THE BIONOMICS OF SOIL NEMATODES IN MANITOBA SOILS

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ABSTRACT

Fifty-one genera of nematodes were found in three types of soil in southern Manitoba. Butlerius spp., Leptonchus spp., and Pseudhalenchus spp. were newly recorded in Canada. Helicotylenchus spp., Tylenchorhynchus spp., Tylenchus spp., Mesorhabditis spp., Panagrolaimus spp., and Eudorylaimus spp., were the most numerous. Clay soils harbored greater numbers of nematodes than sand. Plot A (17.2% sand, 42.8% silt, 40.0% clay) harbored 43 genera, plot B (94.4% sand, 2.7% silt, 2.9% clay) harbored 37 genera, and plot C (21.7% sand, 42.6% silt, 35.7% clay) had 36 genera. Differences in numbers of nematodes between the three plots were correlated with differences of nitrogen (N), potassium (K) and soluble salts in the soil solution, and not to soil type.

In pot experiments, nematode populations in clay and sand under grass were exposed to different levels of N, phosphorus (P) and K. The number of nematodes was greater in clay than in sand, but the difference may have been due to greater plant growth in clay. The number of nematodes decreased as N content in clay increased, whereas nematode numbers increased with the addition of N to the sand. Numbers of dorylaimids were similar in clay and sand. They decreased in number as N treatments were increased from 0 ppm to 600 ppm. Dorylaimids were most numerous at 0 ppm N with 40/400 ppm P/K ratio levels,

and 200 ppm N with 20/200 ppm P/K ratio levels. Tylenchids were more numerous in clay than in sand, and decreased as N treatments were increased in clay. In sand, tylenchids increased in number with higher N treatments. Numbers of non-stylet bearing (NSB) nematodes were similar in clay and sand, but probably would have been more numerous in sand if vegetation had been the same in both soils. Increased N levels produced no change in NSB populations in clay, but were correlated with larger populations in sand. Nematode biomass was greater in clay than in sand, but the difference may have been due to the different vegetative content of the two soils. Biomass was greatest in sand at 200 ppm of N, and in clay at 0 ppm of N. Biomass decreased steadily with increased N treatments.

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INTRODUCTION

Information on soil nematodes in western Canada is scarce, and particularly on the factors which govern their distribution and abundance. This study, therefore, has two distinct, but interrelated objectives;

(1) to survey the nematode fauna in three prairie soils in southern Manitoba, and

(11) to assess from both field and laboratory observations the role of various biotic and abiotic factors in governing the distribution and abundance of nematodes in these soils.

The work was divided into two projects. The first was a survey of prairie soils for nematodes with particular attenion to vegetative cover, moisture content, pH, temperature, soil type, soluble salt content, and to the nitrogen, phosphorus and potassium content. The soil nematodes recovered from the field survey were identified to genus and these genera were compared to genera recovered in other areas of the great plains. The second project was a laboratory study of a mixed population of nematodes in a clay soil and sand soil. Pots were treated with different levels of nitrogen, phosphorus and potassium. The vegetative cover, soil pH, temperature, moisture content, and soluble salt content were recorded also. The experiment did not simulate field conditions, but gave an opportunity to test hypotheses or predictions that arose from field observations.

The hypotheses which were examined were as follows;

(1) that vegetative cover influences the number of nematodes in soil,

(11) that nitrogen, phosphorus and potassium content in the soil determine the numbers of nematodes,

(111) that soil type regulates the number of nematodes,

(1V) that temperature, moisture and pH in arable soils during a normal growing season do not influence the distribution and abundance of nematodes directly, but obviously affect the vegetation.

LITERATURE REVIEW

Introduction

The review will cover the major surveys that have been conducted in various parts of the world. The influence on nematode populations of physical, chemical, and biological factors in the soil are discussed also.

The term "soil nematode" describes free-living, plant and animal parasitic nematodes which spend part or all of their life-cycle in the soil. Only free-living and plant-parasitic nematodes are discussed in this review.

SURVEYS

A review of 124 references on nematode surveys revealed that they can be placed in four arbitrary categories (Appendix 1).

(1) Large-scale general surveys record all genera and species of soil inhabiting nematodes encountered over a large geographical area. This type of survey is concerned with the distribution and abundance of the total nematode fauna. Valuable information is obtained on new species, on new localities for existing species, and on rare species. Twenty-five of the 124 surveys belong to this category.

(11) Large-scale specific surveys are concerned with only one or a few species of soil inhabiting nematodes encountered over a large geographical area. This type of survey

usually examines the distribution and abundance of economically important plant-parasitic species. Information may be gathered on new areas of infestation, on increases in the size of populations and on new plant hosts. The European and Mediterranean Plant Protection Organization issues yearly reports on the geographical distribution of Heterodera rostochiensis Wollenweber, 1923. Twenty-one of the 124 surveys belong to this category.

(111) Restricted general surveys list all the soil inhabiting nematodes encountered within a circumscribed geographical area. This type often examines environmental factors that influence the distribution and abundance of nematode populations. The survey in this thesis, and 55 of the 124 surveys belong in this category.

(1V) Restricted specific surveys record only one or a few species of soil inhabiting nematodes within a circumscribed geographical area. These surveys usually are concerned with specific plant-parasitic nematodes attacking a particular crop plant in an agricultural area. A typical example was the survey in 1965 for H. rostochiensis in potato fields on Vancouver Island conducted by the Federal Plant Protection Division. The remaining 23 surveys were of this type.

THE SOIL ENVIRONMENT OF NEMATODES

Observations on factors that affect the distribution and abundance of nematode populations in soil are based either on field studies or laboratory experiments.

Hypotheses may be formulated from field studies but conclusions should be examined with caution because field conditions are variable and difficult to control. Laboratory projects, such as pot experiments, may be conducted under more controlled conditions, and their conclusions accepted with more confidence. The laboratory studies of Dougherty (1951; 1953), and Mountain (1955) on the culture of nematodes under monoxenic and sterile conditions permit definite conclusions. Laboratory conditions are never exact simulations of field conditions, and conclusions based only on laboratory data may not hold true in the field.

One procedure is to investigate factors in the field, to derive hypotheses, then to test these in the laboratory, and to draw conclusions. This procedure is often neglected and many projects deal with either laboratory experiments or field studies. This is probably a major reason for the conflict of data and conclusions in the literature.

PHYSICAL AND CHEMICAL FACTORS IN THE SOIL ENVIRONMENT

Many of the following references are from field studies but laboratory projects are included also.

Soil Moisture

Soil nematodes are aquatic animals that are surrounded continually by water and upon which they depend for their

activities. Nematodes move in the water films which either surround soil particles, or collect in soil pores.

Soil moisture can be measured by determining the weight loss when soil is heated at 100°C for about 8 hours. Weight loss is then divided by the dry weight of the remaining soil to obtain percent value. Soil moisture is also expressed by the pF scale, in which the measurement of the height of a water column in centimeters is converted to logarithms. The force equivalent to the weight of 100 cm. of water corresponds to a pF of 2; that of 1000 centimeters to a pF of 3; and so on until the extreme force with which water is held by soils is reached. This is approximately 10,000,000 centimeters or a pF of 7. Figure 1 from Russell (1961) shows a relationship between pF and moisture content of a soil.

Survival of soil nematodes increases with increased moisture tension to a pF of 4.2, but increase in numbers is optimal at soil moisture tensions of pF 2 to 3. This led Kable and Mai (1968) to state that survival of nematodes is poor at those moisture levels most satisfactory for increase in the number of nematodes. This paradoxical statement stems from the observation that nematodes are torpid at low moisture levels, and are active at high moisture levels.

