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THE INFLUENCE OF MINERAL FERTILIZER APPLICATION AND PLANT NUTRITION ON PLANT-PARASITIC NEMATODES IN UPLAND AND LOWLAND RICE IN CÔTE D'IVOIRE AND ITS IMPLICATIONS IN LONG TERM AGRICULTURAL RESEARCH TRIALS

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SUMMARY

Mineral fertilizer application and consequent plant nutrition has long been observed to influence associated plant-parasitic nematode population densities, offering the potential as a nematode management option. Observations were made on the influence of mineral fertilizer application on nematode populations on three separate long-term rice experiments, (differential mineral application on upland and on lowland rice, and P application on upland rice) undertaken between 1994 and 1997 in Côte d'Ivoire. In 1995, on upland rice, treatments with K or N withheld from the comprehensive mineral application treatment (range of elements including N, P, K, Ca, Mg and Zn) led to lower densities of *Pratylenchus zeae* at harvest than the comprehensive mineral application. By withholding K or Mg, *Helicotylenchus pseudorobustus* densities were greater than with either the control (no mineral application) or comprehensive mineral application in the same year. No differences were observed between treatments in 1994, or between treatments for densities of other nematode species present (*Meloidogyne incognita*, *Criconemella tescorum*) or for total nematode density. In the lowland rice trial, no treatment effects on nematode species (*Hirschmanniella oryzae* and *Uliginotylenchus palustris*) were observed. In the P application trial on a P-deficient Ultisol, *Heterodera sacchari* densities were lower in treatments receiving 180 kg P ha^{-1}, than untreated in 1995; in 1996 no differences were observed between untreated and 135 kg P ha^{-1}, while in 1997 higher densities of *H. sacchari* were present in 135 kg P ha^{-1} than untreated. Regression analysis of nematode densities against the mineral straw content in the P application trial revealed a negative correlation between *M. incognita* and Mn and Ca, and between *P. zeae* and Zn or Fe. A positive correlation was observed between *Helicotylenchus* spp. and Mg. This study provides strong arguments for taking plant parasitic nematodes into account when planning and executing long-term research trials.

INTRODUCTION

Mineral nutrition is essential to plant growth and development. Variable nutritional status of plants may influence crop resistance to pests and diseases (e.g. Dale, 1988; Engelhard, 1989; Rodríguez-Kábana, 1986). Manipulation of such relationships may therefore provide potential pest and disease management interventions. A

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comprehensive review of the influence of plant nutrition on inherent disease resistance is found in Engelhard (1989), and specifically on rice in Datnoff (1994). The effects of nutrient stresses on plants and how these affect their suitability to herbivorous insects is reviewed in Dale (1988). By comparison, such information for plant-parasitic nematodes is meagre. Largely, the influence of mineral fertilizer or organic waste application on nematode incidence is reported (Rodríguez-Kábana, 1986). Specific studies on the effects of individual nutrients on nematodes have been undertaken, including K (Oteifa, 1953; Terry and Das Gupta, 1973), P (Price *et al.*, 1989; 1995) and most commonly N (e.g. Swain and Prasad, 1991; Prot *et al.*, 1994) but these are, in general, limited.

Within a given field a complex of factors, including soil texture, pH, moisture, temperature, microbial activity of the soil and individual plants, amongst others, combine to affect the release and availability of mineral nutrients (Brady, 1974). With high variability of such factors shown to occur over short distances (IRRI, 1996), interactions of these factors with applied fertilizers are likely to be equally variable. Conversely, interactions may be dependent upon seasonal changes in climate. Rao and Isreal (1971; 1972), showed that physical changes in soil moisture and soil type both affect the way nematodes behave, while Koen (1966) showed how seasonal variations influenced root-knot nematode (*Meloidogyne javanica*) distribution within the soil. While nutrients indeed play an important role in plant health and pest and disease incidence, the magnitude of probable interactions and relationships appear dependent upon a range of interacting factors (Dale, 1988; Datnoff, 1994).

