Effect of KNO_3 on CO_2 exchange rate, nutrient concentration and yield of *Meloidogyne incognita* infected beans

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SUMMARY

One-week-old *Phaseolus vulgaris* plants were inoculated with 4 000 second stage *Meloidogyne incognita* juveniles and fertilized with Hoagland solution containing none, normal, double, or quadruple strength KNO_3 and compared with uninfected controls that received normal strength Hoagland solution. The leaf area and the photosynthetic and dark respiration rates were measured at intervals from 0 (before) to 28 days after inoculation. At 28 days, plant dry weight, number of pods and seeds and the concentration of K, Ca, Mn, Fe, Cu and Zn in the leaves, stems and roots and NO_3 in the leaves were determined. The soil pH, conductance and the soil concentrations of PO_4, Na, B, Mg, and SO_4 were also measured. The photosynthetic rate and respiration rate increased with the addition of KNO_3 in the nematode-infected plants but not higher than in the uninfected controls. The concentration of K in the shoot and NO_3 in the leaves increased while the other elements generally decreased with increasing supplementary KNO_3. In the soil, NO_3, K, Ca, Mn, SO_4 and conductance decreased while the pH increased with decreasing supplementary KNO_3. Fewer pods and seeds were formed in the nematode-infected plants which did not receive supplementary KNO_3. The results show that under the prescribed conditions, for a nematode-infected bean plant to yield closest to the uninfected and fertilized with normal strength Hoagland solution it required a four fold supplement of KNO_3.

RÉSUMÉ

Effets de KNO_3 sur le taux d'échange du CO_2, la concentration en éléments nutritifs et la récolte chez le haricot infesté par Meloidogyne incognita

Des plants de *Phaseolus vulgaris* âgés d'une semaine ont reçu un inoculum de 4 000 juvéniles de second stade de *Meloidogyne incognita* et une solution de Hoagland contenant des doses variées de KNO_3 (0, normale, double, quadruple); ces plants ont été comparés à des plants témoins, non infestés, ayant reçu une solution d'Hoagland de composition normale. La surface foliaire, les taux de photosynthèse et de respiration nocturne ont été mesurés à des intervalles s'étageant de 0 (avant inoculation) à 28 jours après l'inoculation. Après 28 jours, ont été déterminés : le poids sec de la plante, les nombres de gousses et de grains, le contenu des feuilles, des tiges et des racines en K, Ca, Mn, Fe, Cu et Zn ainsi que le taux de NO_3 dans les feuilles. En ce qui concerne le sol, ont été déterminés : le pH, la résistivité et les concentrations en PO_4, Na, B, Mg et SO_4. La photosynthèse et la respiration augmentent chez les plants infestés ayant reçu du KNO_3, mais ces valeurs ne dépassent pas celles des témoins non infestés. La teneur en K dans les pieds et en NO_3 dans les feuilles augmente alors que celle de la plupart des autres éléments diminue lorsque la dose supplémentaire de KNO_3 s'accroît. Dans le sol, les taux de NO_3, K, Ca, Mn et SO_4, ainsi que la résistivité, diminuent cependant que le pH augmente lorsque les doses de KNO_3 décroissent. Un nombre plus faible de gousses et de graines sont formés chez les plants infestés qui ne reçoivent pas de doses supplémentaires de KNO_3. Ces résultats montrent que, dans les conditions de cette expérience, les haricots infestés ne peuvent atteindre un rendement voisin de celui des plants non infestés et fertilisés avec une solution de Hoagland de composition normale, que s'ils reçoivent une dose quadruple de KNO_3.