Most species are adversely affected by high soil moisture content. Exceptions are Radopholus oryzae (V. Breda de Han, 1902) Thorne, 1949 and Ditylenchus angustus (Butler, 1913)

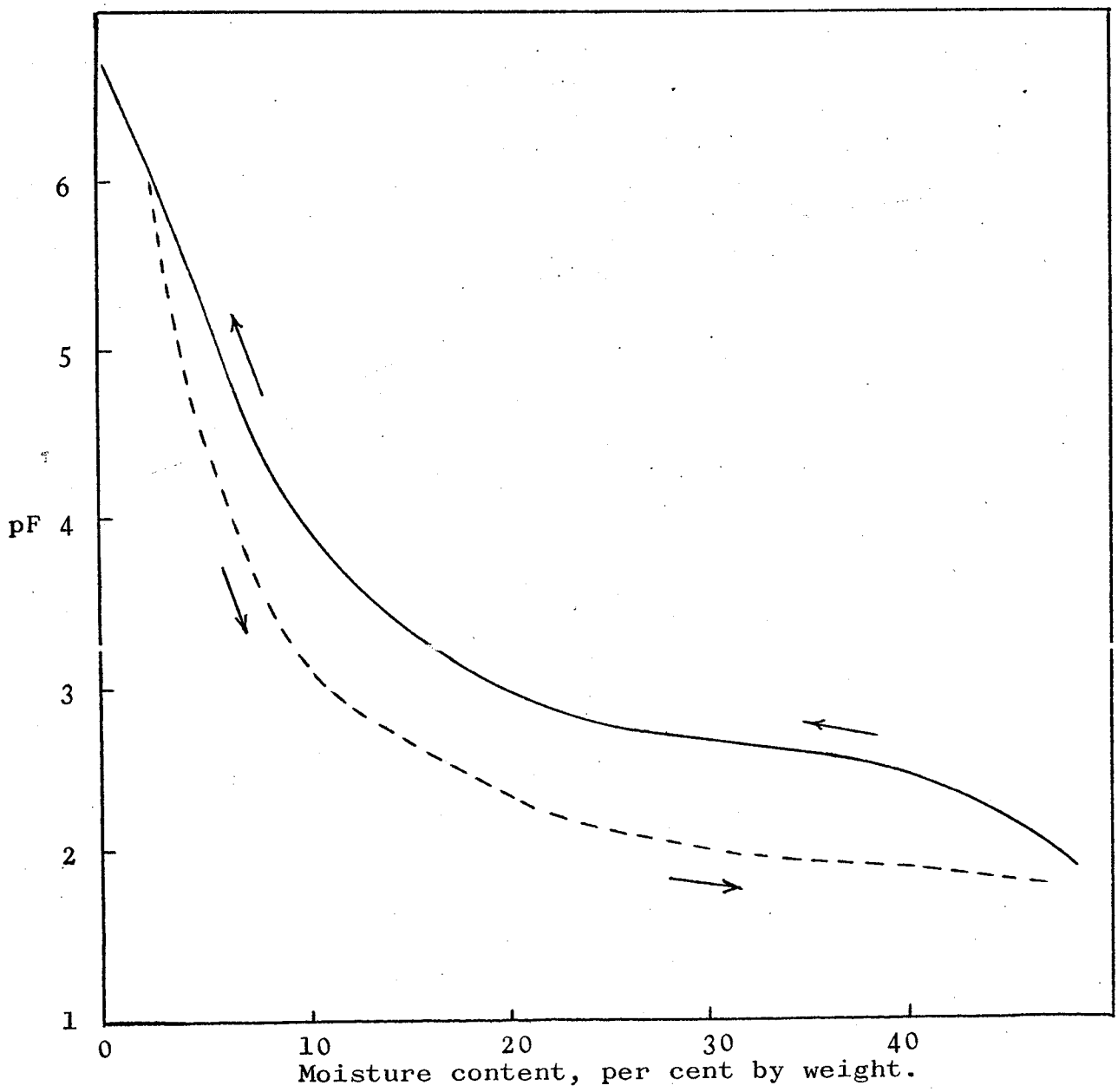

Fig. 1: The pF-moisture content curve for a Rothamsted soil. The solid line shows the relationship for a wet soil as it is allowed to dry slowly, and the broken line for a dry soil allowed to wet slowly (from Russell, 1961, p. 375).

Filipjev, 1936. These species occur in rice paddy fields and are adapted to high moisture.

Tolerance to desiccation and saturation vary between species, but most soil nematodes survive and multiply if the soil is not dry or saturated for extended periods. (Kable, 1965). Root knot nematodes are susceptible to desiccation whereas Ditylenchus dipsaci (Kühn, 1857) Filipjev, 1936 is resistant. Godfrey and Hoshino (1933) found that eggs and juveniles of Heterodera radicicola Müller, 1884 succumbed to low humidity. Low soil moisture inhibited emergence of juveniles from cysts of H. schachtii and H. rostochiensis (Wallace, 1956; Dropkin et al., 1958).

Numbers of bacteria in soil usually increase with increasing moisture content. Fungi are more common in dry agricultural soils (Russell, 1961). The influence of soil moisture on nematodes may be indirect in arable soils; in that moisture may influence the types and size of microbial populations and higher plants, both of which are sources of food for nematodes.

Soil Temperature

Soil temperature is determined by factors which control the transfer of heat into, and out of the soil, such as water content, air temperature and structure of the soil (Wallace, 1963).

Nematodes are affected directly by high or low temperatures.

High temperatures ($>40^{o}C$) are lethal to most nematodes and low temperatures ($<0^{o}C$) immobilize nematodes. Moderate temperatures also affect soil nematodes directly. A temperature of $7^{o}C$ will cause most nematodes to be sluggish while $27^{o}C$ will cause increased activity. But moderate soil temperatures are also important because of the indirect affect on nematodes. Temperature largely determines the kinds and numbers of plants, and these, in turn, influence the soil microbial populations which are food for most soil nematodes. Optimum soil temperatures for nematode development are also best for root growth, so root growth and nematode development closely parallel one another (O'Bannon, 1968). This is expected if one considers the phylogenetic development of soil nematodes, and their habitat around plant roots.

Malek et al. (1965) observed that $20^{o}C$ favoured the greatest increase in numbers of Criconemoides curvatum Raski, 1952 and Trichodorus christiei Allen, 1957. Burkhalter (1928) found that low temperatures at high altitudes had little effect on total numbers of nematodes, but the number of species declined. At 2000 meters in the Alp foothills individuals were abundant, but few species were present, all capable of enduring extreme cold. Helicotylenchus microlobus Darling and Thorne, 1959 populations decreased at $25^{o}C$, but at $30^{o}C$ sharply increased (Castaner, 1966). O'Bannon (1968) observed that the egg hatch of populations of Tylenchulus semipenetrans Cobb, 1917 was ideal at $20^{o}C$ to $30^{o}C$, but inhibited at $35^{o}C$.

Meloidogyne acrita Chitwood, 1949 survived best at 50°F when food was unavailable (Bergeson, 1959). Daulton and Nusbaum (1962) found that eggs of M. hapla Chitwood, 1949 survived longer at -2°C than eggs of M. javanica (Treub, 1885) Chitwood, 1949. They felt that the degree of tolerance of nematodes might be due to the conditions under which they had evolved. Sayre (1964) studied the effects of rapid freezing on M. incognita (Kofoid and White, 1919) Chitwood, 1949 and M. hapla and observed survival for a short period at -40°C. Bosher and McKeen (1954) held D. dipsaci at -80°C in vacuo for 128 days.

Havertz and Grundman (1961) noted that Ditylenchus destructor Thorne, 1945 and D. dipsaci followed Bergmann's principle that smaller individuals of the same species occur at higher temperatures. Malek et al. (1965) found no correlation between different temperatures and body dimensions or stylet length in C. curvatum, but that the average length of T. christiei consistently decreased from the lowest to the highest temperature. Gysels (1964) studied the allometric growth of Panagrellus silusae (de Man, 1913) T. Goodey, 1945 and found that as temperature increased, nematode length decreased.

Hansen and Cryan (1966) noted that the sex ratio of Panagrellus redivivus (Linn, 1767) T. Goodey, 1945 changed from 1:1 at 20°C to mostly males by a temperature of 28°C.

Soil Type

Mechanical analysis is the process of separating a soil

into its component particles, and then estimating the proportion of particles in the various size ranges. The present United States Scale divides a soil into sand, for particles 2.0 - 0.05 mm. in diameter, silt, for particles 0.05 - 0.002 mm. in diameter,and clay, for particles less than 0.002 mm. in diameter. Soils are classified into a number of textural classes or types such as sands, silts, loams, and clays. The name of the textural class being that of the mechanical analysis fraction, or soil separate, whose properties dominate the soil. Loams are soils in which no one fraction dominates.

Grainger (1951) found no correlation between soil type and the severity of cyst infection of Heterodera spp. Seinhorst (1956) found D. dipsaci more abundant and destructive in clay soils, but Wallace (1962) noted that mobility of D. dipsaci was greater in sand soils and that invasion into oat seedlings was similar in clay or sand loam. Kable et al. (1968) stated that the widespread occurrence of high populations of Pratylenchus spp. in sandy soils resulted from the interactions of soil moisture with soil type. Norton (1959) felt that the prevalence of some nematodes is due to the different geological derivations of the soil.

Jones et al. (1964)and Kable (1965) concluded that the greater water holding capacity of the fine particles in clay supplied more metabolic water to nematode populations than a sandy soil would. Norton (1959) found that nematode survival

was greater in clay than in sand at pF 3.0 to 4.2 (dry soil).