On rice, plant-parasitic nematodes can constitute significant production constraints (Bridge *et al.*, 1990). In lowland (flooded) rice *Hirschmanniella* spp. are important pests, causing annual losses estimated at as high as 25 % globally (Hollis and Keoboonrueng, 1984). On upland (dry) rice, numerous nematode species have been associated with rice, although *Pratylenchus zeae* (Plowright *et al.*, 1990), *Meloidogyne* spp. (Diomandé, 1981; Plowright and Hunt, 1994) and *Heterodera sacchari* (Coyne and Plowright, 2000) can be particularly damaging.

This study reports on observations made on the influence of mineral fertilizer applications on nematode incidence on upland and lowland rice. Consistency of observed associations over successive seasons were assessed on three long-term fertilizer application experiments at the West Africa Rice Development Association (WARDA) between 1994 and 1997 in the humid forest and forest-savannah transitional zones, Côte d'Ivoire.

METHODS

Mineral deficiency experiments

Long-term multi-year experiments to determine the status of mineral reserves in (1) a non-irrigated upland soil and (2) a lowland soil under irrigation were located in the forest-savannah transitional zone at M'bé (7.52°N, 5.06°W; altitude 340 m asl). Experiments followed a randomised complete block (RCB) design with plot size measuring 24 m^2, four replications and eight treatments, including untreated

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(zero check) and comprehensive mineral application controls (100 kg N ha^{-1} as urea, 100 kg P ha^{-1} as triple super phosphate, 83 kg K ha^{-1} as KCl, 38 kg Ca ha^{-1} as hydrated lime, 30 kg Mg ha^{-1} as $MgCO_3$ and 5 kg Zn ha^{-1} as $ZnSO_4$). For the remaining six treatments, one of the six elements was omitted. P, K, Ca, Mg and Zn were applied basally at planting; N was applied in three equal splits at planting, tillering and flowering. The site received 1260 mm and 708 mm of rainfall during the 1994 and 1995 growing seasons, respectively. Plots were maintained weed free with regular hand weeding.

(1) Upland mineral deficiency experiment

The upland soil was pH 6.5, low in organic matter, gravelly throughout with sandy clay texture in deeper horizons (0.3–0.5 m). The trial was first planted in 1989 with rice (*Oryza sativa*) cultivar (cv) IDSA6 used throughout. Nematode population densities were assessed at crop maturity during the wet seasons of 1994 and 1995 (6th and 7th successive crops).

(2) Lowland mineral deficiency experiment

In the lowland experiment, the soil type was a sandy clay loam Ultisol, low in organic matter with pH 6.7. The rice (*O. sativa*) cv Bouaké 189 was used throughout. Nematode population densities were assessed in 1995 and 1996 (8th and 9th successive crops). All treatments were assessed in 1995 while only the untreated and the comprehensive nutrient application treatments were assessed in 1996.

(3) Phosphorus application experiment

The P application experiment was on an upland location in the humid forest zone at the IDESSA (Institut des Savannes) station near Man, Côte d'Ivoire (7°20′N, 7°40′W; altitude 500 m asl) in an Ultisol, pH 4.9 with low extractable P (2.7 ppm Bray-1 extractable P). The site received 1396 mm, 1668 mm and 970 mm of rainfall during the 1995, 1996 and 1997 growing seasons respectively. The experiment had a RCB design with four replications. The treatments consisted of four rice (*O. sativa*) cultivars and 5 P levels (0, 45, 90, 135 and 180 kg P ha^{-1} as triple super phosphate) applied in 1993. Assessments were made only on cv IDSA6 and cv WAB 56-125. Individual plots measured 15 m^2 and received 100 kg N ha^{-1} as urea in three splits at planting, tillering and flowering. Plots were maintained weed free with regular hand weeding. Nematode population densities were assessed at crop maturity in 1995, 1996, 1997 (3rd, 4th and 5th successive crops). In 1995 nematode densities from all treatments for cv IDSA6 were assessed, and for 0 and 135 kg P ha^{-1} treatments on cvs IDSA6 and WAB 56-125 in 1996 and 1997.

