

Interpreting Upland Rice Yield and *Pratylenchus zaei* Relationships: Correspondence Analyses¹

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Abstract: Correspondence analyses were used to explore the relationships between yield and populations of *Pratylenchus zaei* in an upland rice field and in a greenhouse experiment. Initial soil (Pi) and final root (Pf) population densities of *P. zaei*, and yield (Y) of rice cv. UPL Ri5 were determined at 490 spots in the field. Very low Y was linked to very high Pf. Low Y was linked to medium or high Pi and medium Pf. Medium to very high Y were clustered with undetectable Pi and very low or high Pf. All yield levels were independent of very high Pi. In the greenhouse experiment where seven nematode inoculum levels and three fertilizer levels were evaluated, low Y was associated with medium or high Pf and high Y with high or low Pf. The analyses indicated that nematode–yield interaction involved a complex, dynamic process, in which the root-carrying capacity probably was a determining factor. Correspondence analysis, which does not require assumptions on the shape of nematode population–yield relationships or on variable distributions, revealed meaningful associations in these complex data sets.

Key words: Correspondence analysis, crop loss, lesion nematode, nematode, nematode–yield relationships, *Oryza sativa*, *Pratylenchus zaei*, rice.

Pratylenchus zaei, is associated with upland rice in Africa, South America, and South and Southeast Asia (3). It is omnipresent in upland rice ecosystems in the Philippines and Indonesia (10,11,17). Control with nematicides (9) or crop rotations (1) have resulted in significant yield increases. Plowright et al. (9) indicated that nematicidal control of low (18/100 cm³ soil) populations of *P. zaei* resulted in yield increases of 13–29%. A constant minimum yield occurred over a wide range of population densities (9). Thus, yield losses may be expected with low population densities of *P. zaei*. Because of this absence of relationship between population densities of *P. zaei* and yield, it is difficult to assess the impact of the nematode in actual field situations and portray nematode–yield or plant growth relationships by using conventional regression techniques.

The objective of this study was to evaluate the potential of correspondence analysis (2,7) as a technique for assessing the relationships between population densities of *P. zaei* and yield of upland rice under

field conditions and in the greenhouse. Correspondence analysis uses categorized information based on quantitative variables. These variables are replaced by classes that represent discrete ranges. With correspondence analysis, categorized data can be analyzed by means of contingency tables, i.e., matrices relating classes of paired categorized variables. Correspondence analysis has been used to analyze data sets in botanical and fish ecology (2), and in nematology to analyze nematicide data from field experiments (4) and the effects of nematodes on the growth and nitrogen fixation of groundnut (6). The technique has also been applied to plant disease epidemiology (12,13) and the analysis of yield loss due to multiple pathogens (14).

MATERIALS AND METHODS

Field experiment: The experiment was conducted from June to October 1989 in a field located at the International Rice Research Institute (IRRI), Los Baños, Philippines. The field, previously cropped to rice from June to October 1988 and held fallow from October 1988 to June 1989, was direct seeded with rice cultivar UPL Ri5 in rows 20 cm apart with 10 cm spacing in the row. Nitrogen (ammonium sulfate, 40 kg/ha) (N) was applied at plowing and

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again at maximum tillering. *Pratylenchus zaeae* was the only plant-parasitic nematode detected in the field. A 25 × 20 grid with intersections 2 m apart was superimposed on the field. Numbers of *P. zaeae* (Pi and Pf) and yield were determined for plants at each grid intersection. Nematodes were extracted from 200 cm³ soil with a combination of sieving and modified Baermann funnel methods (16) and from 3 g roots by macerating for 15 seconds in a blender and then placing them on a modified Baermann funnel for 48 hours (16). Ten plants were damaged by stem borers or tungro disease, leaving 490 samples to be analyzed. Relationships between yield and initial and final nematode population densities were analyzed using step-wise regression and correspondence analysis.