Pratylenchus penetrans (Cobb, 1917) Chitwood and Oteifa, 1952, P. zeae Graham, 1951, T. christiei and Meloidogyne spp. reproduced more rapidly in sand than in clay soils (Endo, 1959; Thomason, 1959; Van Gundy et al., 1964; O'Bannon and Reynolds, 1961).

Dropkin (1955) stated that no clear relationship existed between soil type and distribution of nematodes, but Seinhorst (1956) observed that the distribution of D. dipsaci was related to soil type. Winslow (1964) concluded that the presence or absence of nematodes was determined by the soil type and the crop cover.

Experimental data, together with field observations of previous workers, suggest that most plant nematode species cause greater plant damage in sand soils than in clay soils (Wallace, 1963). Perhaps the greater mobility in sand soils is important to plant nematodes in reaching plant roots. Fungal and bacterial feeding tylenchids in clay soil may not need this mobility since microorganisms usually are more numerous in clay than in sand soils.

Hydrogen Ion Concentration (pH)

Evidence on the influence of pH on soil nematode populations is contradictory, but most nematodes apparently survive and reproduce best in the pH range that is beneficial for most plants. The contradictory evidence may be due to

the difficulty in determining soil pH accurately. The pH of a soil depends on the salt concentration in the soil solution and the CO_2 concentration in the soil atmosphere, both of which are constantly changing. Rarely can one obtain a really accurate measurement of soil pH, even if one measures it in a suitable salt solution (Russell, 1961).

Peters (1926) stated that no relation existed between soil pH and cyst concentration of H. rostochiensis from various districts in England. Simon (1955) found that the level of H. schactii infestations increased as the soil pH increased from 5 to 8. Banage and Visser (1965) observed that a pH range of 6.5 to 8.0 was optimum for most soil nematode populations, and that the acid molecule was the chief toxic factor. The population size of Tylenchulus semipenetrans in sweet orange seedlings was reduced at pH 3.3 to 4.3 but not at 5.6 to 7.6. The influence of soil pH may be associated with other soil factors such as salt concentration and microbial populations (Van Gundy and Martin, 1961).

Ellenby (1946) observed that emergence of juveniles from cysts of H. rostochiensis decreased as pH declined from 6.7 to 4.0 and ceased at pH of 3.4. Ellenby felt that extremes of pH inhibited emergence. Robinson and Neal (1956) found that the optimum pH range for the emergence of H. rostochiensis juveniles was between 2 and 3 in aqueous solutions of hydrochloric, citric and fumaric acid.

Koen (1967) showed that Pratylenchus brachyurus

(Godfrey, 1929) T. Goodey, 1951 survived best in a pH range of 5 to 7, and that P. penetrans tolerated a pH range of 5.1 to 6.5, typical of most agricultural soils, but occurred most often at a pH range of 5.5 to 5.8. Jiminez - Millan (1962) observed that Rhabditis spp. even when collected from an acid soil, had maximum reproduction at pH 8. The reason for the increased nematode reproduction at pH 8, maybe that Rhabditis spp. are bacterial feeders, and bacterial populations usually are larger in slightly basic soils than in neutral or acid soils.

Soil Atmosphere

Oxygen, carbon dioxide and other gases such as nitrogen that may affect nematodes are those which diffuse from the atmosphere into the soil water. Currie (1961) suggested that soil aeration is not only a function of soil depth and rate of diffusion through the larger pores, but also a function of the size of soil crumbs.

The concentration of O_2 in the soil is controlled by the rate at which O_2 is consumed and is replaced by diffusion from the atmosphere. Similarily, CO_2 is controlled by its rate of production and its diffusion into the atmosphere (Wallace, 1963).

Gases which might influence soil nematodes are those which diffuse into soil water. In heavy wet clays, anaerobic conditions may exist, whereas in dry sandy soils, the gaseous

composition of soil water may resemble that of the atmosphere (Wallace, 1963). The most important effects of soil gases on nematodes are probably indirect; the effect on soil micro-organisms.

Most soil fungi require good aeration. Soil bacteria include groups having degrees of tolerance ranging from strict obligate anaerobes through numerous groups relatively insensitive to the oxygen supply, to strict obligate aerobes (Russell, 1961).

Triffit (1930) observed that juveniles of H. rostochiensis did not emerge from cysts in the absence of O_2 and that the activity of many plant nematodes increased with rising O_2 concentration and decreased with diminishing CO_2 concentrations. Wallace (1956, 1968) observed that Meloidogyne javanica did not hatch when O_2 was absent, and that H. schachtii emerged more rapidly from cycts when soil aeration increased. Triffit's statement that CO_2 was toxic to nematodes is in contrast to Wallace (1963).

Growth and reproduction rates of Caenorhabditis briggsae (Dougherty and Nigon, 1949) Dougherty, 1953 were retarded as O_2 pressure dropped and addition of CO_2 retarded growth slightly (Nicholas and Jantunen, 1966).

Van Gundy et al. (1962) claimed that knowledge on the influence of O_2 on soil nematodes is scanty due to the absence of techniques for accurately measuring O_2 in soil. Wallace (1963) stated that the influence of the full range of oxygen

and carbon dioxide concentration on nematode activity must be determined before the effects of soil aeration can be assessed.

Inorganic Materials in the Soil

Plants utilize many chemicals in the soil, but this review will discuss mainly the influence of nitrogen, phosphorus, and potassium on nematode populations. Other chemical elements will be mentioned briefly to indicate that they may also influence populations.

Nitrogen, phosphorus and potassium are present in many compounds in the soil, but the concern here is with those chemical forms which are available as nutrients to plants.

Nitrogen is present in soil as ammonium ions (NH_4^+) or as nitrate ions (NO_3^-). The main difference between these two ions is that all the NO_3^- in the soil is dissolved in the soil solution, but if the soil contains much clay or humus, much of the NH_4^+ will be present as exchangeable cations adsorbed to the negatively charged clay and humus colloids.

Phosphorus is present in a large number of inorganic and organic compounds in the soil, but plants utilize the ionic forms $H_2PO_4^-$ and $HPO_4^=$ in the soil solution.

The potassium content of the soil is usually high, but the amount of potassium available to plants constitutes only about 1 or 2 percent of the total amount present. The

available form exists as potassium ions (K^+) either in the soil solution or as exchangeable cations adsorbed to the surface of soil colloids.

The soil solution is definitely ionic, the degree depending in part on the concentration. When the soil solution is dilute, a large proportion of the soluble constituents are present as ions. As the solution becomes more concentrated, for example during drought, the molecular proportion increases. Soil nutrients are thus presented to the plant both in ionic and molecular forms (Lyon, Buckman and Brady, 1952; Russell, 1961).

Where interpretations are made, the consensus in the literature is that N, P and K act indirectly. This may be in a variety of ways; namely, (i) the increased microbial populations results in larger populations of microbiverous nematodes (see Foods and Feeding of Nematodes P.23), (ii) the increased plant growth supports higher populations of plant-parasitic nematodes, (iii) the increased populations of predacious fungi deplete the populations of certain nematode species.

Oteifa and Diab (1961) found no consistent agreement in the literature pertaining to the effects of inorganic fertilizers on nematode populations. They stated that the application of N P K fertilizers influence nematode populations for about two months, and that the host plants become more tolerant to the increased nematode populations.

Populations of P. penetrans and Xiphinema americanum Cobb, 1913 under cherry trees decreased when applications of K increased but N or P applications had no effect (Kirkpatrick et al., 1959). But Dwinell and Sinclair (1967)found that populations of P. penetrans under American elms increased when N was added, but decreased when K was introduced. Applications of NH_4NO_3 caused striking increases in the yield of soy beans and were accompanied by increased populations of Heterodera glycines (Ross, 1959). This response was attributed to stimulated root growth which provided more multiplication sites for the nematodes. Martin and Van Gundy (1963) observed that applications of P were associated with increased plant growth and increased Tylenchulus semipenetrans populations. Plant nematode populations were correlated to the amount of N added to corn fields with Helicotylenchus microlobus Darling and Thorne, 1959 responding negatively and Pratylenchus spp. responding positively (Castaner, 1966). Applications of inorganic N to Bermuda grass were followed by higher populations of Belonolaimus longicaudatus Rau, 1958 (Heald and Burton, 1968).

Nematodes are associated in some manner with available K of the plant, and if the K is reduced, nematode damage is increased despite low nematode reproduction (Oteifa and Diab, 1961). Oteifa (1952) observed previously that egg mass production of M.incognita increased considerably when the K level changed from low to medium in the plant. Choi and Lee (1964)

found that when the plant contained increased K, more nematodes occuppied the rhizosphere, and Rhode (1965) stated that additions of K stimulated nematode reproduction.