Nematode assessment

Nematode densities were estimated from soil and roots of six plants per plot, randomly chosen from the inside border row. Samples of roots and rhizosphere soil were removed using a trowel, to a depth of ≈250 mm. Nematodes were extracted from 100 cm^3 and 5 g fresh root sub-samples, using the modified Baermann filter technique (Hooper, 1986) for dry soil and root samples, and the modified flotation and sieving technique (Hooper, 1990) for wet soil from the lowland rice experiment. Nematode densities were assessed after an extraction period of 48 h using a Leica Wild M3C stereomicroscope. The nematode suspension was reduced to 10 cm^3 and the population density estimated from 2×1 cm^3 aliquots. Motile, vermiform nematodes only were assessed, with the exception of eggs of *H. sacchari* in experiment 3, which were also present. Nematodes were identified to species level by David Hunt, CABI Bioscience, UK.

Plant straw characteristics

Crops were harvested at maturity and straw samples in the P application trial in 1995 were analysed for percentage N, P, K, Ca, Mg, and ppm of Fe, Mn and Zn for each plot. For total nitrogen content, straw samples were digested with sulphuric acid and hydrogen peroxide and analysed using a Kjeldahl steam distillation. For P, K, Ca, Mg, Fe, Mn and Zn content, straw samples were digested in a 2:1 mixture of nitric and perchloric acid. Total P in the digest was analysed colorimetrically using the vanadomolybdate yellow colour method. Total K, Ca, Mg, Fe, Mn and Zn were analysed by atomic absorption spectrophotometry (Sahrawat *et al.*, 1998).

Statistical treatment of data

Differences in nematode population densities between treatments were compared with ANOVA using SPSS Inc. for Windows 1995 version, following $log_{10}(n+1)$ transformation of densities. Nematode densities, while assessed separately from roots and soil, were combined for analysis and purposes of presentation because endoparasites (*Pratylenchus, Meloidogyne*, and *Heterodera*) move freely between roots and soil, particularly towards root senescence. Population densities of the ectoparasites are derived from soil only. The relationship between transformed population densities and the nutrient content of straw for each individual plot from experiment 3 (1995 only) was assessed using regression analysis (SPSS).

RESULTS

In the upland mineral deficiency experiment (1) *Meloidogyne incognita*, *P. zeae, Helicotylenchus pseudorobustus* and *Criconemella tescorum* were present throughout the trial area. In the lowland mineral deficiency experiment (2) *Hirschmanniella oryzae* and *Uliginotylenchus palustris* were present. Nematodes present in the P experiment (3) included *H. sacchari, M. incognita, P. zeae, Helicotylenchus dihystera, Helicotylenchus* n. sp. and *Macroposthonia onoensis*. *Xiphinema* n. sp. and *Afenestrata africanus* were also present but rare.

Studies on long-term differential mineral fertilizer treatments in 1994 indicated that the application of the comprehensive mineral application, or omission of any individual mineral from the comprehensive treatment had little influence on nematode

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Table 1. Mean (four replications) nematode population densities (log_{10}(n + 1) transformed) recovered from rice (cv IDSA6) in an upland (1995 and 1996) and (cv Bouaké 189) in an irrigated lowland (1994 and 1995) mineral deficiency experiment, M'bé, Côte d'Ivoire.

	Lowland				Upland									
Treatment†	*H. oryzae*‡		*U. palustris*		*M. incognita*		*P. zeae*		*H. pseudorobustus*		*C. tescorum*		Total	
Year	1995	1996	1995	1996	1994	1995	1994	1995	1994	1995	1994	1995	1994	1995
Zero check	1.58	2.00	0.75	1.13	3.27	3.43	2.90	2.71	2.12	2.14	2.38	2.10	3.52	3.57
Comprehensive	0.83	1.78	1.78	1.16	3.11	3.27	2.56	2.90	2.47	2.12	1.93	2.38	3.35	3.52
Element omitted														
– N	0.66	–	1.52	–	3.51	3.11	2.92	2.56	2.58	2.47	2.43	1.93	3.71	3.35
– P	1.86	–	0.77	–	3.31	3.51	2.66	2.92	2.87	2.58	1.98	2.43	3.55	3.71
– K	0.73	–	1.59	–	3.10	3.22	2.68	2.56	2.62	2.74	2.15	2.23	3.41	3.47
– Ca	1.05	–	1.61	–	3.26	3.10	2.73	2.68	2.59	2.62	2.20	2.15	3.51	3.41
– Mg	1.19	–	1.44	–	3.22	3.32	2.56	2.66	2.74	2.87	2.23	1.98	3.47	3.55
– Zn	1.53	–	1.20	–	3.43	3.26	2.71	2.73	2.14	2.59	2.10	2.20	3.56	3.51
s.e.	ns	ns	ns	ns	ns	ns	ns	0.29	ns	0.52	ns	ns	ns	0.23

†Zero check = no fertilizer application; Comprehensive = comprehensive mineral application controls; the remaining six treatments, one of the six indicated elements was omitted (e.g. N, P, etc.).
‡nematode recovered from 100 cm^3 soil + 5 g roots (fresh weight); – indicates the treatment was not assessed.