Parasitic and abiotic agents affect root uptake rate and translocation of mineral elements within a plant and thus change plant elemental concentrations. Changes in elemental concentration resulting from nematode infection directly or indirectly affect plant-host physiology and final yield (Melakeberhan *et al.*, 1985; Been & Schomaker, 1986) and affect the nutritional value of the crop. Commercial fertilizer consisting of a single or combination of elements may be used to improve crop yield by it 1) supplementing existing levels in the soil and 2) compensating for losses that result from pathogens such as nematodes (Trudgill, 1980; Spiegel *et al.*, 1982). In plant disease situations, where more than one element is affected, the use of commercial fertilizers could be improved if the effects of the pathogen on the host physiological processes that affect crop yield were better understood. In studies of the physiology of *Meloidogyne incognita*-infected bean plants that received normal strength Hoagland solution, Melakeberhan, Webster and Brooke (1985), showed a significant decrease in

photosynthetic rate and crop yield with increasing nematode inoculum level and duration of infection. These findings were associated with leaf chlorosis, premature abscission and with changes in nutrient elemental concentrations (Melakeberhan *et al.*, 1987). Among other elements, the concentration of K in the shoots of nematode-infected plants, and the photosynthetic rate based on shoot K concentration decreased with increasing nematode infection from one week after inoculation (Melakeberhan *et al.*, 1987). The authors proposed that : 1) *M. incognita* decreases photosynthetic rate by decreasing the level of K in the leaves, and 2) the chlorosis symptoms suggested that N (and possibly other elements) related deficiencies, and/or a combination of these, decreases host-physiological activity and results in lower productivity. The present study was done to determine if increasing the levels of KNO_3 in normal strength Hoagland solution could alleviate the detrimental effect of *M. incognita* infection on CO_2 exchange rate, chlorosis, nutrient status and growth of *Phaseolus vulgaris* compared with those receiving the normal strength of Hoagland solution.

Materials and methods

Steam sterilized soil (1:1 sand : silt mix) was analyzed for nutrient concentrations, conductance and pH status. The concentrations of NO_3, PO_4, K, Ca, Na, Mg, Cu, Fe, Mn and Zn were determined in five soil samples (350 g/sample), using inductively coupled plasma atomic emission spectrometry (Church, 1981) and that of B using the azomethine method (Upor, Mohai & Novak, 1985). Conductance and soil pH were determined using saturation paste extraction and a 1:2 (v/v) soil : water slurry, respectively (Tran & Van Leirop, 1981). The soils from each treatment described below were analyzed by the same methods at the end of the experiment.

Three days after germination, *Phaseolus vulgaris* L. cv. Topnotch Golden Wax seedlings were transplanted into a 9 × 7.5 cm round plastic pots. Two days later (0 time), the CO_2 exchange rate and leaf area of twenty seedlings was measured and fertilized with normal strength Hoagland and Arnon (1939) solution (HS) without KNO_3.

In a four replication experiment, one-week-old plants were inoculated with 4 000 second stage *Meloidogyne incognita* (Kofoid & White, 1919) Chitwood, 1949, juveniles/pot and subjected to four levels of fertilization : HS (normal strength) without KNO_3 (Nem 0 K), HS (Nem 1 K), HS + double strenght KNO_3 (Nem 2 K) and HS + quadruple strength KNO_3 (Nem 4 K). A fifth treatment, with HS and no nematodes (0 Nem 1 K) was included. A full factorial design was not used for two reasons : *i)* the CO_2 exchange rate measuring system allowed the measurement of only 20 plants per day during the stable photosynthetic period of these plants (Melakeberhan, Webster & Brooke, 1984), and *ii)* the known physiological and yield differences between infected and non-infected plants that we reported (Melakeberhan, Webster & Brooke, 1985; Melakeberhan *et al.*, 1987) were from plants that received normal strength HS, which was considered as the optimum fertilizer regime (Melakeberhan, Webster & Brooke, 1984).

Plants were arranged randomly in a growth chamber and watered on alternate days with similar amounts of tap water or with their particular nutrient treatment.