Bassus (1960) found that the nematode population doubled in number after the addition of $CaCO_3$ to raw humus. He attributed this to the increase in microorganisms on which microbivorous nematodes feed. Dolliver et al. (1962) found in a laboratory study that Aphelenchus ritzemabosi Schwartz, 1911 reproduction was inhibited by low Ca ion medium, but not in Zn, Fe, Mn, Mg and K ions media.

Osmoregulation and Osmotic Pressure: The osmotic pressure of the soil solution depends on the amount of salt and ions (K^+, $HPO_4^{=}$, NO_3^-) present in the soil water; hence, as the soil dries the osmotic pressure of the soil solution increases (Russell, 1961). All plants and most soil organisms, including nematodes are exposed to the osmotic pressure of the soil solution.

Differences in osmotic potential between the nematode's fluids and the soil solution occur with changes in concentrations of dissolved salts in soil water, and water and salts move through the nematode cuticle to restore osmotic equilibrium. Increases in osmotic potential occur as the soil dries and water is drawn from the nematode. Many species of nematodes tolerate variations of osmotic pressure but the ability to regulate has been determined in only a few species (Wallace, 1963).

The stretching of the alimentary canal of Rhabditis terrestris Stephenson, 1942 in distilled water suggested that the periphery of the body swells more rapidly than the gut, indicating that water is exchanged faster through the external surface than through the gut. Prolonged immersion in distilled water reduced swelling and normal movement returned. This indicated active osmotic regulation involving the excretory tubules, phasmids and amphids (Stephenson, 1942). Stephenson's observations contradicted the idea that free living nematodes possessed an impermeable cuticle that could withstand osmotic changes.

Dropkin et al. (1958) noted a decrease in the hatch of M. javanica eggs at higher concentrations of NaCl and an increase in hatch in distilled water. The movement of juveniles of H. schachtii and D. dipsaci in the soil was affected only by moisture content and not by osmotic potential (Blake, 1961). Stated differently, movement depended on the thickness of water films surrounding the soil particles and was independent of the osmotic potential until the solute concentration was high enough to cause plasmolysis of the nematodes. The osmotic concentration of the soil solution in most fertile soils never reaches this level.

There are few studies of nematode populations in relation to soil conductivity. Conductivity is expressed as the reciprocal of the resistance in ohms of the solution; in millimhos per centimeter of soil solution.* The millimhos per

*Metson, A.J. 1965. Methods of Chemical Analysis for Soil Survey Samples. N.Z. Dept. Sci. Ind. Res. Soil Bur. Bull. 12.

cm. values can be converted to percent total soluble salt concentration in the soil solution. Russell (1961) stated that soil conductivity readings of 4.0 or less indicate that the amount of soluble salts in the soil solution will not obstruct the absorption of nutrients by plant roots. The influence of conductivity values of 4.0 or less on soil nematodes is not known.

Organic Materials in the Soil

The literature, largely based on field studies, suggests that organic materials affect nematode populations indirectly, as do inorganic materials. Organic materials are added to the soil in the form of animal or green manures. Manures increase the amount of organic colloids which hold more ions of plant nutrients than inorganic clay colloids.

Linford *et al*. (1938) and Oteifa *et al*. (1964) observed that the addition of organic matter to the soil was associated with the increase of saprozoitic nematodes, nematode catching fungi, predacious nematodes, and mites. Van der Laan (1956) found that organic manuring increased the populations of natural enemies of nematodes. He also discovered half-grown nematodes in plants, leading him to suspect that plants developed resistance to plant nematodes. The addition of steer dung, alfalfa, wood shavings, oat hay and chicken manure to the soil was associated with an increase in the number of mocrophagous

nematodes and predacious fungi (Mankau, 1962).

Oostenbrink (1961) noted that the number of Pratylenchus spp. on various crops was lower in plots treated with farmyard manure, than those treated with inorganic fertilizers. The application of organic manure was associated with decreased cyst populations of H. schactii, and Duddington et al. (1956) speculated that increased predacious fungal activity depleted the eelworm population. Johnson (1962) observed a decrease in M. incognita when oat straw was added to a tomato crop.

BIOLOGICAL FACTORS IN THE NEMATODE ENVIRONMENT

The biological factors in the nematode environment are the soil fauna and flora which may influence directly or indirectly, the distribution and abundance of nematodes. Bacteria and fungi provide food for nematodes, or nematodes may be consumed by predacious fungi, decomposed by bacteria, or attacked by predacious nematodes. Symbiotic relationships are formed between certain nematode species and soil fungi or bacteria. Plant roots can influence nematode populations directly, by providing food for plant-parasitic nematodes, or indirectly by supporting microbial populations in the root rhizosphere, upon which saprobic nematodes feed.

Foods and Feeding of Nematodes

The main foods of soil inhabiting nematodes are soil microorganisms and the contents of plant rootlets.

Soil nematodes can be divided into three types based on mouth structure; namely on the presence or absence of a buccal stylet, and on the type of stylet. These structures generally reflect particular feeding habits of nematodes.

The three nematode types are:

(i) the tylenchids, encompassing nematodes belonging to the order Tylenchida.

(ii) the dorylaimids, encompassing nematodes belonging to the superfamily Dorylaimiodea in the order Dorylaimida.

(iii) the non-stylet bearing nematodes.

In the Tylenchida the stylet is a hollow cuticular structure, usually with basal knobs. In most species of the superfamily Dorylaimoidea the stylet is also hollow, but has a different origin, developing subventrally from a tooth or teeth, and is often asymmetrical; basal knobs are usually absent (Wallace, 1963).

The orders Tylenchida and Dorylaimida contain many plant-parasitic representatives, which utilize the stylet to puncture the cellulose wall of plant cells, and feed on the protoplasm. Many more species of the Tylenchida and Dorylaimida are microbivorous and are believed to feed mainly on fungi. The chemical composition of fungal cell walls are

complex but cellulose and chitin are the main constituents (Alexopoulos, 1964). The buccal stylet of nematodes probably punctures fungal cell walls and plant cell walls in a similar manner.

The non-stylet bearing nematodes lack the typical buccal stylet and usually possess a hollow stoma. Most of the species in this group are thought to ingest bacteria and minute particles of organic debris.

Symbiosis of Nematodes with Fungi and Bacteria

Plant-parasitic nematodes and fungi often appear to interact in a plant disease complex. Plant nematodes provide a portal of entry for fungi, and the fungi provide a more favorable environment for the nematodes. The plant nematodes also may lower the resistance of the plant to fungal disease.

Nematode populations increased when associated with Verticillium spp. (Dwinell and Sinclair, 1967; Powell, 1963). Panagrolaimus spp. were isolated from Kentucky blue-grass infected by Helminthosporium spp. Leaves containing nematodes usually were more damaged than leaves infected by the fungi alone (Pepper, 1965). Benedict and Mountain (1956) studied Rhizoctonia solani Kühn and Pratylenchus minyus Sher and Allan, 1953 on winter wheat in southern Ontario. The combined effect of the fungus and the nematode on growth was twice as great as the effect when either one or the other parasite acted alone.

Nematode - bacterial interactions appear to be largely a wound and/or vector relationship. Probably in complex diseases involving nematodes and bacteria, the nematode serves as a vector or as an entry agent. Host changes that aid the bacteria may occur, such as disruption of the biochemistry of the host plant following nematode attack.

Pitcher and Crosse (1958) observed that Corynebacterium fascians caused leafy gall in strawberries, and Aphelenchoides ritzemabosi (Schwartz, 1911) Steiner, 1932 caused alaminate leaves. Together, the two organisms caused the typical cauliflower disease of strawberries. Bacterial pathogens of plants are few compared with fungi or viruses and many are foliar parasites already provided with an efficient means of dispersal caused by rain splashes (Pitcher, 1963). Everard and Feder (1959) observed that aureomycin, a product of eubacteria, at low concentrations caused the increase of populations of certain soil nematodes.

Competition

Nematodes in Relation to Other Soil Organisms: Nematodes occupy a distinct ecological niche in the soil, so much so that Haarlov (1960) considered that nematodes are in little direct competition with microarthropods (Wallace, 1963). Nematodes may compete with bacteria and fungi for nutrients, but it appears that large bacterial and fungal populations usually

are associated with large nematode populations.

Nematodes in Relation to Other Nematodes: Oostenbrink (1965) speculated that the polyphagy of most nematode species and a weakness of interspecific competition allow the establishment of several species side by side, and explains the polyvalence of natural populations. Consider the competition between fungi and bacteria in the soil; if bacteria flourish to the detriment of fungi, bacterial feeding nematodes will predominate over fungal feeders. The presence or absence of many nematode species may depend primarily on the food source available, and not on the competetive ability of individual species.

