Spatial Dynamics of Disease Symptom Expression During *Phytophthora* Epidemics in Bell Pepper

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ABSTRACT

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Epidemics caused by *Phytophthora capsici* were monitored in three commercial fields of bell pepper (*Capsicum annuum*) in order to characterize the spatial progression of symptom expression over time and to provide evidence for possible mechanisms of inoculum dispersal. Spatial dynamics were characterized using two-dimensional distance class analysis. Symptom expression was nonrandom in each field, and quadrats containing dead plants or plants with wilt, crown lesions, or stem lesions were clearly aggregated. Wilting preceded crown symptoms, suggesting that root infection and subsequent colonization to crowns of plants occurred most frequently. Large clusters of dead plants or plants with wilt or crown lesions were observed, and these clusters changed in size over time. Aggregation of pairs of quadrats containing plants with wilt symptoms or dead plants also was greater within than across rows in three of four fields and occurred unidirectionally for long distances down rows, which suggests the importance of movement of surface water along rows in spread of disease. In one field, across-row spread of disease was evident and radial development of symptom expression was observed. Wilted plants occurred in a circular area surrounding a large aggregation of dead plants or plants with crown lesions. Drainage of surface water, possibly containing inoculum, both within and across rows may have been responsible for this radial pattern of disease progression. Incidence of plants with stem lesions was low in all fields. Clusters of plants with stem lesions were initially small and did not increase until late in the season in areas where plants with crown lesions were observed previously. Splash dispersal of inoculum from soil to stems, leaves, or fruits and aerial dispersal were apparently not important mechanisms of dispersal in these fields.

Phytophthora capsici Leonian causes a root and crown rot as well as an aerial blight of leaves, fruit, and stems on bell pepper (*Capsicum annuum* L.) (9,17). Infection results in rapid wilting and death of plants (2,9,17). Because *Phytophthora* species are polycyclic, dispersal of inoculum from previously infected plants may play a significant role in the development of epidemics within seasons (3). The spatial dimensions of *Phytophthora* epidemics can change during a single season and should reflect the primary dispersal mechanisms that function in a given field (17).

The *P. capsici*–pepper pathosystem is more complex than other *Phytophthora* pathosystems because the pathogen can infect virtually all parts of the plant and can be dispersed by at least four distinct mechanisms: inoculum movement from root to root in the soil, surface irrigation or rain water dispersal, splash dispersal from soil, and aerial dispersal from sporulating lesions on leaves, stems, or fruit. Disease symptom expression is a potential indicator of pathogen dispersal mechanisms in fields. Plants with crown lesions preceded by wilting are likely to have become infected from soil inoculum via roots (15,17). The pathogen can be readily isolated from roots of severely wilted plants that do not exhibit aboveground lesions in the field (15). Infections of stems, leaves, or fruit would indicate splash and/or aerial dispersal of inoculum to aboveground plant parts.

Inoculum of *P. capsici* may move from root-to-root in the soil via root growth to inoculum, inoculum movement to roots (zoospore movement in saturated soil), or root-to-root contact, as is possible in the *P. parasitica* Dastur var. *nicotianae* (Breda de Haan) Tucker–tobacco system (4,20). It is expected that the change in the spatial pattern of disease will occur slowly in this scenario and will reflect the spatial pattern of initial inoculum. The primary change in spatial pattern will occur within rows, the occurrence of new foci may be rare, and the degree of aggregation of disease will change little with time.

Inoculum of *Phytophthora* species can also move with surface irrigation water and rainfall and can be dispersed long distances through fields (7,11,16,21,22). Dispersal of inoculum of *P. parasitica* from point sources to tomato roots in soil was limited to less than 2 m from the initial inoculum source; however, spread to fruit on the surface of saturated soil in irrigation furrows was extensive, and the pathogen occurred in free water at distances of up to 68 m from infestation sites during furrow irrigation (11). The amount of rainfall and the frequency of irrigation can have large effects on the rate of development of Phytophthora blight on bell pepper, amount of pathogen spread, area under the disease progress curve, and subsequent yield (1,2,15,19). Within-row spread of disease caused by *P. capsici* was predominant, although across-row spread was observed in pepper fields later in the season (1,17). Movement of inoculum down rows in surface rain or irrigation water will increase the rate of disease development. Long-distance, unidirectional spread may be detected within many rows. This type of pathogen dispersal also was observed with *P. p. nicotianae* on tobacco (20).

P. capsici produces pedicellate sporangia on infected tissue that can be splash-dispersed aerially from plant to plant and splash-dispersed locally from soil to aboveground parts of plants (1,9,19). Plant-to-plant spread of *P. capsici* resulted in severe disease in fumigated plots in fields with high amounts of rainfall, whereas less plant-to-plant spread occurred in fields with low amounts of rainfall (15). *P. p. nicotianae* can be splash-dispersed to the crowns of plants by rainfall to distances of 5 m in the field (20). Splash dispersal of inoculum also plays a major role in the spread of *P. cactorum* (Lebert & Cohn) J. Schröt., the causal agent of leather rot on strawberries (10,14). Disease will increase rapidly if inoculum from soil is splash-dispersed to aerial parts of plants with rainfall or overhead irrigation, and rapid rates of disease increase (both temporal and spatial) will occur. Disease foci may expand within and across rows, and new foci may occur close to existing foci.

Long-distance dispersal of inoculum from sporulating lesions on leaves, stems, or fruits will result in rapid disease increase on aerial parts of the plant. The degree of aggregation of disease will decrease rapidly as focal expansion occurs within and across rows and as new foci develop and overlap. This mechanism of dispersal is probable for the *P. infestans* (Mont.) de Bary–potato system.

We have recently described the spatial development of disease incidence in three commercial bell pepper fields that were naturally infested with *P. capsici* (17). The spatial pattern of diseased plants was nonrandom in each field, and cluster size increased over time. Disease spread occurred over long distances within many rows (17). The temporal dynamics of symptom expression also were reported in our previous work. Changes in the spatial patterns of disease symptom expression have not been described previously for this or any other soilborne pathogen. The objectives of this study were: 1) to characterize changes in the spatial pattern of symptom expression over time in fields of bell pepper studied previously that contained natural inoculum of *P. capsici* and 2) to gain preliminary evidence of the important mechanisms of dispersal that were operative in this pathosystem.

MATERIALS AND METHODS

The data reported here were collected as a part of a series of 1992 field experiments for which many of the methods were described previously (17). Experiments were conducted in three commercial pepper fields in which the soil was infested naturally with *P. capsici* and disease was observed in previous years. All fields were located in the coastal plain region of North Carolina, and soil texture was reported previously (17). In each field, the presence of *P. capsici* was confirmed by isolations from infected plants plated on PARPH medium (8).