The photosynthetic and dark respiration rates, leaf area measurements and the number of buds, flowers and/or pods were determined at 0 time (which was five days after germination and two days before inoculation), and at 3, 7, 14 and 21 days after inoculation (Melakeberhan, Webster & Brooke, 1984). At 28 days after inoculation, dry weights of leaves, stems and roots and numbers of pods and seeds were determined. The photosynthetic and dark respiration rate measurements (at 22.5 ± 1°; 750 $\mu E\ m^{-2}\ s^{-1}$ and air flow rate of 4.5 $1\ mn^{-1}$) were as described in Melakeberhan, Webster and Brooke (1984).

Pellets of approximately 140 mg/cm^2 in thickness of ground, dried samples from leaves, stems and roots of each plant were prepared for X-ray energy spectroscopy analysis of K, Ca, Mn, Fe, Cu and Zn (Stump *et al.*, 1979). The reproducibility error of the concentrations of the elements was ± 7.6 %. The NO_3 in the leaves was determined as described for the soil.

Data from each sampling date were analyzed using an analysis of variance and the Newman-Keul test. The changes in leaf area, and the photosynthetic and dark respiration rates for each treatment with duration of infection were analyzed using linear regression.

Results

At the beginning of the experiment, the concentration of NO_3 in the soil was higher while those of Ca and Na were slightly lower than normal for potting soils (Tab. 1). The concentration of each of the other elements were considered normal. At the end of the experiment, there was no significant change in the amount of PO_4, Na, B, Fe and Zn in the soil of any of the treatments (Tab. 1). The NO_3 and K concentration and the conductivity (salts) of soil from the Nem 2 K and Nem 4 K treatments increased ($P \leqslant 0.05$) compared with those of other treatments. The pH values of the soil decreased with nematode treatment and with increasing KNO_3 applications. Calcium and SO_4 were significantly lower ($P \leqslant 0.05$) in the Nem 0 K and Nem 1 K compared with that of the uninfected controls and in the Nem 4 K, and Mn was significantly higher ($P \leqslant 0.05$) in the Nem 2 K compared with the Nem 0 K treatments (Tab. 1). Copper was significantly higher in the Nem 0 K and Nem 1 K treated soils than in soils from any other treatment (Tab. 1).

Table 1

Nutrient elemental concentration (g/ml), conductance (dS/m) and pH status of soil before the planting (0 time) of *Phaseolus vulgaris* and at 28 days after potassium nitrate treatment of the *Meloidogyne incognita* infected bean plants. Note : Treatment abbreviations refer to those listed in the methods. Means followed by the same letters are not significantly different from others on the same line at $P \leqslant 0.05$ (n = 4).

ELEMENTS	*0 Time*	*0 Nem 1 K*	*Nem 0 K*	*Nem 1 K*	*Nem 2 K*	*Nem 4 K*
PO_4	100.80	119.50	120.75	107.75	112.25	121.00
Na	27.00	23.75	23.00	20.25	25.00	21.75
B	0.23	0.64	0.57	0.51	0.57	0.66
Fe	48.60	41.95	44.55	47.10	47.10	41.80
Zn	0.64	0.63	0.58	0.63	0.65	0.65
NO_3	105.80	90.25 *c*	66.50 *c*	100.25 *c*	261.25 *b*	435.50 *a*
K	86.00	135.50 *c*	38.25 *c*	143.25 *c*	511.25 *b*	1000.00 *a*
Ca	220.00	326.25 *a*	218.25 *b*	213.00 *b*	291.25 *ab*	329.50 *a*
Mg	20.00	53.75 *ab*	30.75 *c*	41.00 *bc*	58.50 *ab*	71.50 *a*
SO_4	20.60	49.30 *a*	28.35 *c*	31.00 *c*	37.70 *b*	45.25 *a*
Cu	0.38	1.03 *b*	1.25 *a*	1.18 *a*	0.98 *b*	0.88 *b*
Mn	7.70	4.88 *ab*	4.48 *b*	5.75 *ab*	6.33 *a*	5.08 *ab*
Conductance	1.19	1.00 *c*	0.73 *c*	1.08 *c*	3.41 *b*	7.38 *a*
pH	4.62	4.93 *a*	4.78 *b*	4.75 *b*	4.53 *c*	4.48 *c*

About twelve days after inoculation, chlorosis developed in the primary leaves of the KNO_3 deficient treatment. By 21 days after inoculation, these symptoms had developed on all primary leaves of the Nem 0 K and Nem 1 K treated plants, in 75 % of the Nem 2 K and in 25 % of the Nem 4 K and of the control plants. Abscission of the yellowed leaves occurred about one week later. More galls were visible on the Nem 0 K treated plants than on those of the other treatments.