Greenhouse experiment. The experiment was conducted in a temperature-controlled greenhouse set for 22 C at night and 28 C during the daytime. Five seeds of rice cultivar UPL Ri5 were sown per 25-cm-d clay pot filled with 8 dm³ autoclaved soil. Ten days after seedling emergence, plants were thinned to one per pot and inoculated with 0, 10, 50, 100, 500, 1,000, or 5,000 *P. zaeae* juveniles and adults per plant. Three levels (40, 80, and 160 kg/ha) of nitrogen (ammonium sulfate) were divided equally over applications at seeding, maximum tillering, and panicle initiation. Treatments were arranged in a randomized complete block design with five replications. At harvest, root fresh weight, number of panicles, and grain weight were recorded for each plant. Nematode population densities were estimated from soil and roots as for the field experiment. Relationships between yield, initial and final nematode population densities, and quantity of nitrogen applied were analyzed using ANOVA, step-wise regression, and correspondence analysis.

Correspondence analysis: Correspondence analysis (2,5,8) is a multivariate statistical technique used to analyze a series of contingency tables. The initial quantitative variables are categorized (i.e., converted

into classes), and represented by their frequencies (i.e., numbers of plants that fall into categories of yield, Pi, and Pf). As in principal component analysis, a series of axes is defined. Each class contributes to their definition. Each axis accounts for a fraction of the total information represented by the contingency tables. The contribution of a given class (i.e., a categorized variable) to the information contained in a contingency table is called inertia (2,5) because it is computed as its frequency times the squares distance to the origin of axes. The resulting graphs are pictorial representations of the contingency tables (5). Interpretation of graphs is based on the contribution of axes to the description of the data set, and on the proximity of points representing classes of the different variables (5). For variables that can be associated with a progression from low to high, such as yield or nematode population density, the successive classes in the graph can be linked to one another, and the shape of the resulting path of increasing yield or nematode population density is considered, along with axes and other variables.

The variation of yield ($Y = \text{g of grain per plant}$) was analyzed as a response to nematode population density (Pi and Pf) in the field experiment. Five classes were established for each of three variables. For Y, the classes and their lower and upper boundaries were as follows: very low Y ($0 \leq Y_1 < 7.9$), low Y ($7.9 \leq Y_2 < 12.3$), medium Y ($12.3 \leq Y_3 < 16.6$), high Y ($16.6 \leq Y_4 < 23.8$), and very high Y ($23.8 \leq Y_5 \leq 68$). For nematode Pi (number of *P. zaeae* /dm³ soil), the five classes and their lower and upper boundaries were as follows: undetectable Pi ($Pi_1 = 0$), low Pi ($0 \leq Pi_2 < 5$), medium Pi ($5 \leq Pi_3 < 30$), high Pi ($30 \leq Pi_4 < 130$), and very high Pi ($130 \leq Pi_5 \leq 1650$). For Pf (number of *P. zaeae* /g root), the five classes and their lower and upper boundaries were as follows: very low Pf ($0 \leq Pf_1 < 121$), low Pf ($121 \leq Pf_2 < 226$), medium Pf ($226 \leq Pf_3 < 407$), high Pf ($407 \leq Pf_4 < 672$), and very high Pf ($672 \leq Pf_5 \leq 4508$). Two contingency

tables were built ($Y \times P_i$) and ($Y \times P_f$) and bracketed together [$(Y \times P_i) + (Y \times P_f)$] to define axes and to calculate contributions and coordinates of classes (2,8) (Table 1).