Fields were cultivated and prepared by growers using standard cultural practices (18). Beds were shaped with 1 m between rows and planted with a single row of plants per bed. Within-row plant spacing was 30 cm. Grower transplanting equipment did not permit individual plants to be established in regular, equally spaced lattices within the fields; thus, data were collected from contiguous 1-m^2 quadrats that contained two or three transplants of the susceptible pepper cultivar Jupiter. In fields one and two, 20 rows were divided into 20 quadrats per row; in field three, 40 rows were divided into 70 quadrats per row. For field three, data were analyzed separately (20 rows × 35 quadrats) for the upper and lower portions to account for differences in slope and drainage.

Incidence of disease on individual plants within quadrats was assessed 9 times in field one, 10 times in field two, and 3 times in field three. Each plant was examined for specific types of disease symptoms: wilted plants without visible lesions, plants with crown lesions, plants with stem lesions above the soil line, plants with fruit lesions, plants with leaf lesions, and dead plants. Disease incidence data were mapped for each symptom type at each assessment time for each field.

Two-dimensional distance class analysis (5,12) was used to characterize the spatial arrangement of plants with different symptom types. We used 2DCLASS software (13) to analyze data from

TABLE 1. Spatial statistics form two-dimensional distance class analysis of disease symptom expression data from epidemics in bell pepper caused by natural inoculum of *Phytophthora capsici* in field one

Day of year	Percentage of quadrats with diseased plants	SCFs[a] (+)	SCFs[a] (−)	Minimum cluster size Core[b]	Minimum cluster size Reflected[c]	Total no. of clusters	Effect[d] Within row	Effect[d] Across row
Wilt without lesions								
174	4.5	29	0	6	3(3),4,6	6	4	3
177	4.0	31	0	2	2,3(2),4,5,8	7	2	2
181	5.5	34	0	19	2,11	3	6	5
188	6.8	34	0	28	0	1	6	4
195	11.0	38	13	35	0	1	6	4
202	15.8	51	72	51	0	1	11	6
211	15.8	48	75	41	2,4	3	7	6
Crown lesions								
177	5.0	40	0	27	2,11	3	8	3
181	5.8	41	0	6	16(2)	3	5	4
188	8.0	38	0	7	2,3,12(2)	5	4	3
195	8.5	40	0	8	2(2),3(2),7,13	7	5	3
202	8.8	37	0	7	2(3),5,8(2)	7	4	3
211	16.8	44	44	42	2	2	12	5
Dead plants								
181	4.5	40	0	26	2,10	3	6	4
188	5.5	45	0	32	2,11	3	7	4
195	9.5	52	15	48	2,2	3	13	5
202	12.0	38	18	33	4	2	11	4
211	15.3	50	54	48	0	1	13	6
Stem lesions[e]								
211	15.6	37	10	13	2,3,7,9	5	7	2

[a]Number of [X, Y] distance classes in which the observed standardized count frequency (SCF) was significantly greater than (+) (upper confidence limit on the level of significance $P \leq 0.05$) or less than (−) (lower confidence limit on the level of significance $P \geq 0.95$) expected under a random spatial pattern. The minimum percentage of SCFs greater than expected needed to indicate nonrandomness was 5% of the total distance classes, or 20 SCFs.

[b]The minimum core cluster size was defined as the number of significant and adjacent [X, Y] distance classes (including the [X, Y] distance class, [0,0]) that formed a discrete, contiguous group in the upper left-hand corner of the distance class matrix.

[c]Minimum reflected core cluster size was defined as the number of significant and adjacent [X, Y] distance classes that formed discrete, contiguous groups elsewhere in the two-dimensional distance class matrix. A cluster was counted if two or more SCFs were adjacent in an [X, Y] distance class. Number in parentheses = number of reflected clusters of size indicated.

[d]Within-row and across-row effects were interpreted as the greatest number of significant and adjacent SCFs detected in any [X] or [Y] distance class matrix. For within-row and across-row effects adjacent to the [X, Y] distance class [0,0], a value of 1 was added to the total number of adjacent and significant SCFs.

[e]Percentage of quadrats with stem lesions remained below 1% until day 211, so other data are not shown.

each time of disease assessment and each symptom type separately as described previously (17). Number of [X, Y] distance classes in which the observed standardized count frequency (SCF) was significantly greater than (upper confidence limit on the level of significance $P \leq 0.05$) or less than (lower confidence limit on the level of significance $P \geq 0.95$) expected under a random spatial pattern was calculated. The minimum percentage of SCFs needed to indicate nonrandomness was 5% of the total distance classes (20 in fields one and two, 70 in field three). Expected count frequencies were determined by 400 computer simulations.

The minimum core cluster size was defined as the number of significant and adjacent [X, Y] distance classes (including the [X, Y] distance class, [0,0]) that formed a discrete, contiguous group in the upper left-hand corner of the distance class matrix (12,13). Minimum reflected core cluster size was defined as the number of significant and adjacent [X, Y] distance classes that form discrete, contiguous groups elsewhere in the two-dimensional distance class matrix. Minimum cluster number was defined as the number of contiguous groups of significant [X, Y] distance classes within the distance class matrix. A cluster was counted if two or more SCFs were significant and adjacent in the [X, Y] distance class matrices. Within-row and across-row effects were interpreted as the greatest number of significant and adjacent SCFs detected in any [X] or [Y] distance class matrix. For within-row and across-row effects adjacent to the [X, Y] distance class [0,0], a value of 1 was added to the total number of adjacent and significant SCFs.

RESULTS

Disease incidence by symptom type. Disease symptom types observed in all fields included wilted plants without lesions, plants with crown lesions, plants with stem lesions, and dead plants. No fruit or leaf lesions were observed.

The percentage of quadrats containing plants with wilt symptoms, plants with crown lesions, or dead plants increased over time from 4.5 to 15.8, 5.0 to 16.8, and 4.5 to 15.3 in field one (Table 1) and from 5.8 to 16.5, 12.8 to 23.5, and 10.8 to 31.0 in field two (Table 2), respectively. The incidence of quadrats with plants with stem lesions remained below 1% for most of the season but increased to 15.6 and 10.5% at the last assessment time in fields one and two, respectively (Tables 1 and 2).