Table 2

The effect of *Meloidogyne incognita* on plant weight and yield components of *Phaseolus vulgaris* plants at 28 days after inoculation. Note : Treatment abbreviations refer to those listed in the methods. Means followed by the same letters are not significantly different from others in the same column at $P \leqslant 0.05$ (n = 4).

TREATMENT	*PLANT DRY WEIGHT (g)*					*YIELD number/plant*	
	Leaf	*Stem*	*Shoot*	*Root*	*Total*	*Pods*	*Seeds*
Nem 1 K	0.87 *a*	0.60 *a*	1.46 *a*	0.39	1.85 *a*	6.00 *a*	28.50 *a*
Nem 0 K	0.41 *c*	0.30 *b*	0.70 *b*	0.30	1.00 *b*	3.00 *c*	11.25 *c*
Nem 1 K	0.35 *c*	0.37 *b*	0.72 *b*	0.30	1.02 *b*	4.00 *bc*	14.50 *bc*
Nem 2 K	0.58 *bc*	0.37 *b*	0.95 *b*	0.27	1.22 *b*	4.00 *bc*	16.25 *b*
Nem 4 K	0.69 *ab*	0.46 *ab*	1.14 *ab*	0.29	1.43 *ab*	5.25 *ab*	23.25 *ab*

The leaf dry weight of all nematode-infected plants, except Nem 4 K, was significantly ($P \leqslant 0.05$) less than in the 0 Nem 1 K plants and was higher in Nem 4 K plants than in the Nem 0 K and Nem 1 K treated plants (Tab. 2). The stem, shoot and total plant weight of the uninfected controls was significantly higher ($P \leqslant 0.05$) than for all but the Nem 4 K treatment. None of the treatments differed significantly in root weight (Tab. 2). Nematode treatment significantly ($P \leqslant 0.05$) decreased total plant dry weight in all treatments, except for the Nem 4 K treatment, compared with the uninfected (0 Nem 1 K) treatment. At 28 days after inoculation, the number of pods and seeds in the uninfected controls was higher ($P \leqslant 0.05$) than in all but the Nem 4 K treatment, and those of Nem 4 K were higher than the Nem 0 K (Tab. 2).

There was no significant difference in total leaf area in any of the treatments except at the last sampling date when that of the Nem 4 K treated plants was significantly higher ($P \leqslant 0.05$) than that of the Nem 0 K and Nem 1 K treatments (Tab. 3). The leaf area of all treatments increased ($P \leqslant 0.01$) with duration of infection until primary leaf abscission (Tab. 3).

The photosynthetic rate of the Nem 0 K treated plants was significantly less than that of 0 Nem 1 K treatment from 14 days after inoculation, and was significantly less in all nematode treatments, except Nem 4 K, from 21 days after inoculation (Tab. 3). From 21 days onwards, the photosynthetic rate of all nematode infected plants generally increased with increasing levels of KNO_3. The dark respiration rate of all nematode infected plants was significantly higher ($P \leqslant 0.05$) than for the uninfected controls at three days after inoculation (Tab. 3). The photosynthetic rates of all treatments decreased ($P \leqslant 0.01$) with time and the regression slopes of the 0 Nem 1 K and Nem 4 K plants were similar to each other and different from those of the other treatments (Tab. 3). Twenty one days after inoculation, the dark respiration rate of the Nem 2 K and Nem 4 K treated plants was higher than that of Nem 0 K treated plants and at the last sampling date the respiration rate of the Nem 0 K was significantly lower than that of the 0 Nem 1 K and Nem 4 K treatments. The dark respiration rate of all nematode treatments decreased ($P \leqslant 0.01$) with duration of infection (Tab. 3).