In the greenhouse experiment, the two variables that may be visualized as final outputs of the rice-nematode system were used to define the axes using a Burt table (5) (Table 2): the grain weight (g) per plant (Y) and the number of nematodes recovered from roots per plant at harvest (Pf). The other variables, i.e., number of panicles (P), root fresh weight (R), quantity of nitrogen applied in kg/ha (N), and initial number of nematodes per plant (Pi), were considered as additional variables and were superimposed on the defined axes. The consideration of a few variables (Y and Pf) allows axes to be generated that are easy to interpret through the examination of the contributions of variables to axes. The superimposition of additional variables (P, R, N, and Pi) on the framework of axes allows exploration of the re-

TABLE 1. Contingency table for number of plants/class from a field experiment to determine the relationships between yield of upland rice cv. UPL Ri5 and population densities (PD) of *Pratylenchus zeae*.

Nematode population class†	Yield class‡				
	Y1	Y2	Y3	Y4	Y5
Pi1	25	34	35	36	37
Pi2	10	8	11	10	2
Pi3	23	22	15	17	21
Pi4	16	20	15	18	18
Pi5	24	16	19	17	21
Pf1	11	18	23	23	22
Pf2	21	16	20	20	21
Pf3	20	25	19	18	17
Pf4	16	18	19	21	24
Pf5	30	23	14	16	15

† Y = yield (g of grain per plant), Y1 = very low Y ($0 \leq Y1 < 7.9$), Y2 = low Y ($7.9 \leq Y2 < 12.3$), Y3 = medium Y ($12.3 \leq Y3 < 16.6$), Y4 = high Y ($16.6 \leq Y4 < 23.8$), and Y5 = very high Y ($23.8 \leq Y5 \leq 68$).

‡ Pi = initial *P. zeae* population density (number per dm³ soil), Pi1 = undetectable Pi (Pi1 = 0), Pi2 = low Pi ($0 \leq Pi2 < 5$), Pi3 = medium Pi ($5 \leq Pi3 < 30$), Pi4 = high Pi ($30 \leq Pi4 < 130$), and Pi5 = very high Pi ($130 \leq Pi5 \leq 1650$). Pf final *P. zeae* population density (number per g root), Pf1 = very low Pf ($0 \leq Pf1 < 121$), Pf2 = low Pf ($121 \leq Pf2 < 226$), Pf3 = medium Pf ($226 \leq Pf3 < 407$), Pf4 = high Pf ($407 \leq Pf4 < 672$), and Pf5 = very high Pf ($672 \leq Pf5 \leq 4508$).

TABLE 2. Number of plants in each class using data from a greenhouse experiment designed to evaluate the effects of *Pratylenchus zeae* and nitrogen on growth and yield parameters of upland rice cv. UPL Ri5.

Class†	Class‡					
	Y1	Y2	Y3	Pf1	Pf2	Pf3
Y1	31	0	0	8	11	12
Y2	0	39	0	14	18	7
Y3	0	0	35	10	8	17
Pf1	8	14	10	32	0	0
Pf2	11	18	8	0	37	0
Pf3	12	7	17	0	0	36
R1	19	15	1	10	17	8
R2	9	19	7	10	15	10
R3	3	5	27	12	5	18
P1	23	4	0	8	11	8
P2	8	29	7	12	18	14
P3	0	6	28	12	8	14
N1	21	12	2	15	14	6
N2	9	18	8	10	15	10
N3	1	9	25	7	8	20
Pi0	3	5	7	15	0	0
Pi1	8	13	9	7	12	11
Pi2	11	8	11	4	14	12
Pi3	9	13	8	6	11	13

† Y = yield (g per plant): Y1 = low Y ($0 \leq Y1 < 6$), Y2 = medium yield ($6 \leq Y2 < 10$), and Y3 = high yield ($10 \leq Y3 \leq 25$). Pf = final nematode population (numbers per plant): Pf1 = low Pf ($0 \leq Pf1 < 10,000$), Pf2 = medium Pf ($10,000 \leq Pf2 < 40,000$), and Pf3 = high Pf ($40,000 \leq Pf3 \leq 265,000$). R = fresh root weight in g per plant: R1 = low R ($0 \leq R1 < 20$), R2 = medium R ($20 \leq R2 < 32.5$), and R3 = high R ($32.5 \leq R3 \leq 60$). P = number of panicles per plant: P1 = low P ($0 \leq P1 < 5$), P2 = medium P ($5 \leq P2 < 8$), and P3 = high P ($8 \leq P \leq 15$). N = quantity of applied nitrogen (kg/ha): N1 = 40, N2 = 80, and N3 = 160. Pi = initial number of *P. zeae* inoculated per plant: Pi0 = 0, Pi1 = 10 or 50, Pi2 = 100 or 500, and Pi3 = 1,000 or 5,000.