Table 2. Mean (four replications) nematode densities (log_{10}(n + 1) transformed) recovered from rice (cv IDSA6) at harvest in a P application trial on a P deficient Ultisol, Man, Côte d'Ivoire in 1995.

P kg ha^{-1}	*M. incognita*†	*P. zeae*	*Helicotylenchus* spp.	*M. onoensis*	*Xiphinema* n.sp.	*H. sacchari*	Total
0	2.42	2.45	1.06	2.04	0.73	2.54	3.13
45	2.69	2.63	0.65	1.32	1.27	2.29	3.14
90	2.61	2.55	0.56	2.24	1.40	2.31	3.13
135	2.47	2.41	1.16	1.92	0.79	2.36	3.15
180	2.12	2.47	1.95	2.02	0.80	1.92	3.03
s.e.	ns	ns	1.21	ns	ns	0.59	ns

†nematodes recovered from 100 cm^3 soil + 5 g roots (fresh weight).

population densities at crop maturity (Table 1). In the upland experiment (1) in 1995 however, higher mean densities of *P. zeae* ($p \leq 0.05$) were observed in the comprehensive mineral application treatment and with P withheld than in treatments with either K or N withheld, and higher mean *H. pseudorobustus* ($p \leq 0.05$) populations in treatments with K or Mg withheld than the comprehensive mineral application treatment or the zero check. With P withheld, total mean nematode populations (all species combined) were greater ($p \leq 0.05$) than when either K or Ca were withheld. The 1994 results, however, did not reflect those obtained in 1995. In the lowland rice experiment (2) no differences in nematode population densities were recorded between treatments, although densities were relatively low over both years.

In the P application experiment (3) in 1995, *H. sacchari* densities from roots and soil were lower ($p \leq 0.05$) on cv IDSA6 when P was applied at 180 kg ha^{-1} than on untreated plots (Table 2). In 1996, however, higher densities of *H. sacchari*

Table 3. Mean (four replications) nematode densities ($\log_{10}(n+1)$ transformed) recovered at harvest from rice (cv IDSA6 and cv WAB 56-25) at two application rates of P on a P deficient Ultisol, Man, Côte d'Ivoire in 1996 and 1997.

Cultivar Year	P Kg ha^{-1}	*M. incognita*†		*P. zeae*		*H. sacchari*		*Helicotylenchus* spp.		*M. onoensis*		*Xiphinema* n. sp.		Total	
		1996	1997	1996	1997	1996	1997	1996	1997	1996	1997	1996	1997	1996	1997
IDSA6	0	1.48	–	1.15	2.22	2.23	3.11	1.26	0.82	–	1.77	1.48	–	2.41	3.21
	135	1.97	–	1.15	2.02	2.58	3.06	1.66	0.66	–	1.93	1.56	–	2.76	3.17
	s.e.	ns	–	ns	ns	0.32	ns	ns	ns	–	ns	ns	–	ns	ns
WAB 56-125	0	0.92	–	2.24	1.72	2.43	2.75	0.19	0.6	–	1.53	1.13	–	2.71	2.92
	135	0.59	–	2.24	2.32	2.13	2.29	0.97	1.53	–	2.0	1.03	–	2.57	2.75
	s.e.	ns	–	ns	ns	ns	ns	ns	ns	–	ns	ns	–	ns	ns
	Interaction P × cultivar‡	*	–	ns	ns	ns	*	*	ns	–	ns	ns	–	ns	ns

†nematodes recovered from 100 cm^3 soil + 5 g roots (fresh weight); – indicates nematodes not present.
‡interaction significantly different at $p \leq 0.05$ (*); ns – not significantly different.