The percentage of quadrats with plants with wilt symptoms, plants with crown lesions, or dead plants changed over time from 11.4 to 11.2, 3.6 to 7.4, and 4.2 to 9.5 in the upper portion of field three (Table 3) and from 23.1 to 19.1, 26.6 to 31.1, and

TABLE 2. Spatial statistics from two-dimensional distance class analysis of disease symptom expression data from epidemics in bell pepper caused by natural inoculum of *Phytophthora capsici* in field two

Day of year	Percentage of quadrats with diseased plants	SCFs[a] (+)	SCFs[a] (−)	Minimum cluster size Core[b]	Minimum cluster size Reflected[c]	Total no. of clusters	Effect[d] Within row	Effect[d] Across row
Wilt without lesions								
181	5.8	24	0	18	7	2	7	3
188	7.3	29	0	15	3,8	3	6	3
195	10.5	47	7	11	2,32	3	8	5
202	12.3	55	11	14	2,6,31	4	11	4
211	15.5	61	26	37	24	2	17	4
217	16.5	59	19	45	2,3,10	4	17	3
Crown lesions								
168	12.8	26	30	26	0	1	6	5
171	13.0	30	27	26	4	2	6	5
174	13.5	29	28	25	4	2	6	5
177	13.8	29	32	27	2	2	6	5
181	14.0	31	35	26	5	2	6	5
188	15.8	45	50	32	14	2	7	6
195	16.8	48	55	32	17	2	7	6
202	19.8	60	94	31	30	2	7	6
211	23.0	59	115	33	27	2	8	6
217	23.5	62	134	36	27	2	8	6
Dead plants								
168	10.8	26	18	25	2	2	6	5
171	11.0	25	24	25	0	1	6	5
174	10.8	24	20	24	0	1	6	5
177	11.5	25	24	26	0	1	6	5
181	13.5	32	33	27	4	2	6	5
188	14.5	42	37	27	16	2	6	6
195	18.5	43	67	37	6	2	8	6
202	21.0	60	115	37	24	2	8	6
211	29.0	62	119	28	34	2	10	5
217	31.0	60	118	28	33	2	9	5
Stem lesions[e]								
211	9.3	40	1	19	2,2,3,5,5	6	11	3
217	10.5	35	3	13	2,2,4,8	5	5	3

[a]Number of [X, Y] distance classes in which the observed standardized count frequency (SCF) was significantly greater than (+) (upper confidence limit on the level of significance $P \leq 0.05$) or less than (−) (lower confidence limit on the level of significance $P \geq 0.95$) expected under a random spatial pattern. The minimum percentage of SCFs greater than expected needed to indicate nonrandomness was 5% of the total distance classes, or 20 SCFs.

[b]The minimum core cluster size was defined as the number of significant and adjacent [X, Y] distance classes (including the [X, Y] distance class, [0,0]) that formed a discrete, contiguous group in the upper left-hand corner of the distance class matrix.

[c]Minimum reflected core cluster size was defined as the number of significant and adjacent [X, Y] distance classes that formed discrete, contiguous groups elsewhere in the two-dimensional distance class matrix. A cluster was counted if two or more SCFs were adjacent in an [X, Y] distance class.

[d]Within-row and across-row effects were interpreted as the greatest number of significant and adjacent SCFs detected in any [X] or [Y] distance class matrix. For within-row and across-row effects adjacent to the [X, Y] distance class [0,0], a value of 1 was added to the total number of adjacent and significant SCFs.

[e]Percentage of quadrats with stem lesions remained below 1% until day 202, so other data are not shown.

30.1 to 42.4 in the lower portion of field three (Table 4), respectively. The incidence of quadrats with plants with stem lesions was also low in these fields and remained below 2% in the upper portion of field three and below 14% in the lower portion of field three over the season (Tables 3 and 4).

Two-dimensional distance class analysis. *Field one.* Nonrandom distributions of pairs of quadrats with plants with wilt symptoms (Fig. 1A and C), plants with crown lesions (Fig. 1E and G), and dead plants (Fig. 1I and K) were observed between day 181 and 211 in field one. Minimum core cluster size of plants with wilt symptoms, plants with crown lesions, or dead plants increased from 19 to 41, 6 to 42, and 26 to 48 distance class units (count

TABLE 3. Spatial statistics from two-dimensional distance class analysis of disease symptom expression data from epidemics in bell pepper caused by natural inoculum of *Phytophthora capsici* in the upper portion of field three

Day of year	Percentage of quadrats with diseased plants	SCFs[a] (+)	SCFs[a] (−)	Minimum cluster size: Core[b]	Minimum cluster size: Reflected[c]	Total no. of clusters	Effect[d]: Within row	Effect[d]: Across row
Wilt without lesions								
209	11.4	281	184	130	2(2),4(2),5,10,11,14,18,32,38	12	33	7
216	13.5	354	211	110	3,233	3	31	9
223	11.2	358	254	95	2,3,254	4	31	10
Crown lesions								
209	3.6	152	0	29	2(11),3(5),4(2),6,7,10(2),12	23	5	2
216	4.8	141	3	93	2(4),3,4,8,11	9	18	4
223	7.4	142	72	116	2(2),5(2)	5	32	4
Dead plants								
209	4.2	180	4	8	2(12),3(2),9,10,19,20,25,40	21	17	4
216	5.1	228	37	15	2(6),3(3),6,7,17,147	14	13	6
223	9.5	218	96	28	2(5),3(4),4(2),5,7,9,16,28(2),54	19	17	5
Stem lesions								
209	1.5	107	0	2	2(10),3(5),4,5,7(2),10(2)	22	4	4
216	1.1	87	0	8	2(7),3(5),4,5(2),17	17	16	2
223	1.1	103	0	4	2(13),3(5),4(3),5,8	24	3	4

[a]Number of [X, Y] distance classes in which the observed standardized count frequency (SCF) was significantly greater than (+) (upper confidence limit on the level of significance $P \leq 0.05$) or less than (−) (lower confidence limit on the level of significance $P \geq 0.95$) expected under a random spatial pattern. The minimum percentage of SCFs greater than expected needed to indicate nonrandomness was 5% of the total distance classes, or 70 SCFs.

[b]The minimum core cluster size was defined as the number of significant and adjacent [X, Y] distance classes (including the [X, Y] distance class, [0,0]) that formed a discrete, contiguous group in the upper left-hand corner of the distance class matrix.

[c]Minimum reflected core cluster size was defined as the number of significant and adjacent [X, Y] distance classes that formed discrete, contiguous groups elsewhere in the two-dimensional distance class matrix. A cluster was counted if two or more SCFs were adjacent in an [X, Y] distance class. Number in parentheses = number of reflected clusters of size indicated.

[d]Within-row and across-row effects were interpreted as the greatest number of significant and adjacent SCFs detected in any [X] or [Y] distance class matrix. For within-row and across-row effects adjacent to the [X, Y] distance class [0,0], a value of 1 was added to the total number of adjacent and significant SCFs.