relationships between the two groups of variables, through the examination of the contributions of axes to these variables that are not used in the definition of axes. Four classes were defined for Pi: Pi null (Pi0 = 0), low Pi (Pi1, 10, and 50), medium Pi (Pi2, 100 and 500), and high Pi (Pi3, 1,000 and 5,000), and three classes were defined for the six other variables: low Y ($0 \leq Y1 < 6$), medium yield ($6 \leq Y2 < 10$), high yield ($10 \leq Y3 \leq 25$), low P ($0 \leq P1 < 5$), medium P ($5 \leq P2 < 8$), high P ($8 \leq P \leq 15$), low R ($0 \leq R1 < 20$), medium R ($20 \leq R2 < 32.5$), high R ($32.5 \leq R3 \leq 60$), low N (N1 = 40), medium N (N2 = 80), high N (N3 = 160), low Pf ($0 \leq Pf1 < 10,000$), medium Pf

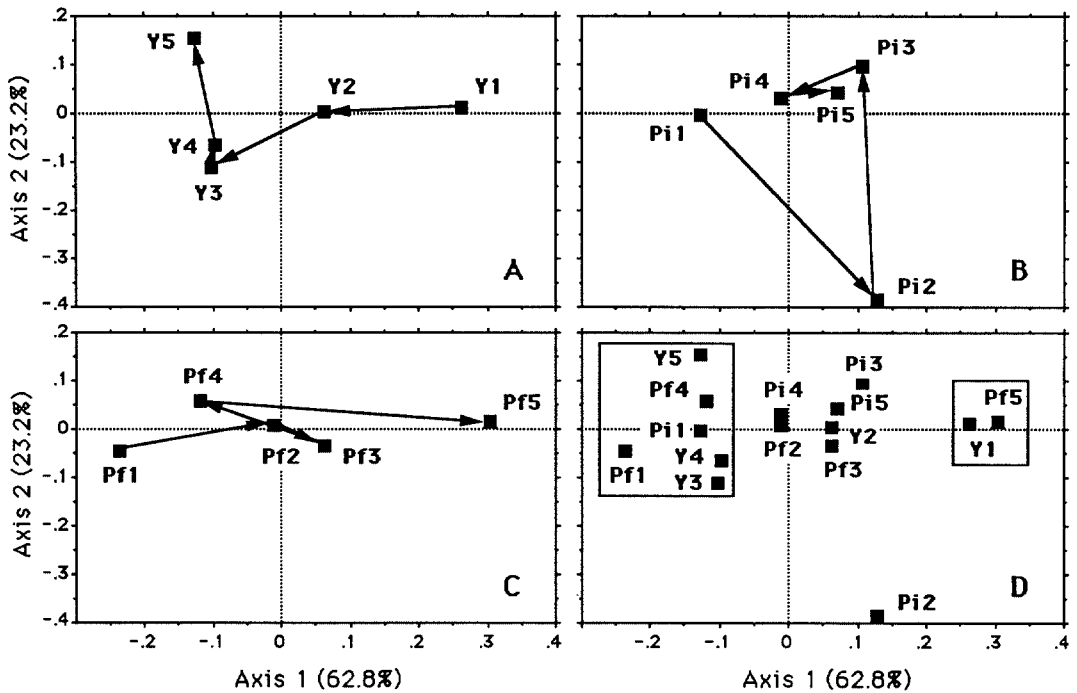


FIG. 1. Correspondence analysis of data from a field experiment showing two-dimensional representations of upland rice yield (Y), initial soil population of *Pratylenchus zeae* (Pi), and final root population of *P. zeae* (Pf) classes using axes 1 and 2. A) Path for increasing Y from very low Y (Y1) to very high Y (Y5). B) Path for increasing Pi from undetectable Pi (Pi1) to very high Pi (Pi5). C) Path for increasing Pf from very low Pf (Pf1) to very high Pf (Pf5). D) Associations between variables indicated by the analysis.

gression along the path of increasing Y (Fig. 1A). The progression along the path of increasing Pi was irregular. Y1 was associated with Pf5. Y5 was associated with any initial nematode population size except Pi2. Y5 was also associated with Pf1 and Pf4, but not Pf5.