Predator - Prey Relationships

Predacious Nematodes: Some of the most effective natural enemies of soil inhabiting nematodes are other nematode species. Chief among these are the members of the family Mononchidae which occur in most soils and fresh water (Thorne, 1961). Linford and Oliveira (1937) observed species of Dorylaimus, Discolaimus and Actinolaimus feeding on other nematodes, and they considered that predation by these stylet-bearing nematodes was more important than that of the non-stylet bearing mononchids.

Predacious Fungi: More than 100 species of nemat-

ophagous fungi were designated belonging to the Phycomycetes and to the class Moniliales of the Fungi Imperfecti (Esser and Sobers, 1964).

Capstick (1957) observed that predation of soil nematodes by fungi was accomplished mostly by penetration of the cuticle by hyphae growing out of sticky conidia or ring structures. Fungi with ring type traps are more efficient predators than fungi with adhesive traps (Cooke, 1963). Pramer (1964) noted that the fungi Arthrobotrys, Dactylaria, Dactylella and Trichothecium were encountered most often. He observed also that nematode trapping fungi are not obligate predators but can grow on organic substrates. In pure culture many fungi do not form traps but if nematodes are added, hyphal differentiation occurs and traps are produced. The hyphal response is induced by a substance, produced by the nematodes, that is not yet analyzed.

Plants and Plant Roots

Plant roots may be the major environmental factor affecting soil nematodes. They act directly as a food supply and indirectly by carrying large concentrations of microorganisms on their surface. Plant root respiration reduces the oxygen and increases the carbon dioxide content of the soil atmosphere and soil solution. The physical presence of roots also alter the soil structure. Plants affect soil

temperature by intercepting radiation from the sun and by reducing heat loss during the night. The uptake of ions and liberation of CO_2 by plant roots alter the soil pH (Jenkins and Taylor, 1967; Jones, 1960).

Soil and plant nematodes accumulate around plant roots. Weiser (1956) advanced the hypothesis that plant roots possess a repellant and an attractant, the balance between the two determining whether or not the plant attracts nematodes. Bergman and Van Duuren (1959) suggested that bacteria in the rhizosphere attracted nematodes, but Blake (1962) showed that plant-parasitic nematodes move toward roots in the absence of bacteria, indicating that root exudates are important. Oostenbrink (1961) observed that agricultural crops have a marked influence on numbers and types of nematodes, with the last crop being most important.

DISTRIBUTION OF SOIL NEMATODES

Nielsen (1949) gave data for vertical distribution in various soil types. In beach sand with the water table 80 cm. below the surface nematodes were distributed throughout the whole depth except for the top 5 cm. In cultivated soils with complete vegetative cover most nematodes were in the top 5 to 8 cm. with 50% in the top 1 cm. With no vegetative cover less nematodes existed in the top few cm. but most were in the top 7 cm. In cultivated fields nematodes were distributed evenly

with the depth of root penetration of the crop.

In the Broadbalk Wilderness of England where vegetative cover was complete, nematodes were most abundant in surface soil. In the wheat crop where soil was partially covered, most of the nematodes occurred at 6 to 8 cm. The vertical distribution of Rotylenchus pumulus (Perry in Perry, Darling and Thorne, 1959) Sher, 1961 and Helicotylenchus vulgaris Yuen, 1964 was not related to the amount of roots in the soil (Yuen, 1966).

Steiner and Heinly (1922) found that soil nematodes may occur to a depth of 25 feet, but most were in the top 2 to 3 inches in uncultivated soils, while in cultivated soils they were distributed throughout the cultivated layer. Peters (1953) found that soil nematodes are most numerous vertically in the top 2 inches and horizontally in the region of the roots, especially in grasses. Depth distribution of plant nematodes was associated with the depth distribution of the host plants (Winslow, 1960; Kerr, 1967; Sumner, 1967). Bassus (1960) observed that the vertical distribution of nematodes were concentrated in the organic layers and suggested that food requirements and climate determine the difference in distribution. Koen (1967) in South Africa observed that Pratylenchus penetrans concentrated in the organic layers at a depth of 20 cm.

The vertical distribution of Ditylenchus dipsaci in soil of an oat plot resembled that for other nematodes, except that after a rain they concentrated at the surface (Wallace,

1962). Wallace and Greet (1964) noted that Tylenchorhynchus icarus Wallace and Greet, 1964 were concentrated at about 5 cm. Potter (1967) observed that Belonolaimus longicaudatus Rau, 1958 juveniles and adults were concentrated at 15 to 30 cm. and were sparse at 30 to 45 cm. and 0 to 15 cm. Criconemoides ornatum Raski, 1958 and Tylenchorhynchus claytoni Steiner, 1937 were most numerous at 0 to 15 cm. and least numerous at 30 to 45 cm. Potter postulated that nematodes at 30 to 45 cm. represented an overwintering population. In India, Mukhopadhyaya and Prasad (1968) found more juveniles of Tylenchorhynchus than adults at 0 to 10 cm., and most adults were at 10 to 20 cm.

FIELD SURVEY

METHODS

General

The field survey consisted of sampling prairie soils for nematodes. The influence of vegetative cover, moisture content, pH, temperature, soil type, soluble salt content, nitrogen, phosphorus and potassium on nematode populations was examined.

Sampling

Three field pastures (plots) were sampled in southern Manitoba (Table 1). The plots were 100 foot squares subdivided into nine equal subplots. The centre of each subplot contained a circle 6 feet in diameter (Figure 2). A one-inch diameter soil probe was used to remove 10 soil cores, randomly from the 0 to 6 inch and 6 to 12 inch levels within each circled area.

Sampling dates were August, September and November of 1967, and May, July, August, September and November of 1968. In 1967 the plots were sampled at levels of 0 to 6 inches and 6 to 12 inches. In 1968 only 0 to 6 inches was sampled. Samples were taken in 1968 only from subplots 1, 5 and 9 of

TABLE I

Description of plots.

Plot	Mechanical analysis United States Scale	Year when last cultivated	Location
A	17.2% sand 42.8% silt 40.0% clay	Virgin soil	Tp. 2, Rge. 1W, Sec. 15, S.E. 1. (Near Altona).
B	94.4% sand 2.7% silt 2.9% clay	1959	Tp. 9 , Rge. 6W, Sec. 22, S.E. 2. (Near Portage la Prairie).
C	21.7% sand 42.6% silt 35.7% clay	1945	Tp. 14, Rge. 5W, Sec. 1, N.W. 13. (Woodlands Pasture).

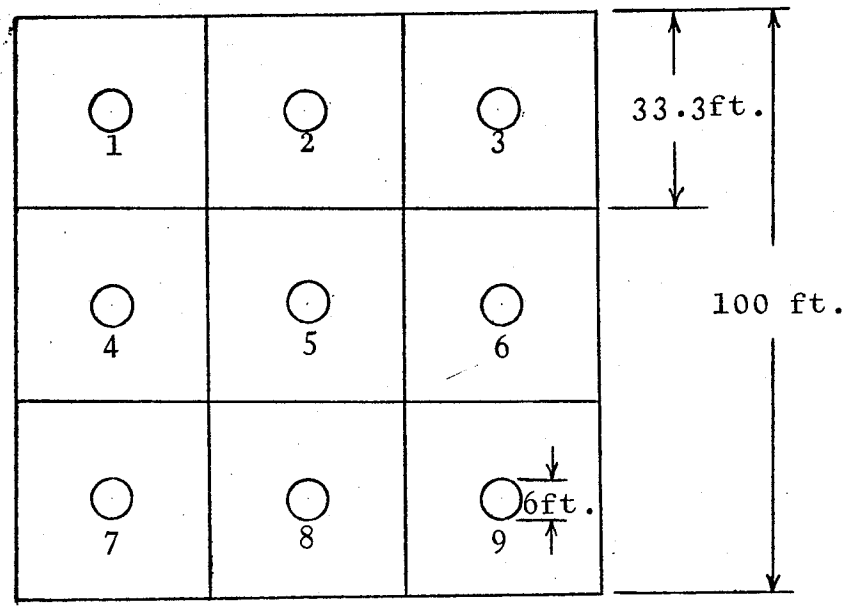

Fig. 2: Diagram of a plot with subplots.