TABLE 4. Spatial statistics from two-dimensional distance class analysis of disease symptom expression data from epidemics in bell pepper caused by natural inoculum of *Phytophthora capsici* in the lower portion of field three

Day of year	Percentage of quadrats with diseased plants	SCFs[a] (+)	SCFs[a] (−)	Minimum cluster size: Core[b]	Minimum cluster size: Reflected[c]	Total no. of clusters	Effect[d]: Within row	Effect[d]: Across row
Wilt without lesions								
209	23.1	139	353	65	2(3),3,4(2),17,33	9	8	10
216	28.2	123	235	38	2,5,37,39	5	7	7
223	19.1	109	58	24	2(5),3(2),4,8,16,23	12	7	5
Crown lesions								
209	26.6	253	906	254	0	1	14	21
216	27.4	255	890	255	0	1	16	20
223	31.1	266	565	150	2,5,109	4	15	14
Dead plants								
209	30.1	279	908	280	0	1	15	21
216	32.5	282	934	283	0	1	14	22
223	42.4	309	948	310	0	1	17	21
Stem lesions								
209	13.6	193	581	194	0	1	13	18
216	14.2	214	564	214	0	1	15	20
223	6.5	102	22	91	2,5	2	8	13

[a]Number of [X, Y] distance classes in which the observed standardized count frequency (SCF) was significantly greater than (+) (upper confidence limit on the level of significance $P \leq 0.05$) or less than (−) (lower confidence limit on the level of significance $P \geq 0.95$) expected under a random spatial pattern. The minimum percentage of SCFs greater than expected needed to indicate nonrandomness was 5% of the total distance classes, or 70 SCFs.

[b]The minimum core cluster size was defined as the number of significant and adjacent [X, Y] distance classes (including the [X, Y] distance class, [0,0]) that formed a discrete, contiguous group in the upper left-hand corner of the distance class matrix.

[c]Minimum reflected core cluster size was defined as the number of significant and adjacent [X, Y] distance classes that formed discrete, contiguous groups elsewhere in the two-dimensional distance class matrix. A cluster was counted if two or more SCFs were adjacent in an [X, Y] distance class. Number in parentheses = number of reflected clusters of size indicated.

[d]Within-row and across-row effects were interpreted as the greatest number of significant and adjacent SCFs detected in any [X] or [Y] distance class matrix. For within-row and across-row effects adjacent to the [X, Y] distance class [0,0], a value of 1 was added to the total number of adjacent and significant SCFs.

includes 0,0 in the distance class matrix) between day 181 and day 211 in field one (Table 1; Fig. 1B, D, F, H, J, and L). The number of reflected core clusters decreased over time, as several reflected core clusters of plants with wilt symptoms, plants with crown lesions, or dead plants coalesced with the core cluster (Table 1; Fig. 1D, H, and L). Fewer pairs of quadrats containing wilted plants occurred in the upper left-hand corner of the field, as indicated by the large number of significantly lower SCFs in *X* value distance classes [7–16] (open circles in Fig. 1D, H, and L).

The incidence of quadrats containing plants with stem lesions in field one was less than 1% until day 211, when incidence reached 15.6% (Fig. 1M). Distinct noncontiguous foci of diseased plants with stem lesions were observed in field one (Fig. 1M). Minimum core cluster size of plants with stem lesions was 13 distance class units at day 211. Four distinct reflected core clusters of quadrats containing plants with stem lesions were apparent and separated by one to three rows in field one (Fig. 1N).

Aggregation within rows of pairs of adjacent quadrats containing plants with wilt symptoms, plants with crown lesions, or dead plants was apparent and was greater than the aggregation observed across rows between day 181 and day 211 in field one (Table 1). Aggregation within rows of pairs of adjacent quadrats containing plants with stem lesions was observed only at day 211, since disease incidence was below 1% prior to this time (Table 1; Fig. 1N). For example, [*X, Y*] distance classes [1,0–6], [1,0–11], [1,0–12], and [0,1–6] indicate significant row effects for wilted plants, plants with crown lesions, dead plants, and plants with stem lesions, respectively, at day 211 (Fig. 1D, H, L, and N).

Field two. Significant, nonrandom distributions of pairs of quadrats with plants with wilt symptoms were observed at most disease assessment times between day 181 and day 217 in field two (Table 2; Fig. 2A and C). Minimum core cluster size was 18 at day 181 (Fig. 2B) and increased to 45 distance class units between day 181 and day 217 (Table 2).