When the variables were plotted against axes 1 and 3, a clear path of increasing yield was also observed (Fig. 2A), and the paths of increasing Pi (Fig. 2B) and increasing Pf (Fig. 2C) were similar to those observed with axes 1 and 2 (Fig. 1). Three clusters (Fig. 2D), represented by different associations between classes, can be identified along the path of increasing yield. In a first cluster, Y1 was associated with low Pi2 but not with Pi1, and with Pf5. In a second cluster, Y2 was associated with Pi3, Pi4, and Pf3. In the third cluster, Y3, Y4, and Y5 were associated with Pi1, Pf1, and Pf4. In addition, Pi5 was equally distant from

any yield class, indicating the independence of very high initial nematode population and any yield level.

Greenhouse experiment: An ANOVA indicated significant effects of nitrogen amount applied ($P = 0.0001$), initial number of nematodes ($P = 0.01$), and a significant nitrogen \times Pi ($P = 0.06$) interaction on yield variation. Yield variation could further be described by the regression equation:

$$Y = 3.22 + 0.055 N - 10^{-6} (5.847 N \cdot Pi)$$

which accounts for a significant ($P < 0.05$) although small proportion of variation ($R^2 = 0.465$).

Correspondence analysis yielded four axes accounting for 39.6, 26.7, 21.4, and 12.3% of total inertia, respectively. Variables with a positive sign were: axis 1—Y2,