In all treatments, the concentration of K in the leaves and stems significantly increased while Ca significantly decreased ($P \leqslant 0.05$) between the Nem 0 K and Nem 4 K treatments (Tab. 4). Manganese concentration in the leaves and stems of the uninfected controls and Nem 4 K was significantly ($P \leqslant 0.05$) lower than for the other treatments (Tab. 4). The leaf and stem Fe of the Nem 0 K was significantly ($P \leqslant 0.05$) higher than in all other treatments (Tab. 4). The leaf Zn concentration was significantly ($P \leqslant 0.05$) lower in the Nem 4 K treatment than that for all other treatments, and in the stem, Nem 0 K Zn was significantly lower ($P \leqslant 0.05$) than in the 0 Nem 1 K and Nem 4 K treatments. None of the elements in the roots changed significantly (Tab. 4).

Table 3

Influence of potassium nitrate on leaf area (dm^2) and photosynthetic and dark respiration rate (mg CO_2 dm^{-2} h^{-1}) of *Meloidogyne incognita* infected *Phaseolus vulgaris* plants at each sampling date and the change of these parameters over a period of 28 days. Note : Treatment abbreviations refer to those listed in the methods. Means followed by the same letters are not significantly different from others in the same column at $P \leq 0.05$ (n = 4).

	DAYS AFTER INOCULATION						*CHANGE OVER 28 d*
TREATMENT	*0*	*3*	*7*	*14*	*21*	*28*	*Regression slopes*
				Leaf Area			
0 Nem 1 K	0.47	1.22	1.57	2.19	2.28	1.56 *ab*	0.27
Nem 0 K	0.42	1.04	1.25	1.61	1.95	1.18 *b*	0.20
Nem 1 K	0.45	1.13	1.34	1.78	1.97	1.27 *b*	0.20
Nem 2 K	0.42	1.13	1.37	1.83	2.04	1.49 *ab*	0.24
Nem 4 K	0.46	1.15	1.43	1.81	2.12	1.80 *a*	0.29
				Photosynthetic Rate			
0 Nem 1 K	11.5	8.7 *ab*	7.9	6.3 *ab*	4.2 *a*	4.8 *a*	— 1.4
Nem 0 K	11.0	10.8 *a*	8.3	4.5 *c*	1.6 *c*	2.0 *b*	— 2.1
Nem 1 K	12.9	7.4 *b*	8.1	6.5 *ab*	0.7 *c*	2.3 *b*	— 2.1
Nem 2 K	12.6	9.2 *ab*	7.5	5.1 *bc*	2.2 *b*	3.3 *ab*	— 2.0
Nem 4 K	9.7	8.9 *ab*	7.3	6.1 *ab*	3.3 *ab*	3.1 *ab*	— 1.4
				Dark Respiration Rate			
0 Nem 1 K	2.3	0.7 *b*	0.8	0.6	0.9 *ab*	1.5 *a*	— 0.1
Nem 0 K	2.6	1.1 *a*	0.8	0.8	0.8 *b*	0.7 *c*	— 0.3
Nem 1 K	2.2	1.1 *a*	0.8	0.6	0.9 *ab*	0.9 *bc*	— 0.2
Nem 2 K	2.4	1.3 *a*	0.7	0.6	1.1 *a*	1.0 *bc*	— 0.2
Nem 4 K	2.1	1.2 *a*	0.8	0.4	1.1 *a*	1.2 *ab*	— 0.3

Generally the K and Ca concentrations were higher in the leaves and stems than in the roots while Mn, Fe and Cu tended to be more concentrated in the roots than the leaves and stems (Tab. 4). The Cu concentration of the plant were not significantly changed by any of the treatments.