Similarly, nonrandom distributions of pairs of quadrats con-

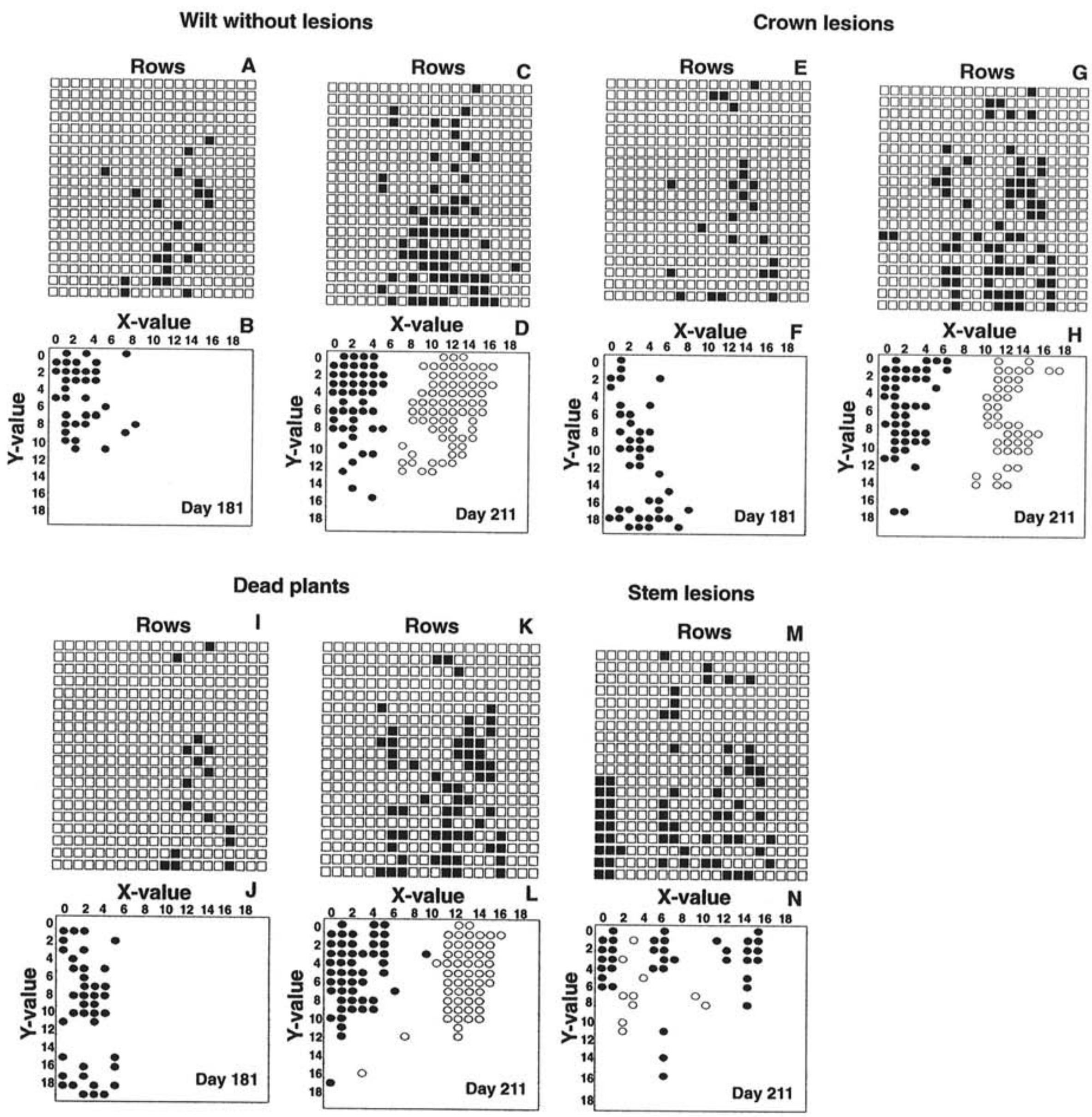

Fig. 1. Spatial pattern of epidemics caused by *Phytophthora capsici* on bell pepper in a 20 row × 20 column lattice of contiguous quadrats in field one in: **A** and **C, E** and **G, I** and **K,** and **M,** and two-dimensional distance class analysis of the spatial pattern in **B** and **D, F** and **H, J** and **L,** and **N** for plants with wilt symptoms, plants with crown lesions, dead plants, and plants with stem lesions at day 181 and day 211, respectively. Solid square = quadrat with at least one diseased plant, open square = quadrat with symptomless plants, solid circle = [*X, Y*] distance class with a standardized count frequency greater than expected at $P \leq 0.05$, and open circle = distance class with a standardized count frequency lower than expected at $P \geq 0.95$.

taining plants with crown lesions (Fig. 2E and G) and dead plants (Fig. 2I and K) were observed between day 181 and day 217 in field two. A large cluster of diseased plants with crown lesions (Fig. 2E) and dead plants (Fig. 2I) was apparent in the lower right-hand corner of the field at day 181. The minimum core cluster size of plants with crown lesions increased with time (Fig. 2F and H), but the minimum core cluster size of dead plants did not increase to a great extent over time (Table 2; Fig. 2J and L). In contrast to field one, only a single reflected core cluster of plants with crown lesions or dead plants was observed to increase over time, and this reflected cluster did not coalesce with the core cluster (Table 2; Fig. 2H and L). Many SCFs lower than expected were observed in *Y* value distance classes 7–16 (open circles in Fig. 2H), indicating that fewer pairs of quadrats contained plants with crown lesions in the upper part of the field at day 217.

Plants with stem lesions occurred in random noncontiguous foci at day 202, and no distinct clusters were apparent (Fig. 2M). Nonrandom distribution of quadrats with plants with stem lesions occurred at day 217 (Fig. 2N), and the minimum core cluster size of plants with stem lesions was 13 distance class units. Four distinct reflected core clusters of quadrats containing plants with stem lesions were apparent (Fig. 2O).

Aggregation within rows of pairs of adjacent quadrats containing plants with wilt symptoms, plants with crown lesions, or dead plants was greater than aggregation observed across rows between day 181 and day 217 in field two (Table 2; Fig. 2B and D). Aggregation within rows of pairs of adjacent quadrats containing plants with stem lesions was also greater than aggregation across rows at day 211 and day 217 (Table 2; Fig. 2O).

Upper portion of field three. Nonrandom distributions of pairs of quadrats containing plants with wilt symptoms (Fig. 3A and C), plants with crown symptoms (Fig. 3E and G), and dead plants (Fig. 3I and K) were observed at most disease assessment times between day 209 and day 223 in the upper portion of field three. Minimum core cluster size of plants with wilt symptoms decreased over time (Fig. 3B and D), whereas minimum core cluster size of plants with crown lesions (Fig. 3F and H) and dead plants (Fig. 3J and L) increased over time in this field (Table 3). The size of the reflected core cluster of plants with wilt symptoms was larger than the size of the reflected core clusters of plants with other symptom types by day 223 (Fig. 3D, H, and L).