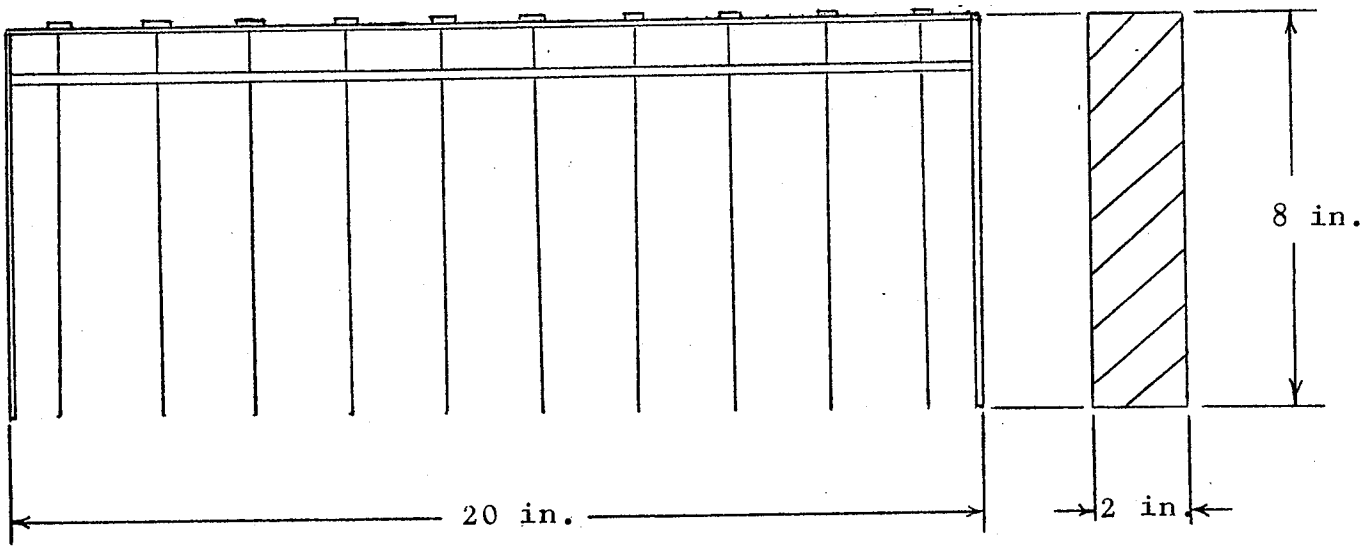

Fig. 3: Apparatus for determining vegetative cover.

plots A (clay) and B (sand) during November. No samples were obtained from plot C (clay loam) during September and November of 1968. The soil cores from each subplot were mixed thoroughly, placed in plastic bags, and transported to the laboratory for nematode extraction.

Vegetation Cover

Vegetation composition was assessed by selecting a large number of points. For each point the presence or absence and identification of plants was determined. Plants were identified in the field, or in the laboratory in more difficult cases. This technique is well suited to short, dense swards such as closely grazed pastures and golf courses (Brown, 1954).

The apparatus for selecting points consists of a frame (wood or metal) 20 inches long, made of two horizontal bars spaced about an inch apart and attached to vertical legs which rest on the ground (Levy and Madden, 1933). The horizontal bars each contain ten holes 2 inches apart so that ten steel pins (bicycle wheel spokes) can move vertically up and down in a set course (Figure 3). The frame is usually 8 inches high for short swards.

Of the various ways of recording hits on vegetation, only those hits on the base of the plant were counted in this study. Recording of basal vegetation is more rapid and is used where vegetation is neither too varied, nor sparsely distributed.

Levy and Madden (1933) considered 100 points sufficient to assess the dominant species, and 400 points to determine the less abundant species in a pasture. Four hundred point readings were taken from each plot in this project. The combined readings from each plot were expressed in terms of a percent or ratio. Two hundred hits out of 400 point readings would indicate that 50% or 0.50 of the ground surface was covered by basal vegetation. Ratio values facilitated the calculation of the percent of dominant vegetation.

Factors Measured in Soil Environment

Soil moisture was recorded during each sample date, except May in 1968. Approximately 2 cubic inches of soil were removed from the 2 to 4 inch level and sealed in small aluminum tubes. In the laboratory the soil was weighed, autoclaved for 24 hours at 100°C, and reweighed to determine the percentage weight of moisture (weight of moisture divided by dry weight of soil).

Soil temperature was recorded on the same date as soil moisture. Temperatures were measured on the surface, and at one, three and five inch depths and the mean calculated from the four recordings. A stainless steel dial type centigrade scale thermometer was used.

Soil samples from each subplot in August 1967 and July 1968 were analyzed for nitrogen, phosphorus, potassium, pH

and soil conductivity (soluble salt content) by the Department of Soil Science, University of Manitoba. Soil collected in November 1968 from subplots 1 and 9 of plots A and B were analyzed as above to determine if any of the soil factors changed drastically during the growing season.

Nematode Extraction

Fifty grams of soil were removed from each plastic bag and the nematodes extracted. A modified Baermann Funnel (BF) technique was employed in 1967 and a modified sugar-flotation (SF) technique was utilized in 1968.

The SF technique was similar to the modified centrifugal flotation technique (Caveness and Jensen, 1955). The 50g. aliquots of soil were mixed with water to break up large aggregates and then poured onto a 40 mesh screen with a 325 mesh screen underneath. A jet of water washed the soil through the 40 mesh screen. The residue on the 325 mesh screen was washed into four 30 ml. centrifuge tubes and water added to bring the suspension to the top of the tubes. The tubes were centrifuged at 2500 RPM for two minutes. The supernatant liquid was discarded and a sugar solution of 1.17 specific gravity was added to the residue in the centrifuge tubes. The residue and sugar solution were mixed and then centrifuged for 2 minutes at 2000 RPM. The supernatant liquid was poured onto a 325 mesh screen and the residue containing the nematodes

was washed from the screen into a Cobb counting dish (Cobb, 1918).

The 50g. aliquots of soil for the BF technique were mixed with water and passed through screens as described for the SF technique. The BF consisted of a 4 inch diameter plastic ring, one-half inch deep, and covered at one end by loosely woven muslin. A two layer facial tissue was placed on the muslin and the soil residue from the 325 mesh screen washed onto the tissue. The plastic ring with the soil was placed in a 6 inch glass funnel which was filled with water to the level of the soil. The bottom of the funnel was attached to a clamped rubber tube. The soil was left in the funnel for 24 hours at 74°F. One hour prior to draining the nematode suspension, the plastic ring containing the soil was removed and the water swirled to dislodge nematodes attached to the slanted portion of the funnel. Approximately 5 ml. of nematode suspension were drained into a Cobb counting dish.

To compare the extraction efficiency of the BF and SF technique, a known number of a mixed population of living nematodes was inoculated into 50g. of autoclaved clay or sand. The inoculated soil was then processed through the BF or SF technique and the percentage recovery of nematodes determined. This procedure was replicated 10 times.

Nematode Preservation and Mounting

The nematodes in the Cobb dishes were examined and counted with a stereomicroscope (50X). About 20% of the nematodes were removed randomly from the counting dish, heat killed and stored in 5% formalin or in TAF. The nematodes in formalin were placed later on a glass slide and examined with a compound Wild Microscope (640X). Nematodes requiring closer study were placed in 95% methanol 5% glycerine solution, heated for 30 minutes at 55°C and then mounted permanently in glycerine on Cobb slides. Other nematodes were placed in a 5% glycerine solution and the water slowly evaporated over several weeks and then mounted (Goodey, 1963). Permanent slides of nematodes were studied under the oil immersion lens (1600X).

Nematode Identification

Specimens were identified to the generic level and where possible to the specific level.

The nematodes were classified according to Goodey (1963). The species in the genus *Tylenchus* were identified according to Thorne and Malek (1968). The priority of *Hexatylus* over *Neotylenchus* was recognized (Nickle, 1968).

Identifications were confirmed by Dr. G. Thorne (University of Wisconsin) and Mr. R.H. Mulvey (Canada Department

of Agriculture, Ottawa). Specimens were compared to those specimens in the Canadian National Collection of Nematodes, Ottawa.

Statistical Analyses

The application of Bartlett's test indicated heterogeneity of variance in the number of nematodes per sample. This was probably caused by a clumped distribution of nematode populations. Raw data were converted to logarithmic values and geometric means were calculated.

The samples collected from the plots on July 3, 1968 were examined by an analysis of covariance on the number of nematodes recovered and the associated amounts of N, P, K, pH and conductivity in the soil. Each subplot was considered a replicate.

Comparison of the Numbers of Nematode Types

The relative numbers of dorylaimids, tylenchids, and non-stylet bearing nematodes (including all genera that do not belong in the orders Tylenchida and Dorylaimida) were compared. The separation into the three types was based on the criteria discussed earlier (see P. 23, Lit. Rev.).

FIELD RESULTS

Sampling

The geometric means in Table II are based on nine 50g. soil samples collected from each plot during each sample date, except for September, and November 1968, when three 50g. samples were collected. The 6 to 12 inch samples from all the plots contained less nematodes than the 0 to 6 inch samples, and were dropped from the sampling programme after 1967.