Discussion

There was a significant positive correlation between high supplementary KNO_3 and the concentration of K and NO_3 in the leaves, the photosynthetic rate and the seed yield of nematode infected plants compared with nematode treatments that were deficient in KNO_3 (Tabs 2, 3, 4). Four times the normal strength of KNO_3 fertilization was required for a nematode-infected plant to yield similar to a nematode-free plant receiving a normal balance of nutrients (Tab. 2). This increased the leaf concentration of K and NO_3 to over two and seven times, respectively, compared with that of the non-infected plants (Tab. 4).

The decrease (approx. 50 %) in leaf and stem dry weight and in the number of seed pods (Tab. 2) caused by *Meloidogyne* infection of the roots supports earlier reports for nematode infections (Trudgill, 1980; Melakeberhan, Webster & Brooke, 1985). Root dry weight was not significantly affected by the nematode infection (Tab. 2) or by the KNO_3 treatments despite the development of root galls or the significant decrease in soil pH.

Meloidogyne infection appeared to temporarily stimulate dark respiration levels of the bean plants three days after inoculation (Tab. 3). Thereafter, progressive senescence of the primary leaves and, by 21 days, growth of the secondary leaves obscured any further effect by the nematodes on respiration, which confirms earlier observations (Melakeberhan, Webster & Brooke, 1985). By the end of the experiment, supplementary KNO_3 treatments had increased dark respiration levels. By fourteen days after nematode infection, the photosynthetic rate was significantly less in nematode-infected than in non-infected plants (Tab. 3). However, increasing amounts of supplementary KNO_3 increased the photosynthetic rate and by 21-28 days it was not significantly different in the nematode-infected plants from that in uninfected control plants (0 Nem 1 K). The

correlation between increasing KNO_3 supplements in nematode-infected plants with increased leaf K and NO_3 concentration, increased photosynthetic rate and delayed chlorosis points to an interaction between K and NO_3 in the plant. It is known that an abundant supply of NO_3 in the soil of KNO_3 supplemented plants influences the level of leaf nitrate (Shaner & Boyer, 1976) and so prevents early senescence and associated chlorosis. In this particular bean cultivar the seed to seed cycle takes only 45 days and the primary leaves senesce around 21-28 days after germination. Hence, in the nematode-infected plants which are known (Melakeberhan, Webster & Brooke, 1985) to have decreased leaf chlorophyll and consequent chlorosis, receiving supplementary KNO_3 delayed senescence to the level of the controls and this occurred during maturation of the nematode.

Table 4

The relationship between different levels of potassium nitrate treatments and the leaf, stem and root elemental concentration (ppm) of *Meloidogyne incognita* infected *Phaseolus vulgaris* plants at 28 days after inoculation. Note : Treatment abbreviations refer to those listed in the methods. Means followed by the same letters are not significantly different from others in the same column at $P \leq 0.05$ (n = 4).

TREATMENT	*ELEMENTAL CONCENTRATION*						
	NO_3	*K*	*Ca*	*Mn*	*Fe*	*Cu*	*Zn*
				Leaf			
0 Nem 1 K	800 *c*	77 592 *c*	2 275 *bc*	1 511 *b*	861 *c*	31.0	66.1 *a*
Nem 0 K	650 *c*	40 091 *d*	3 361 *a*	2 124 *a*	3 671 *a*	28.9	64.6 *a*
Nem 1 K	1 050 *c*	66 667 *c*	2 988 *ab*	2 208 *a*	1 887 *bc*	26.2	67.5 *a*
Nem 2 K	3 000 *b*	113 175 *b*	2 307 *b*	1 914 *a*	2 528 *b*	24.5	64.7 *a*
Nem 4 K	6 025 *a*	160 518 *a*	2 038 *bc*	1 549 *b*	954 *c*	30.7	53.0 *b*
				Stem			
0 Nem 1 K		45 746 *c*	791 *bc*	349 *b*	502 *b*	18.3	71.7 *a*
Nem 0 K		32 282 *d*	1 384 *a*	662 *a*	930 *a*	18.5	51.8 *b*
Nem 1 K		48 337 *c*	1 337 *ab*	676 *a*	571 *b*	15.6	62.7 *ab*
Nem 2 K		74 250 *b*	1 063 *bc*	687 *a*	551 *b*	19.7	59.7 *ab*
Nem 4 K		103 203 *a*	1 045 *c*	403 *b*	431 *b*	11.8	69.7 *a*
				Root			
0 Nem 1 K		62 926	1 195	4 414	11 580	88.8	104.0
Nem 0 K		43 886	879	3 323	11 724	71.8	107.0
Nem 1 K		47 649	1 148	3 725	11 604	79.3	105.8
Nem 2 K		72 658	1 112	5 213	10 006	69.0	123.5
Nem 4 K		49 693	875	4 022	8 387	63.8	118.5