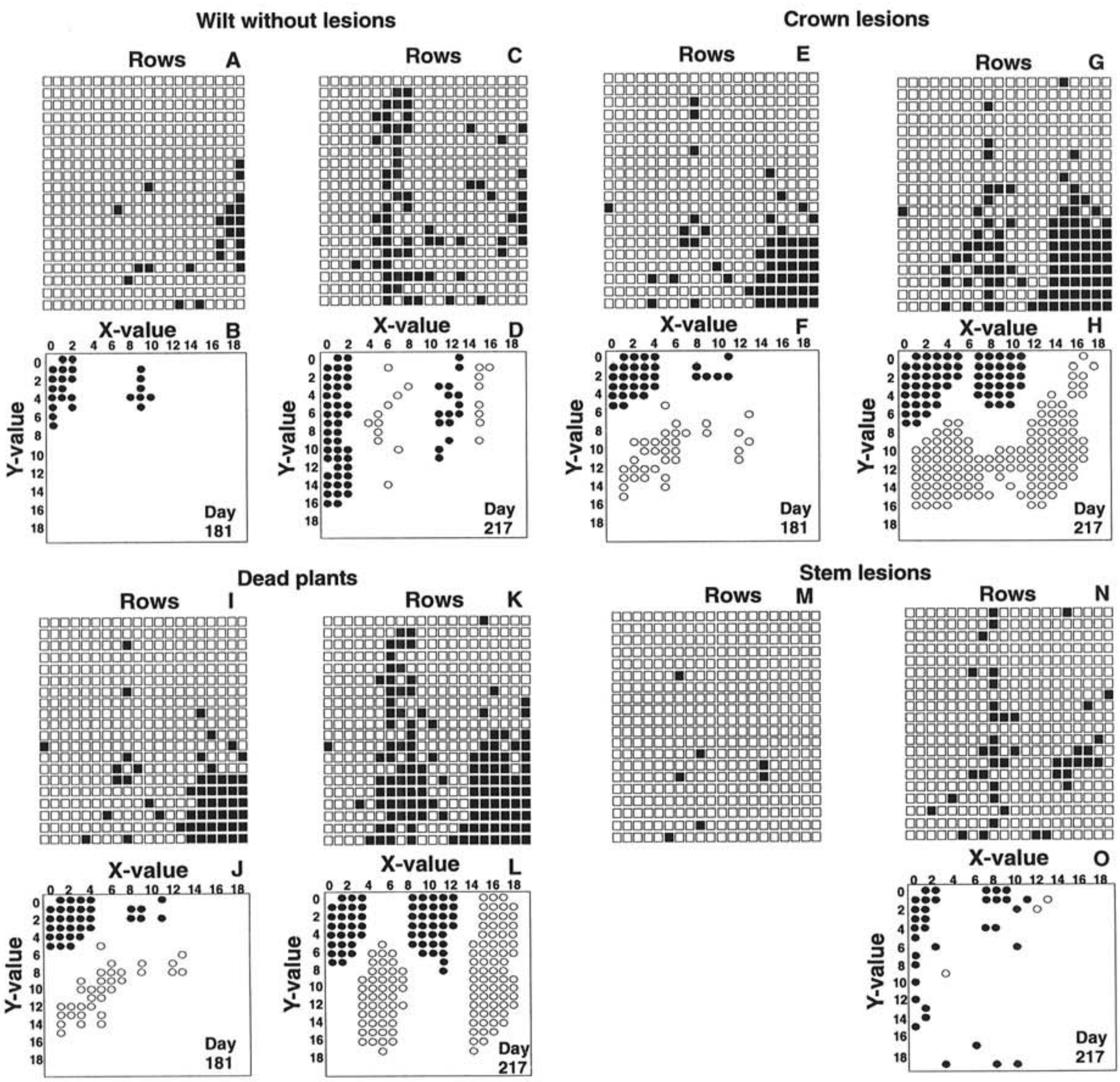

Fig. 2. Spatial pattern of epidemics caused by *Phytophthora capsici* on bell pepper in a 20 row × 20 column lattice of contiguous quadrats in field two in: **A** and **C, E** and **G, I** and **K,** and **M** and **N,** and two-dimensional distance class analysis of the spatial pattern in **B** and **D, F** and **H, J** and **L,** and **O** for plants with wilt symptoms, plants with crown lesions, dead plants, and plants with stem lesions at day 181 and day 217, respectively. Solid square = quadrat with at least one diseased plant, open square = quadrat with symptomless plants, solid circle = $[X, Y]$ distance class with a standardized count frequency greater than expected at $P \leq 0.05$, and open circle = distance class with a standardized count frequency lower than expected at $P \geq 0.95$.

Aggregation within rows of pairs of adjacent quadrats containing plants with wilt symptoms, plants with crown lesions, and dead plants was greater than aggregation across rows at all disease assessment times in the upper portion of field three (Table 3; Fig. 3D, H, and L). A large number of SCFs lower than expected were observed in X value distance classes 5–25, indicating that fewer pairs of adjacent quadrats contained plants with wilt, plants with crown lesions, or dead plants in the center of the field at day 223 (open circles in Fig. 3D, H, and L).

The incidence of quadrats containing plants with stem lesions remained low in this field (Fig. 3M and O). Although several reflected core clusters of plants with stem lesions were observed in the upper portion of the field, these clusters were scattered and did not develop within or across rows to a great extent (Fig. 3N and P).

Lower portion of field three. Quadrats in a large circular area in the lower portion of field three contained plants with wilt symptoms (Fig. 4A and C). Minimum core cluster size of plants with wilt symptoms decreased between day 209 and day 223 (Table 4; Fig. 4B and D).

Dead plants and plants with crown lesions occurred in a central cluster inside the circular area of wilted plants in this field (Fig. 4E, G, I, and K). Minimum core cluster size was 254 for plants with crown lesions and 280 for dead plants at day 209 (Table 4; Fig. 4F and J). Minimum core cluster size for plants with crown lesions decreased over time (Fig. 4F and H), but a large reflected cluster approximately nine rows away from the core cluster was apparent at day 223 (Fig. 4H) and was visible in the field map (Fig. 4G). Reflected core clusters of dead plants were not observed at day 209 or day 223 (Fig. 4J and L), since dead plants were clustered in a central area of the field (Fig. 4I and K). In contrast to the other fields, strong across-row effects were evident for plants with crown lesions, dead plants, and plants with stem lesions at most disease assessment times in this field (Table 4).

Fewer quadrats contained plants with stem lesions (Fig. 4M) than other symptom types in the lower portion of field three, and the incidence of quadrats containing plants with stem lesions decreased over time as plants died (Table 4; Fig. 4M and O). Minimum core cluster size of plants with stem lesions decreased