The number of nematodes in plot A decreased sharply from August to September in 1967, but in 1968 the number increased from May to July, and then changed little during the remaining months. The number of nematodes in plot B was greatest in September, 1967, but in 1968, the number increased through the summer with the peak recorded in November. The number of nematodes in plot C remained uniform in 1967 and 1968.

The change from the extraction technique of 1967 to that of 1968 prohibited comparison of the total number of nematodes extracted from the plots in two years.

Plot A yielded the greatest number of nematodes in 1967 and 1968, though considerable fluctuation in nematode recovery was recorded between sample dates. Plot B yielded the least number of nematodes in the two years.

TABLE II

Geometric means of the number of nematodes extracted from 50g. soil samples collected at depths of 0 to 6 inches and 6 to 12 inches (in brackets).

Sampling Dates			Field Plots		
			A	B	C
1967	Aug.	24	1002(83)	170(31)	437(49)
	Sept.	27	347(78)	316(39)	468(123)
	Nov.	1	246(42)	204(34)	468(115)
1968	May	24	484	181	671
	July	3	863	353	562
	Aug.	24	828	276	512
	Sept.	24	995	505	---*
	Nov.	15	955	555	---*

* Data for these sampling dates were lost.

Vegetation Cover

Seventeen species of plants were found, with Bromus inermis Leyss (awnless Brome grass) and Poa compressa L. (wire grass) constituting 88-95% of the total vegetation. The complete list of plant species is given in Appendix II.

The ground level (basal) vegetation cover was 47%, 30% and 22% in plots A, C and B respectively. The total above ground plant growth was not measured but the sward in plot A was denser than in plot C, and much more so than in plot B.

Vegetation density and total above ground growth gives an indication of root growth, though no direct correlation exists (Russell, 1961).

Soil Measurements

Soil temperatures that were recorded simultaneously with moisture determinations are shown in Table III. Data for September 24 and November 15, 1968 were lost. These measurements were not recorded in 1967. Plots A and C had similar moisture contents, but plot B had substantially less. In all plots, percent moisture tended to increase with the approach of winter, while soil temperature decreased correspondingly.

TABLE III

Percent soil moisture content and soil temperature (°C) recorded from field plots in 1968. Temperature in brackets.

Sampling dates	Plots		
	A	B	C
July 3	33.6(19.5)	12.4(23.0)	40.1(19.5)
Aug. 24	39.7(15.5)	16.1(14.5)	43.1(16.0)
Sept. 24	39.2(11.5)	16.0(11.0)	---
Nov. 15	44.1 (3.0)	17.2 (1.0)	---

Nematode Extraction

The sugar-flotation technique (SF) extracted more nematodes from clay or sand than the Baermann Funnel technique (BF). The SF recovered approximately 42% of the nematodes from clay and 38% of the nematodes from sand. The BF extracted approximately 25% of the nematodes from clay or sand. The BF showed greater variability in nematodes extraction from individual soil samples, and was dropped from the sampling programme after 1967.

The percent recovery and the standard error of the two extraction techniques are given in Appendix 111.

Nematode Identification

The survey recovered 8 orders of soil inhabiting nematodes, encompassing 21 families and 51 genera. Butlerius spp., Leptonchus spp., and Pseudhalenchus spp. were newly recorded in Canada. Specimens in the orders Dorylaimida and Tylenchida contained plant-parasitic nematodes. The complete list of identified genera and the plots from which they were recovered is given in Appendix 1V.

Statistical Analyses

The total number of nematodes recovered from the 50g.

field samples for July 3, 1968 were analyzed by means of the analysis of variance (ANOVAR) and covariance (COVAR). The numbers of nematodes recovered from the other sampling dates were not analyzed statistically because the soil factors (N, P, K, pH and soil conductivity) were determined only for July 3, 1968. The application of these factors to numbers of nematodes recovered during other sampling dates would not be valid, because N, P, etc., of the soil can change with time.

The raw data for all sampling dates are listed in Appendix V.

The significant F value for soils in the ANOVAR was accounted for when the COVAR introduced the soil factors or covariates of N, P, K, pH and soil conductivity. According to the data, the numbers of nematodes were not influenced significantly by the soil types, but by the N, P, K, pH and soil conductivity in the soil (Table 1V).

The standardized partial regression coefficients assessed the relative importance of the individual soil factors (Table V). Soil conductivity, K and N were the three most important factors influencing nematode numbers, of which K was approximately twice as important as soil conductivity, or soluble salt content, and 2.5 times as important as N. Phosphorus and pH were relatively unimportant.

TABLE IV

ANOVAR and COVAR of numbers of nematodes recovered from the July 3, 1968 soil samples.

	ANOVAR				COVAR			
Source	DF	MS	F	Sig.	DF	MS	F	Sig.
Soils	2	.3385	12.77	.01	2	.004	0.12	ns
Error	24	.0265	---	---	19	.033	---	---
Total	26				21			

TABLE V

Partial and standardized partial regression coefficients of the soil properties.

	N	P	K	pH	cond.
Partial Reg.Coeff.	.0061	-.0003	.0002	.0340	.1077
Stand. Reg. Coeff.	.2062	-.0191	.5169	.0687	.2419

Comparison of the Numbers of Different Nematode Types

Nematodes recovered from the July 3, 1968 sampling date were divided into 3 types, based on the presence or absence of a buccal stylet, and on the type of stylet (see P.23 Lit. Rev.). The numbers of each type found in the three plots are summarized in Table Vl.

The numbers of dorylaimids recovered from clay plot A, and sand plot B were similar, but less than the number recovered from clay plot C. Numbers of tylenchids were highest in plot A, and second highest in plot C. Sand plot B contained the lowest number of tylenchids. The greatest number of non-stylet nematodes was recovered from plot A, with plot B and C yielding substantially lower numbers.

Different nematode groups fluctuated over a period of time. The greatest range was in plot B where dorylaimids made up 36% of the total population in September 1968, and only 8% in November 1968.

TABLE VI

Geometric means of the three nematode groups recovered from the July 3, 1968 soil samples (50g. units).

Plot	dorylaimids	tylenchids	non-stylet
A	72	364	337
B	77	96	110
C	126	251	92

LABORATORY EXPERIMENT

METHODS

General

The laboratory experiment investigated the influence of nitrogen, phosphorus, potassium, soil type, and vegetative cover on populations of soil nematodes. The experiment did not simulate field conditions, but gave an opportunity to test hypotheses that arose from field observations.

Soil Preparation

Three replicates of 16 different treatments of nitrogen (N), phosphorus (P) and potassium (K) were made on sand (98.3% sand, 0.7% silt, 1.0% clay) and on clay (12.1% sand, 39.2% silt, 48.7% clay). Prior to treatment, the two soil types were autoclaved for 48 hours at 100°C, and then 500g. placed in each 4 inch plastic pot. A soil analysis was also performed on the two soils prior to treatment.

Applications of N, P and K were made with solutions of ammonium nitrate (NH_4NO_3), potassium chloride (KCl), and potassium phosphate (K_2HPO_4). Ammonium nitrate has an atomic weight of 80 with N constituting 28. To add 100 parts per million (ppm) of N to 500g. of soil, $100/10^6 \times 500 = .05$g. of

N, or 80/28 X .05= .1428g. of NH_4NO_3 dissolved in about 20ml. of water is needed. The desired N solutions were obtained by diluting a concentrated NH_4NO_3 stock solution. Solutions of KCl and K_2HPO_4 were added to the soil in a similar way to obtain the desired levels of P and K.

An analysis was performed on the soil immediately after treatments, and recorded lower levels of N, P and K than introduced in the applications (Table Vll). This is because the soil analysis is a somewhat empirical method and does not record all the N, P and K in the soil.

When NH_4NO_3, KCl and K_2HPO_4 are added to soil, they separate into NH_4^+, NO_3^-, K^+, Cl^- and $HPO_4^=$ ions. The soil analysis records only N in the NO_3^- ions in the soil solution, and not NH_4^+ ions, which are adsorbed to the surface of the negatively charged soil colloids. The K^+ are also adsorbed by the soil colloids, but this method of analysis records the majority of K^+ ions except for those which are incorporated into the soil particles. Phosphate ions in the soil solution are precipitated by the soil, and extraced with sodium bicarbonate, but the first extraction usually only records about 50% of the phosphate. Additional treatment with sodium bicarbonate will recover more phosphate ions, but this was not done in this analysis. The results of the soil analysis, except for NO_3^- ions, can vary with different soil types (Dr. R. Soper, Dept. of Soil Science, Personal Communication).

When N, P and K applications were completed, each pot

TABLE VII

Additions of N, P and K to soils and amounts recorded by soil analysis after treatments (ppm).