The extended photosynthetic period of the leaves of KNO_3 treated plants increased the level of K in the leaves which increased the CO_2 exchange rate and this may also increase the recirculation of photosynthate within the plant (Ashley & Goodson, 1972). The relationship between increased K concentration in the leaves and the CO_2 exchange rate, particularly photosynthetic rate, parallels the common phenomenon in healthy plants that receive external supplementary K (Torimitsu *et al.*, 1985). Although we measured only the total concentration, it is possible that intracellular accumulation of K in the leaves (Geiger & Conti, 1983) influenced stomatal regulation and so favouring a higher CO_2 exchange rate (Outlaw, 1983). This probably enhances the movement of other ions to maintain the anion and cation equilibrium. The overall effect is improved physiological performance and a significantly increased yield (Tab. 2) compared with that which occurred in nematode-infected plants which received normal strength HS with similar nematode levels (Melakeberhan *et al.*, 1985).

Bean, a glycophyte plant, and *M. incognita* are sensitive to high salt concentrations (Viglierchio, Croll & Gortz, 1969; Nassery & Jones, 1976), and associated with the increase in K and NO_3 concentration in the shoots of the high supplementary KNO_3 treatment is the change in concentration of other nutrient elements and pH in the soil. These changes affect the ionic equilibrium in the soil and influence the soil-water potential, which could alter the uptake by and/or metabolism of

the elements (Johansen, Edwards & Loneragan, 1968) and subsequently result in their unbalanced distribution within the plant. Although the number of nematodes in the roots was not estimated, the decreased galling in the Nem 4 K treatments indicates that the nematode's ability to develop and/or induce galling may have been impaired as the salt concentration increased in the soil and/or the pH decreased (Tab. 1). With the increased salt concentration in the soil, one could have expected salinity problems to affect photosynthesis (Wignarajah, Jennings & Handley, 1975; Seeman & Critchley, 1985) and thereby to decrease plant growth (Lahaye & Epstein, 1971). In this study, however, this was not the case because Na did not increase, and the high NO_3 and SO_4 in the soil of the high supplementary KNO_3 treatments, may have offset possible salinity problems by decreasing the soil pH. This, emphasizes the need for identifying the exact processes of overcoming the nematode stress with minimum disturbance to the ionic balance in the soil.

In summary, K and NO_3, whose translocation to the shoots might have been impeded by the nematode's demand for consumption, could be two of the " root-derived (translocated) factors " referred to by Loveys and Bird (1973) that influence photosynthesis in nematode-infected plants. The results show that the physiological and growth response of *M. incognita*-infected beans can be improved by applying KNO_3 to the soil. It took four times the normal strength of KNO_3 for a nematode-infected plant to yield at about the same level as an uninfected plant receiving normal strength HS (controls). Increasing the concentration of KNO_3 application to nematode-infected plants appears to delay chlorosis, prolong the photosynthetic period and rate, and so increase productivity of the infected plants. Increasing the concentration of KNO_3 is associated also with changes in soil pH and conductivity and, depending on the experimental conditions, the plant response could vary. Further studies could lead to improved fertilizer programs to compensate for nematode damage.

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