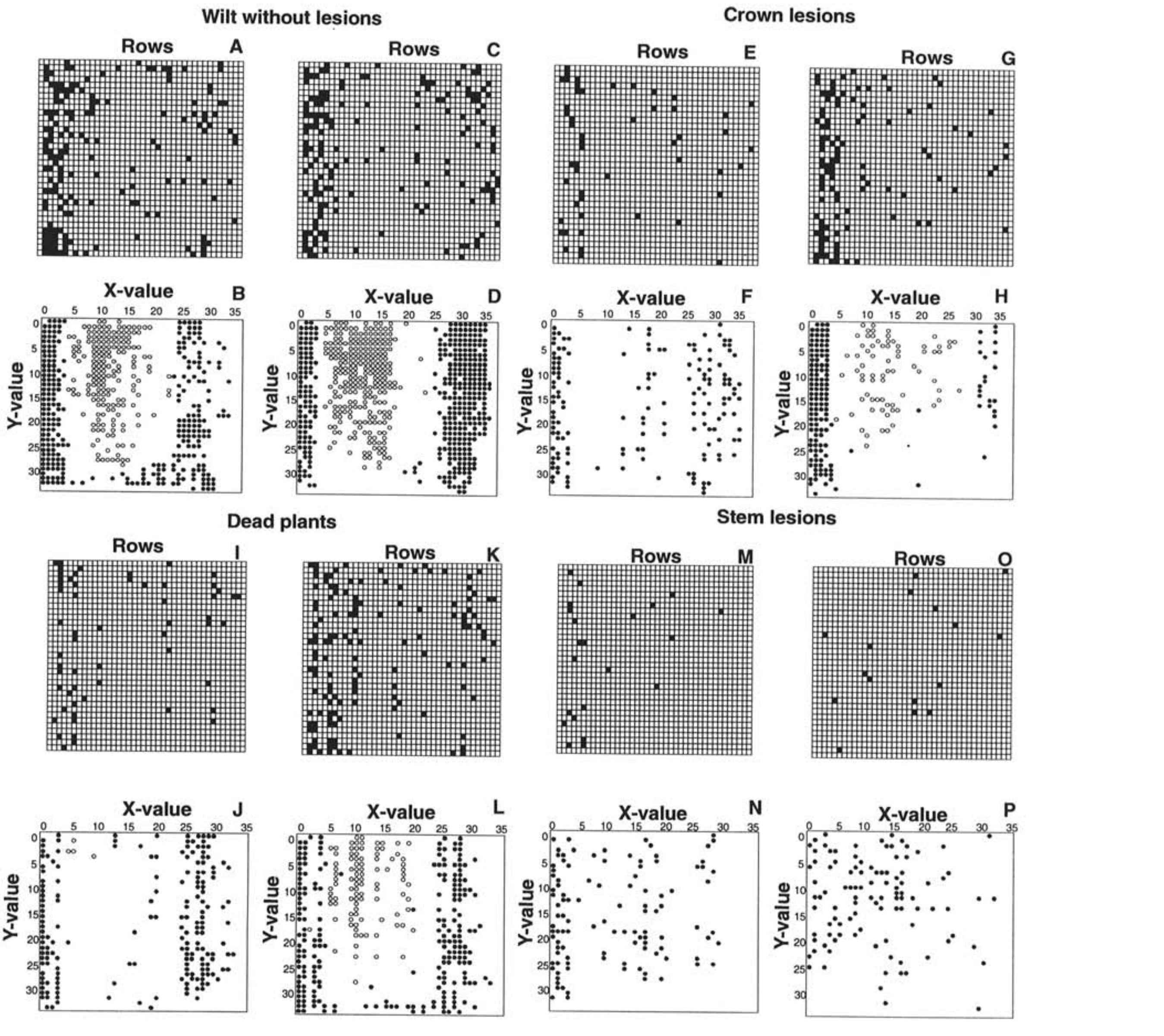

Fig. 3. Spatial pattern of epidemics caused by *Phytophthora capsici* on bell pepper in a 40 row × 35 column lattice of contiguous quadrats in the upper half of field three in: **A** and **C**, **E** and **G**, **I** and **K**, and **M** and **O**, and two-dimensional distance class analysis of the spatial pattern in **B** and **D**, **F** and **H**, **J** and **L**, and **N** and **P** for plants with wilt symptoms, plants with crown lesions, dead plants, and plants with stem lesions at day 209 and day 223, respectively. Solid square = quadrat with at least one diseased plant, open square = quadrat with symptomless plants, solid circle = $[X, Y]$ distance class with a standardized count frequency greater than expected at $P \leq 0.05$, and open circle = distance class with a standardized count frequency lower than expected at $P \geq 0.95$.

from 194 to 91 between day 209 and day 223 (Table 4; Fig. 4N and P).

Many SCFs lower than expected were observed in X value distance classes 24–39 and Y value distance classes 23–34, indicating that fewer pairs of quadrats contained plants with wilt, plants with crown lesions, or dead plants in areas around the edge of field three at day 209 and day 223 (Fig. 4B, F, J, L, and N).

DISCUSSION

The final incidence of crown infections was greater than the final incidence of wilted plants or plants with stem lesions in two of four fields examined, whereas in two fields, the incidence of wilted plants was greater than or equal to the incidence of plants with crown lesions. Wilting of plants preceded the observation of crown lesions in this and other studies we have conducted with this pathogen in the field (15,17). No infection of leaves or fruit was observed. These data suggest that root infection and subsequent colonization to the crowns of plants occurred in these fields and demonstrate the importance of soil inoculum in this pathosystem. We previously (15) isolated the pathogen from wilted plants with infected roots but did not isolate the pathogen from roots in this study, since plant removal from the field would have disturbed the expansion of disease foci. We believe that both inoculum dispersal to roots (either via root-to-root contact, inoculum movement to roots in soil, or root growth to inoculum) and surface water dispersal were important mechanisms of dispersal of inoculum of *P. capsici* in naturally infested fields in this study.

Aggregation of pairs of quadrats containing plants with wilt, plants with crown lesions, plants with stem lesions, or dead plants was greater in most cases within rows than across rows in three of the four fields examined. Largest differences in aggregation of disease were generally observed later in epidemic development when disease incidence was highest. In some fields, an increase in focal expansion occurred simultaneously within several adjacent rows and accounted for the smaller differences between within-row and across-row effects in these fields (Fig. 2E, G, I, and K).