($p \leq 0.05$) were present at the higher P application rate of 135 kg ha^{-1} compared with untreated. No differences in nematode population densities were observed between these treatments in 1997 (Table 3). *Helicotylenchus* spp. densities were lower ($p \leq 0.05$) in low P application rates than high application rates in 1995, a trend (non-significant) reflected in 1996 and 1997. No other differences were observed between nematode densities and P application rates over the three-year study period for cv IDSA6.

On cv WAB56-125 (1996 and 1997) in experiment (3), no differences ($p \leq 0.05$) were observed in nematode densities following the application of P in 1996 (Table 3). Over the three seasons of study however, the nematode community structure varied. For instance, population densities of *M. onoensis* were high in 1995, were low and occurring too erratically to be analysed in 1996, but were again present throughout the experimental area in 1997. *M. incognita* were present in high densities in 1995, were relatively low in 1996 and were too few to analyse in 1997. *Xiphinema* n.sp. were present in low densities during the first two seasons but occurred too erratically to analyse in the third. During 1996 *H. sacchari* densities differed ($p \leq 0.05$) between treatments on cv IDSA6 but not on cv WAB56-125. In 1997 no differences in nematode densities were observed between treatments, although fewer *H. sacchari* were recovered from P treated plots of WAB56-125. This suggests that the influence of rice P nutrition on nematode infection may be dependent upon host susceptibility to the nematode.

Analysis of cv IDSA6 straw nutrient content and nematode infection in 1995 (Table 4) showed that no single nutrient was correlated with population densities of more than one nematode species. Total N ranged from 0.77 to 1.56 %, P from 0.05 to 0.11 %, K from 0.79 to 2.0 %, Ca from 0.1 to 0.34 %, Mg from 0.3 to 0.11 %, Fe from 46 to 784 ppm, Mn from 149 to 443 ppm, and Zn from 7 to 17 ppm. The presence of *Helicotylenchus* spp. was positively correlated with Mg ($p \leq 0.05$); *M. incognita* was negatively correlated with either Mn ($p \leq 0.01$) or Ca ($p \leq 0.05$); *P. zeae* was negatively

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Table 4. Regression coefficient (r) between nematode population densities ($\log_{10}(n + 1)$ transformed) and mineral content of rice (cv IDSA6) straw in 1995 in a P application trial on a P deficient Ultisol.

Mineral	*M. incognita*[†]	*P. zeae*	*H. sacchari*	*Helicotylenchus* spp.	*M. onoensis*	*Xiphinema* n. sp.
N	0.31	0.37	−0.02	−0.34	0.05	0.14
P	−0.15	0.42	−0.13	0.25	0.11	0.21
K	−0.35	−0.02	0.14	0.31	0.11	−0.38
Ca	−0.53*[‡]	0.08	−0.14	0.35	−0.12	−0.20
Mg	−0.42	−0.28	−0.14	0.54*	−0.08	−0.19
Fe	−0.18	−0.49*	−0.25	0.14	0.06	0.24
Mn	−0.63**[‡]	−0.19	−0.03	0.33	−0.17	−0.13
Zn	0.21	−0.4*	0.04	0.03	0.05	0.02

[†] $n = 20$.
[‡] significant at $p \leq 0.05$ (*) and $p \leq 0.01$ (**).

correlated with either Fe or Zn ($p \leq 0.05$). No correlations were observed between densities of any other nematode species and a specific nutrient in the straw.

DISCUSSION

The availability of nutrients and the consequent nutritional status of plants has the capacity to influence the relationship between the plant and its pests and diseases. However, consistent results are not always obtained for such observations between studies. It appears that a large number of extraneous factors need to be taken into consideration before recommendations on the use of fertilizers as a management option, can safely be made. When assessing the influence of plant nutrient stresses on insects, Dale (1988), considered it wise to consider the relationships among soil, plant and insects as an active interplay of the three biological systems that are themselves prone to be acted upon by many ecological factors. Moreover, the high diversity and often varied results obtained by workers were related to such factors, resulting in studies with single plant nutrients individually in a reductionist approach. This however, we find inconsistent with Dale's (1988) own observation, that individual minerals are likely to behave differently in the presence of the various intrinsic and extrinsic factors. This is likely to be more relevant under tropical, than temperate conditions where chemical and biological processes tend to be faster, and where the number of potential interactions ultimately greater. For instance, tropical nematode communities are much more diverse, and generally have much shorter life cycles than their equivalents in temperate climates (Luc *et al.*, 1990).