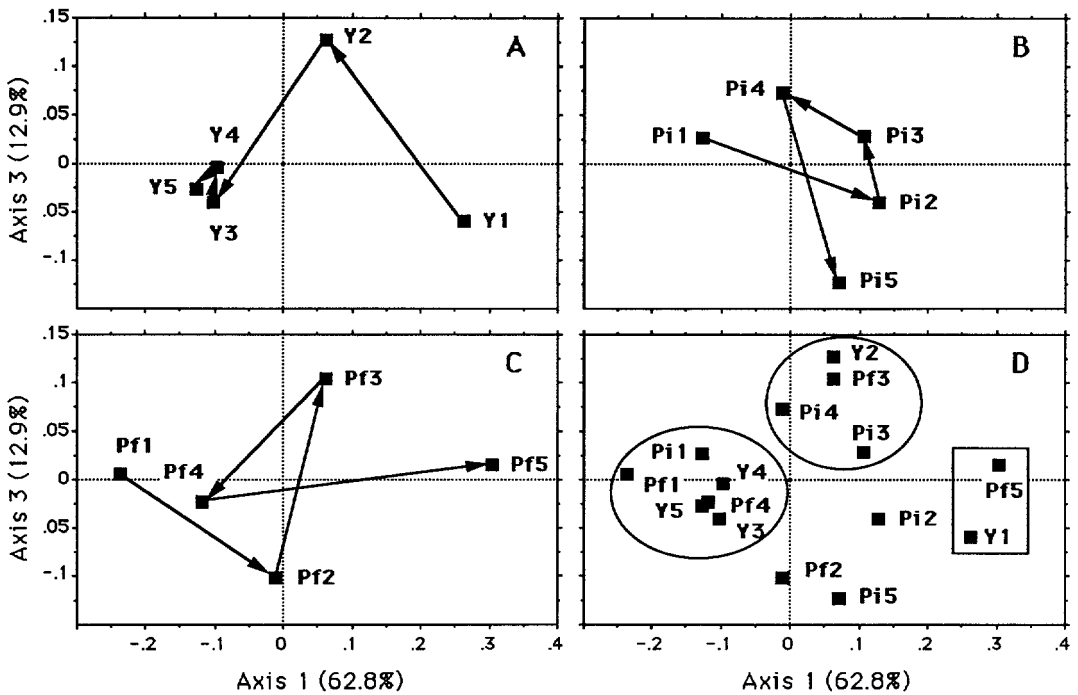


FIG. 2. Correspondence analysis of data from a field experiment showing two-dimensional representations of upland rice yield (Y), initial soil population of *Pratylenchus zae* (Pi), and final root population of *P. zae* (Pf) classes using axes 1 and 3. A) Path for increasing Y from very low Y (Y1) to very high Y (Y5). B) Path for increasing Pi from undetectable Pi (Pi1) to very high Pi (Pi5). C) Path for increasing Pf from very low Pf (Pf1) to very high Pf (Pf5). D) Associations between variables indicated by the analysis.

Pf1, and Pf2; axis 2—Y1, Pf2, and Pf3; axis 3—Y1 and Pf1. All other variables had negative signs (Table 4). The two first axes accounted for most of the inertia of the yield classes (56, 74, and 69% for Y1, Y2, and Y3, respectively) (Table 5). These two axes also accounted for most of the inertia

of the Pf classes (57, 66, and 75% for Pf1, Pf2, and Pf3, respectively) (Table 5). Axis 1 accounted for the path of decreasing root fresh weight and nitrogen input and contrasted P2 and P3. Axis 2 contrasted R1 and R3, P1 and P3, N1 and N3, and Pi0 from any other nematode inoculum level.

TABLE 4. Relative weight and contribution to axes of each class of the correspondence analysis matrix (Burt table) of data from a greenhouse experiment investigating the effect of *Pratylenchus zae* and nitrogen on yield of upland rice cv UPL Ri5.

Class†	Relative weight	Axis 1		Axis 2		Axis 3	
		Contribution to axis (%)	Sign	Contribution to axis (%)	Sign	Contribution to axis (%)	Sign
Column and row							
Y1	0.148	1.07	—	34.17	+	34.17	+
Y2	0.186	27.83	+	3.60	—	3.60	—
Y3	0.167	21.10	—	12.23	—	12.23	—
Pf1	0.152	2.57	+	32.19	—	32.19	+
Pf2	0.176	16.19	+	16.19	+	16.19	—
Pf3	0.171	31.25	—	1.61	+	1.61	—

† + Y = yield (g per plant): Y1 = low Y (0 ≤ Y1 < 6), Y2 = medium yield (6 ≤ Y2 < 10), and Y3 = high yield (10 ≤ Y3 ≤ 25). Pf = final nematode population (number per plant): Pf1 = low Pf (0 ≤ Pf1 < 10,000), Pf2 = medium Pf (10,000 ≤ Pf2 < 40,000), and Pf3 = high Pf (40,000 ≤ Pf3 ≤ 265,000).

TABLE 5. Contribution of axes to each class of the correspondence analysis matrix (Burt table) of data from a greenhouse experiment investigating the effect of *Pratylenchus zeae* and nitrogen on yield of upland rice cv UPL Ri5.