Patterns of disease changed with time and initially reflected

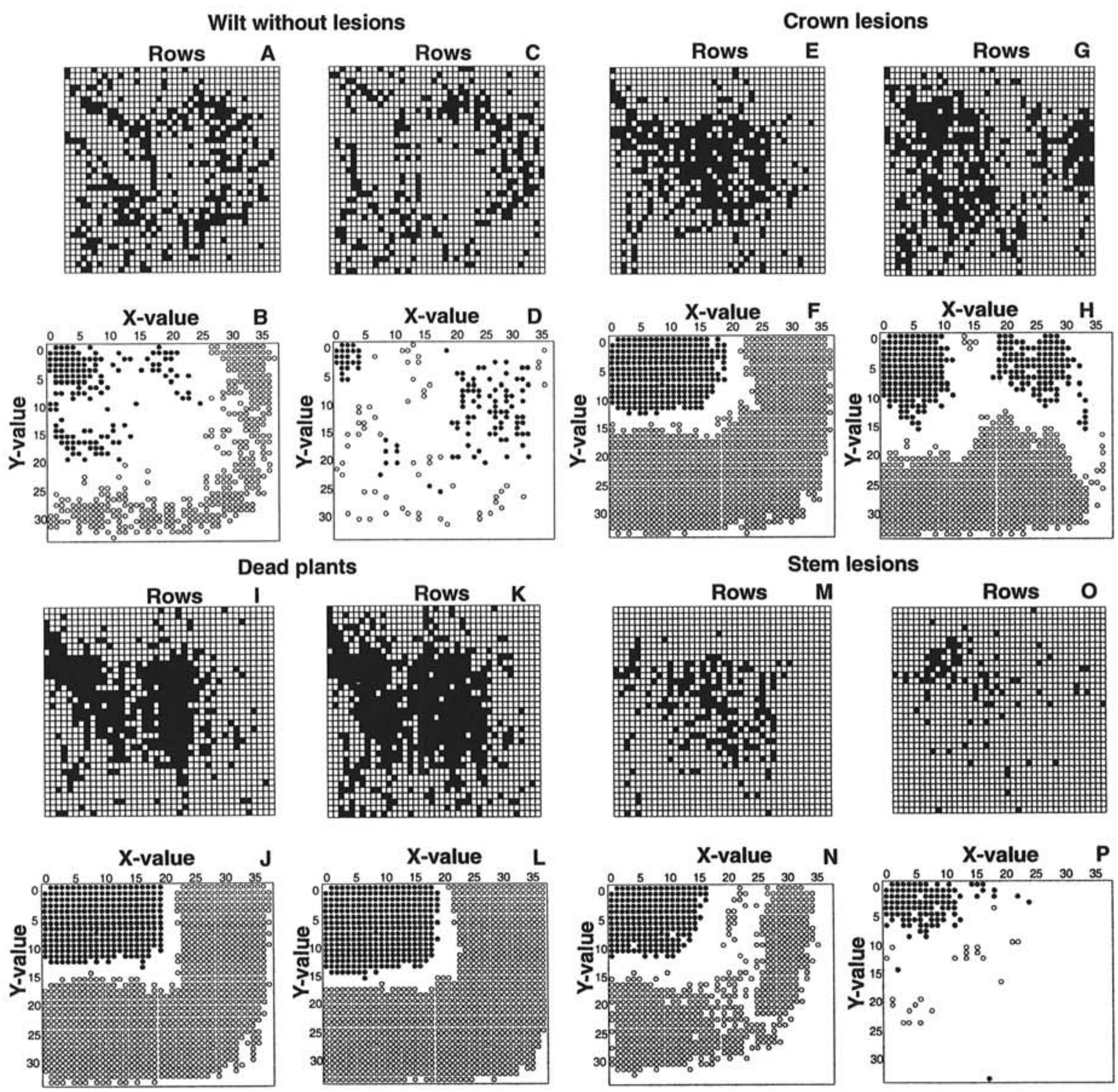

Fig. 4. Spatial pattern of epidemics caused by *Phytophthora capsici* on bell pepper in a 40 row × 35 column lattice of contiguous quadrats in the lower half of field three in: **A** and **C, E** and **G, I** and **K,** and **M** and **O,** and two-dimensional distance class analysis of the spatial pattern in **B** and **D, F** and **H, J** and **L,** and **N** and **P** for plants with wilt symptoms, plants with crown lesions, dead plants, and plants with stem lesions at day 209 and day 223, respectively. Solid square = quadrat with at least one diseased plant, open square = quadrat with symptomless plants, solid circle = $[X, Y]$ distance class with a standardized count frequency greater than expected at $P \leq 0.05$, and open circle = distance class with a standardized count frequency lower than expected at $P \geq 0.95$.

the pattern of soil moisture and inoculum present in the fields (6). We sampled quadrats for the presence of inoculum and soil moisture at two times during the season in fields one and two. Our data indicate that the spatial pattern of early-season inoculum did not reflect the spatial pattern of final disease or final inoculum (R. P. Larkin et al, *unpublished*). There are limitations to our current methods of detection of soil inoculum of *P. capsici*, including lack of germination of oospores on selective media and high minimum threshold levels for detection of various propagule types. Experiments are in progress to improve our detection methods for soil inoculum.

Long-distance, unidirectional increase in numbers of quadrats containing diseased plants within rows and the low level of plants with stem lesions lend support to our hypothesis of dispersal of inoculum via surface water. Because rainwater in furrows was transient, we did not sample water in furrows to determine whether the pathogen was present in surface waters. Therefore, we do not have conclusive data that indicate the presence of the pathogen in surface water. However, surface water from rainfall was reported to disperse *P. capsici* in bell pepper inoculated at point sources in several previous studies and in our work in progress in another field (1,15,19; J. B. Ristaino, *unpublished*). Our work demonstrates the spread of disease over time in commercial fields where natural inoculum in soil was present at the onset of epidemic development.

Lesions on stems of the plants were observed less frequently and later in the season than other symptom types in all four fields, and leaf and fruit infections were not observed. These data suggest that splash and aerial dispersal of soilborne inoculum to leaves, fruits, and stems was less important than spread of inoculum in soil or inoculum dispersal in surface water in these fields (17). Stem lesions generally occurred in areas of the field where crown lesions were previously observed. In some instances quadrats containing plants with stem lesions occurred "downstream" or immediately "upstream" to quadrats containing plants with crown lesions (Fig. 1G and M). Movement of inoculum in surface water within rows followed by splash dispersal of inoculum to the stems probably was responsible for stem lesion development in these cases. The minimum core cluster size of quadrats containing plants with stem lesions also was smaller than the minimum core cluster size of quadrats containing plants with other symptom types in three of four fields, thus supporting our conclusion that splash dispersal to stems, fruits, and leaves and aerial dispersal were less important than other dispersal mechanisms in these fields.

The spatial progression of disease in the lower portion of field three was radial, and across-rows effects were important and larger in this field than in other fields (Table 4). A ring of wilted plants surrounded a large cluster of dead plants and plants with crown lesions in the center of this field (Fig. 4). Standing water was present during disease assessment at day 209, and a drainage area with water that flowed across rows was observed in the field. This drainage of water could explain the significant across-row effects observed for plants with wilt, plants with crown lesions, dead plants, and plants with stem lesions. Similar spread of disease via drainage water from point sources of introduced inoculum has been reported for *P. capsici* in an artificially infested field (19).

A description of "edge effects" was presented in a recent paper on the use of two-dimensional distance class analysis (13). Our data demonstrate a "reverse-edge" effect in that large numbers of quadrats without disease were present around the edge of the lower portion of field three and a central focus of dead plants and plants with wilt, crown, or stem lesions was apparent (Fig. 4). Only three disease measurements were made in the lower portion of field three. However, the spatial dynamics of symptom expression during this time indicated that focal expansion occurred in a circular pattern from a central cluster of diseased plants (23). In our earlier analysis of the spatial pattern of disease incidence in this field, a large core cluster was observed (17). However, the analysis presented here by symptom type enabled us to dissect the composition of this core cluster into its components and to view a central core of dead plants and plants with crown lesions surrounded by a ring of wilted plants (Fig. 4).

Definite large core clusters of quadrats containing plants with wilt or crown lesions or dead plants were apparent in all the fields examined (Tables 1–4). Disease was nonrandom in these fields, and the spatial progression of symptom expression supported the conclusion that infection most often began in the roots and progressed to crown lesions and then to death of the plants. In most cases, the size of the core cluster for each symptom type increased with time. In the upper portion of field three, however, the core cluster size of plants with wilt symptoms tended to decrease with time as plants developed crown lesions or died. Similarly, in the lower portion of field three, the core cluster size of plants with wilt symptoms or stem lesions decreased over time as plants died. The core cluster size of quadrats with dead plants tended to increase over time as disease progressed and plants died.

Two-dimensional distance class analysis allowed us to quantify the spatial dimension of symptom expression during *Phytophthora* epidemics in the fields examined (5,13). The spatial extensity and attributes of epidemics caused by *P. capsici* in naturally infested bell pepper fields changed with time. The probable modes of dispersal of inoculum in the fields studied included within-row spread of disease with surface rainwater and inoculum dispersal to roots and crowns in soil. Studies are in progress to relate the spatial pattern of inoculum and soil moisture in these fields to disease severity. In addition, effects of specific cultural and chemical control strategies on dispersal of introduced inoculum into fumigated bell pepper fields are under investigation.

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