In the current study the intensity of nematode attack was measured (nematodes per unit weight of root), but as the total plant root and shoot weights were not assessed, it is not possible to relate nematode populations to plant growth *per se*, only intensity. Nevertheless, the results showed that under certain circumstances, certain plant nutrients influenced plant parasitic nematode prevalence and/or host susceptibility in rice plants to those nematodes. The results were erratic however, suggesting that the use of mineral application for nematode management should be made with

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caution. There is strong evidence, which demonstrates the nematicidal or nematode suppressing effects of N application (e.g. Rodríguez-Kábana, 1986), but, in order to be effective, N needs to be applied at levels far in excess of those required for crop fertilisation. For instance, Swain and Prasad (1991) observed *Meloidogyne graminicola* density increase on rice following N application up to 80 kg ha^{-1} and marked reductions at 120 kg ha^{-1}. High rates of N fertilizer can result in plant tissue becoming softer as carbohydrates are diverted to protein synthesis instead of cell wall construction (Tisdale and Nelson, 1975). This predisposes plants to increased insect damage (Dale, 1988). However, N that is converted to ammonia in applications, such as urea, possibly exerts selective influence on soil-borne fungi, which may be antagonistic to nematodes (Morgan-Jones *et al.*, 1981). Many soil fungi use ammonia as a preferred N source (Cochrane, 1958). Variable presence of antagonistic fungi may partly explain therefore, why some studies have reported little effect on nematode parasites following N application (Mathur and Prasad, 1972; Prot *et al.*, 1994), in contrast to some of the high levels of nematode suppression reported following N application (Diomandé, 1981; Fademi, 1988). In the current study, omission of N in either of the mineral deficiency experiments influenced only one nematode, *P. zeae*, in 1995 in upland rice, with lower densities present with N withheld compared with the comprehensive mineral application. This observation complicates the interpretation concerning associations between nematodes and fertilizer application. In plots receiving the comprehensive fertilizer treatment, plants are healthier and stronger, as suggested by the higher yield (>100% difference) compared with the zero check (Sahrawat *et al.*, 1993). Healthier plants may support higher rates of nematode multiplication than weaker plants (Seinhorst, 1966). However, with the exception of *P. zeae*, no other nematode species was influenced by the omission of N. By withholding K or Mg, *H. pseudorobustus* densities were greater than in the comprehensive mineral or zero check treatments. This would suggest that individual nematode species are influenced separately by individual minerals, and that the relationship between plant nutrition and nematodes may be dependent upon the presence (interaction) of other minerals.

Observations across experiments were not consistent between seasons in the current study, suggesting that the influence mineral application may have on nematode parasitism may be also influenced by season (climatic factors). Francl (1993), when studying the relationship between edaphic factors and soybean cyst nematode (*Heterodera glycines*), found that Cu appeared negatively associated, but the factor ‘pH, Mg and Cu’ was positively correlated, with the numbers of cysts in the second year. Plowright and Hunt (1994), observed that *M. incognita* density was influenced by fertilizer application in upland rice but not in hydromorphic rice, where water availability is greater, and that the opposite occurred with *P. zeae*. Climatic factors, particularly water availability, which can affect nematode population dynamics (Coyne *et al.*, 2001), probably compounds the influence of mineral availability on nematodes. The competitive capacity of individual species within the nematode community may then affect the ultimate density of individual species (Rao *et al.*, 1984), which will in turn be affected by mineral availability. At WARDA, rainfall during the growing season in 1994 was nearly double that in 1995. These differences, and those at

Man between 1995 and 1997, may account for some of the differences in nematode densities between treatments between seasons during this period.