Class†	Axis 1		Axis 2		Axis 3	
	Contribution to class (%)	Sign	Contribution to class (%)	Sign	Contribution to class (%)	Sign
	Active variable, column and row					
Y1	2.50	-	53.67	+	43.05	+
Y2	68.09	+	5.95	-	4.77	-
Y3	49.58	-	19.42	-	15.57	-
Pf1	6.04	+	51.10	-	40.99	+
Pf2	39.55	+	26.72	+	21.43	-
Pf3	72.78	-	2.54	+	2.03	-
	Additional variable, row					
R1	32.90	+	45.95	+	20.71	+
R2	79.80	+	1.24	+	3.19	-
R3	59.40	-	29.41	-	7.03	-
P1	0.13	+	53.59	+	45.43	+
P2	57.41	+	0.43	-	7.96	-
P3	34.06	-	37.83	-	16.42	-
N1	19.76	+	20.10	+	58.82	+
N2	82.67	+	1.13	+	5.45	-
N3	49.55	-	17.71	-	32.70	-
Pi0	1.21	+	60.70	-	30.96	+
Pi1	13.41	+	15.92	+	47.98	-
Pi2	12.87	-	65.36	+	16.18	-
Pi3	0.01	-	31.64	+	14.57	-

† Y = yield (g per plant): Y1 = low Y ($0 \leq Y1 < 6$), Y2 = medium yield ($6 \leq Y2 < 10$), and Y3 = high yield ($10 \leq Y3 \leq 25$). Pf = final nematode population (number per plant): Pf1 = low Pf ($0 \leq Pf1 < 10,000$), Pf2 = medium Pf ($10,000 \leq Pf2 < 40,000$), and Pf3 = high Pf ($40,000 \leq Pf3 \leq 265,000$). R = fresh root weight (g per plant): R1 = low R ($0 \leq R1 < 20$), R2 = medium R ($20 \leq R2 < 32.5$), and R3 = high R ($32.5 \leq R3 \leq 60$). P = number of panicles per plant: P1 = low P ($0 \leq P1 < 5$), P2 = medium P ($5 \leq P2 < 8$), and P3 = high P ($8 \leq P \leq 15$). N = quantity of applied nitrogen (kg/ha): N1 = 40, N2 = 80, and N3 = 160. Pi = initial number of *P. zeae* inoculated per plant: Pi0 = 0, Pi1 = 10 or 50, Pi2 = 100 or 500, and Pi3 = 1,000 or 5,000.

Plotting all the variables on the first two axes resulted in a complex picture of the relationships between all the variables (Fig. 3A). However, associations were observed. The increases in yield, number of panicles, root weight, and nitrogen input followed similar paths (Fig. 3B). Path of increase in final nematode population was different from paths of increase in root weight (Fig. 3C) and yield (Fig. 3D) between Pf1 and Pf2, but these paths were similar between Pf2 and Pf3. Any initial nematode population above Pi0 may lead to any yield and final nematode population.

DISCUSSION

Analysis of the categorized data set from the field experiment generated corresponding patterns of initial and final nematode populations and yield levels.

The association between yield and final *P. zeae* populations observed by Plowright et al. (9) was confirmed. The association is indicative of a poor growing system (and therefore a poor yield). The analysis suggests the existence of a root tolerance, which would be about 672 nematodes per g of root. Above this level, the nematode population becomes so high that yield is severely affected. The most favorable condition for nematode population build-up coincided with low initial population, rather than a medium or high initial nematode population. A limited carrying capacity of the root system early in the season may account for this response. On the other hand, a high final nematode population was not associated with low yield, but with yield ranging from medium to very high. The large carrying capacity may be attributed to fast growing, potentially