Phosporous is understood to reinforce plant tissue, possibly contributing a physical barrier against pathogens, leading to its role in reducing foliar diseases (Huber, 1990). It is also an important element, which affects the metabolism of other nutrients (Brady, 1974). Regupathy and Subramanian (1972) observed altered mineral metabolism in rice plants with increased rates of NPK fertilizers. High doses of N, P and K influenced the content in the plant of other minerals, with N resulting in a decrease in P, a phenomenon found to occur when P and N fertilizers are jointly applied (Smith, 1964). This may partially explain the higher mean density of *P. zeae* and of total nematode density in 1995 when P was omitted, than when N was omitted from treatments (Table 1). Alternatively, the observation may be related to urea suppressing nematode hatching, which was an observation made by Grosse and Decker (1984) with *Heterodera avenae*. Simon and Rovira (1985), discovered that P utilisation, and consequently plant vigour, was dependent upon nematode density. When studying the effects of P application on wheat infested with *H. avenae* they found that under low nematode densities P application improved crop growth, but that under severely infested conditions, the capacity of the crop to utilise P was impaired. Increased application of P was generally associated with an increase in nematode densities, possibly due to improved plant vigour.

The general balancing effect of K on N and P therefore appears to make K an important component of mixed mineral fertilizer application. In the nutrient deficiency experiment, omission of K in 1995 was associated with lower *P. zeae* population densities, compared with comprehensive mineral application, or with N omitted, and also lower total nematode densities than with P omitted. This suggests that these nematodes may be more abundant in the presence of K. However, no differences were observed in 1994 between these treatments. This contradicts other observations. Oteifa (1953) for instance, concluded that application of K reduced the damage caused by *M. incognita* and Terry and Das Gupta (1973) suggested that application of K reduced densities of *Aphelenchoides besseyi* on rice. Conversely, Quraishi (1985) reported that application of N fertilizers reduced populations of *Xiphinema, Tylenchulus and Rotylenchulus* in grape vineyards, while K and P fertilizers had less effect.

In the current study no significant correlations between any nematode species and N, P or K content of plant tissue (straw) were observed. A number of correlations were observed between some micronutrients and nematode densities. The nature of the relationship and whether the observed correlations are a consequence of the availability of the three main nutrients is unclear. For instance, the high population densities of *M. incognita* in 1995 in experiment (3) may have inhibited the uptake of Mn. Novaretti *et al.* (1987), demonstrated that *M. javanica* interfered with nutrient uptake in sugar cane and Simon and Rovira (1985) suggested that infection with *H. avenae* actually prevents P utilisation in wheat. Conversely, Mn content in the straw may be a consequence of the reallocation of nutrients within the plant when infected with *M. incognita*. During a study on the nutritional disorders in rice following nematode infection, Rao *et al.* (1988), found that Mn, K and Mg decreased in shoots but increased in roots in relation to *M. graminicola* infection. They found a similar relationship with phenols following *Heterodera oryzicola* infection, suggesting that nutrients are mobilised and shifted to different parts of the plant when attacked by nematodes. They concluded that nematodes caused nutritional disorders, which limited the uptake of N and P in particular. In another study, Badra and Elgindi (1979) concluded that mineral application stimulated extensive synthesis of phenols in plant roots, which inversely determined nematode multiplication. Phenol production is associated with natural plant defence mechanisms against nematode and pathogen attack (Pi and Rohde, 1967; Hung and Rohde, 1973). If more detailed studies of this nature could be undertaken, assessing both root and foliar nutrient content, our knowledge of the processes, which lie behind these complex mechanisms, may be better understood. But, as the current study has demonstrated, the magnitude of interrelationships, which may exist between the myriad of factors, is potentially huge. Riggs *et al.* (1989), following studies on potential management options with fertilizers and pesticides for *Heterodera glycines*, proposed that each nematode infested field must be considered separately, taking into account such factors as the nematode population, mineral status of the soil, and soil structure, before applying pesticides and fertilizers.

This study permits two essential observations: firstly, that soil nutrition can influence nematode infestation of upland rice roots. Secondly, nematode infestation may neutralise the potential yield increases of nutrient application. In differential nutrient application studies, therefore, damage incurred by nematodes, which may be greater in some treatments, can mask the nutrient affects to plant growth. Damaged roots are less efficient and less able to utilise applied inputs than healthy, uninfected roots. In long-term fertilizer trials, build-up of nematodes and other soil-borne pests and diseases can develop into substantial constraints to production, and as such require quantification. The current study was, in part, stimulated as a consequence of successive reductions in yield and crop performance.

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