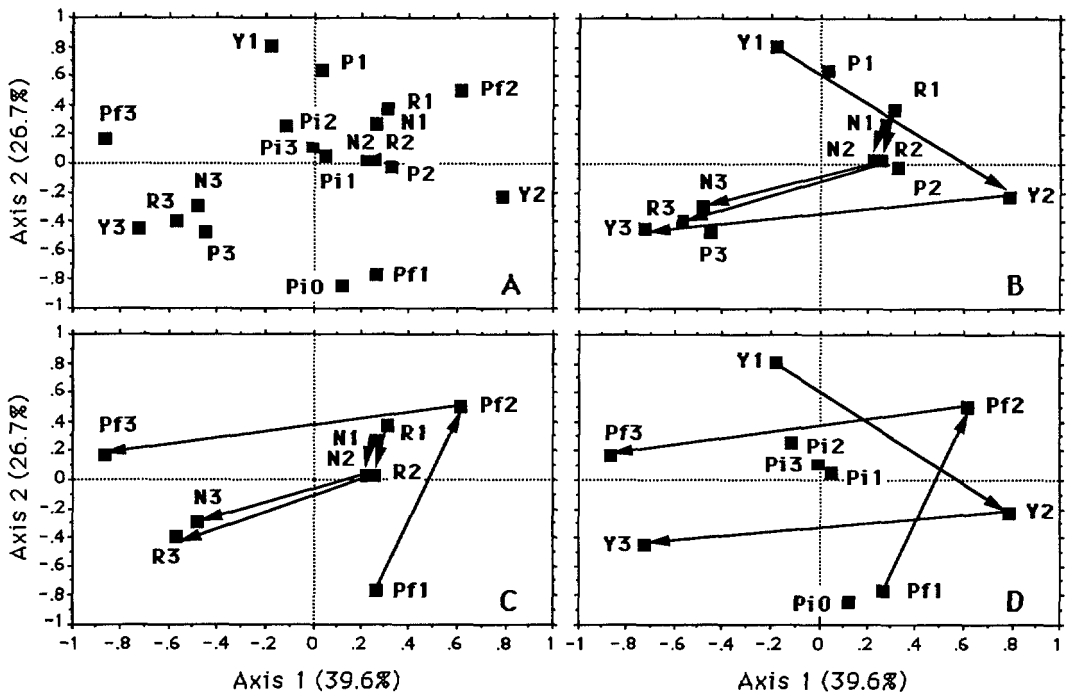


FIG. 3. Correspondence analysis of a greenhouse experiment. A) Two-dimensional representation of yield (Y), panicle number (P), final root weight (R), nitrogen input level (N), initial population of *Pratylenchus zaeae* (Pi), and final population of *P. zaeae* (Pf) classes using axes 1 and 2. B) Paths for increasing Y from low Y (Y1) to high Y (Y3); increasing R from low R (R1) to high R (R3); and increasing N from low N (N1) to high N (N3). C) Paths for increasing R from low R (R1) to high R (R3), increasing N from low N (N1) to high N (N3), and increasing Pf from low Pf (Pf1) to high Pf (Pf3). D) Paths for increasing Y from low Y (Y1) to high Y (Y3) and increasing Pf from low Pf (Pf1) to high Pf (Pf3).

high-yielding plants, and(or) to favorable environmental conditions encountered by the nematode.

Yield and growth characteristics (number of panicles and root weight) were strongly dependent on nitrogen availability. The dynamics of the nematode population and the host growth indicated that equilibrium density of nematode populations was directly dependent on the carrying capacity represented by the host's root system (15). An increase in nematode population limits root growth, which will affect the yield and the nematode multiplication rate. However, an increase in nitrogen availability induces better root growth, producing a better environment for nematode reproduction. The yield of individual plants will depend on their capacity to compensate for injuries caused by the nematode.

Correspondence analysis is a robust,

flexible multivariate method that allows the user to visualize complex relations in contingency tables. It is especially useful when dealing with ordinal (qualitative) variables or with non-normal cardinal (quantitative) variables that do not exhibit linear relations, as in this study. Two independent data sets successfully explained apparent contradictions and illustrated the dynamic nature of the relationships between *P. zaeae* initial and final populations and individual rice plant yield. It may be a powerful tool to reveal trends in complex data sets generated by studies on complex interactions involved in field studies.

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