Treatment no.	Treatment levels			Analysis after treatment					
				Sand			Clay		
	N	P	K	N	P	K	N	P	K
1	0	0	0	0	4	30*	4	10	533*
2	0	20	200	1	14	187	5	16	587
3	0	40	400	0	25	462	6	23	775
4	0	60	600	0	34	705	4	25	954
5	200	0	0	160	4	35	90	6	490
6	200	20	200	130	16	235	136	13	660
7	200	40	400	93	20	380	107	25	820
8	200	60	600	91	35	585	107	35	986
9	400	0	0	194	5	32	241	9	582
10	400	20	200	222	14	220	150	16	680
11	400	40	400	214	21	400	171	19	800
12	400	60	600	189	37	590	166	30	1040
13	600	0	0	340	4	37	319	7	552
14	600	20	200	273	14	215	255	15	680
15	600	40	400	293	25	393	262	25	835
16	600	60	600	340	33	655	310	19	1030

* original soil, classed as treatment No. 1.

was sown with five grams of a surface sterilized seed mixture (C.D.A. Pub. 1008, 1957) of 90% (volume) Poa spp. and 10% Festuca spp.

Inoculation of Nematodes

Nematodes were extracted with the BF technique from the soil of the Buller Building lawn, University of Manitoba. Approximately one thousand live nematodes of a mixed population of approximately 30% Tylenchida, 30% Dorylaimida, and 40% miscellaneous (mostly Rhabditida) were added to each pot. The genera in the inoculant are listed in Table VIII. Because of the time required for separation, inoculations were spread over a 6 day period from September 5 to 11, 1968.

Greenhouse Conditions

The soil was watered every second day. Moisture content in the soil immediately after the addition of water was estimated at, or slightly above field capacity. The pF ranges, or changes in soil moisture content between water additions were not recorded. A hydro-thermograph recorded room temperature and humidity. Room temperature fluctuated between 65°F and 75°F (18°C - 24°C) and the relative humidity was approximately 15%. The pots were exposed to alternate 12 hour periods of light (350 foot candles) and darkness.

Vegetative Cover in Pots

The grass was about one inch tall when nematodes were added to the soil. Immediately prior to nematode extraction, the grass of each pot was cut to soil level, autoclaved at 100°C for 24 hours, and the dry weight recorded.

Nematode Extraction

Nematodes were extracted during January 1969. Two 50g. soil samples from each pot were processed through the SF technique and the nematodes counted in a Cobb dish. The mean of the two counts was used in the statistical analysis. Approximately 100 nematodes were removed at random from eacn separation in the Cobb dish, and identified to genus. At the end of the extraction period, several soil samples were analyzed to determine changes in N P K levels, and in pH and conductivity levels (see Appendix V1).

Nematode Measurements for the Estimate of Biovolume and Biomass

Dorylaimid, tylenchid and rhabditid (non-stylet bearing) nematodes were recovered from the pots. Tylenchids and rhabditids in general were about the same size, with a few exceptions. Dorylaimids, however, were much larger than the two other groups. It was felt that the influence of soil

properties on a mixed population of nematodes of this nature might be more accurately assessed if the nematode biomass was examined, as well as total numbers of nematodes.

Permanent slides of nematode specimens from the pot soil were projected with a camera lucida, and their lengths and greatest diameters were measured by utilizing a micrometer slide. The length of nematodes from lips to anus was multiplied by π and the square of half the greatest diameter to determine the volume of an equivalent cylinder. The body region from the anus to the tip of the tail in most nematodes is often filiform (e.g. Tylenchus spp.), and the inclusion of this region in the total length would introduce unnecessary errors in calculations. Exclusion of this region also helped to offset the error caused by using half the maximum diameter of the nematode, instead of a mean of several diameters measured at several places along the length of the nematode body. The use of the single diameter was more expedient.

Between one and two hundred nematodes from each pot were identified to genus and the quantitative proportion of genera estimated. Volume values obtained for the genera mounted on permanent slides were applied to the same genera identified in the 50g. samples. Nematodes were assumed to have a specific gravity of 1.0 making biovolume equivalent to biomass.

Nielsen (1949) calculated the volume of nematodes by the following method which is quoted directly.

"Given an absolutely cylindrical hypothetical nematode, length 1332 u, diameter 66.7 u. At the magnification that an optical saggital section of this animal represents a square 100 X 5.0mm = an area of $500mm^2$.

This area drawn on a particular type of paper by means of a 'camera lucida' weighs 45.6mg., the volume of this nematode being $\pi r^2 l = \pi \times 2.5^2 \times 100 = 1960$ u l. This hypothetical nematode is used as a standard."

Nielsen, using the dimensions of an example nematode calculated the volume by this method. I used the same dimensions in my method and the volume differed very little from Nielsen's result.

Nielsen stated that the mean specific gravity of soil nematodes is 1.02 which was multiplied by the volume to obtain weight and biomass. A specific gravity of 1 was used in this project.

Statistical Methods

Russell (1961) stated that most soil microorganisms such as fungi and bacteria exist in colonies. This has led most soil nematologists to believe that soil nematodes are also distributed, or clumped in colonies.

The application of Bartlett's test to the appropriate data from the laboratory experiment indicated heterogeneity of variance in the number of nematodes per sample, which was probably caused by the clumped distribution of nematode populations. Raw data was therefore converted to logarithmic values.

Computer analyses were used. The analysis of variance programme (ANOVAR) analyzed the effect of soils, N, P/K ratio and their interactions on nematode numbers, biomass and types. The analysis of covariance (COVAR) analyzed effects of vegetative cover, and various treatments and interactions on nematode types, biomass and total numbers.

LABORATORY RESULTS

Inoculation of Nematodes

A mixed population of approximately one thousand live soil nematodes was inoculated into each pot. Table Vlll lists the genera used for inoculation.

Recovery of Nematode Genera: All the genera in the inoculant were recovered from the pot soil with the SF technique, except for Helicotylenchus spp., which were not found in the sand soil.

Numbers Analyses

Analysis of Total Number of Nematodes: A mixed population of soil nematodes contains many species. However, one can regard all species as occupying a distinct ecological habitat in the soil; the water films which surround the soil particles or collect in soil pores (Haarlov, 1960). This

TABLE VIII

Genera of nematodes taken from Buller Building lawn and used for inoculation. Asterisks indicate the dominant genera.

Achromadora	Mesorhabditis*
Acrobeloides	Monhystera*
Aphelenchoides*	Mylolaimus
Aphelenchus*	Panagrolaimus*
Chiloplacus*	Paraphelenchus
Dorylaimus*	Plectus
Eucephalobus	Tripyla
Eudorylaimus*	Tylenchus*
Helicotylenchus*	Wilsonema
Hexatylus	

concept of the soil nematode population allows the analysis of total numbers of nematodes (see Table 1X).

The total number of nematodes was greater in clay than in sand. Geometric means (GM, singular, GMs, plural) of nematode numbers from the ANOVAR were 401 in clay and 248 in sand. All geometric means were based on nematode recovery from 50g. soil samples. The ANOVAR indicated that the difference in nematode numbers between clay and sand was significant. The COVAR which considered the covariate of vegetative growth, showed that soil type differences were no longer significant, and that the difference in nematode numbers was related perhaps, to the different root content of clay and sand. The mean dry weight of surface vegetation per pot from clay was 3.95g. and 1.91g. from sand, and root weights would approximate these proportions.

The number of nematodes decreased steadily as the N content in clay was increased. In sand there was an initial increase in nematode numbers associated with 200 ppm N, but more N did not increase the number of nematodes (see Table X). Both the ANOVAR and COVAR showed that soil - N interactions were correlated to changes in nematode numbers.

Analysis of Total Numbers of Dorylaimids: Dorylaimids and tylenchids possess buccal stylets which influence their feeding habits (see Lit. Rev. P.23). The foods of dorylaimids and tylenchids are plants or microorganisms, especially fungi. Non-stylet bearing nematodes are believed to feed

TABLE IX

ANOVAR and COVAR for nematode numbers.

Source	ANOVAR				COVAR			
	DF	SS	F	Sig.	DF	SS	F	Sig.
Replication	2	0.265	---	---	---	---	---	---
Soil	1	1.129	16.98	.01	1	0.145	2.09	ns
N	3	0.438	2.20	ns	3	0.288	1.38	ns
P/K	3	0.047	0.24	ns	3	0.087	0.42	ns
Soil-N	3	1.317	6.61	.01	3	1.389	6.66	.01
Soil-P/K	3	0.116	0.58	ns	3	0.187	0.90	ns
N-P/K	9	0.682	1.14	ns	9	0.880	1.41	ns
Soil-N-P/K	9	0.127	0.22	ns	9	0.354	0.57	ns
Error	62	4.120	---	---	62	4.382	---	---
Total	95	8.240			94	8.238		

TABLE X

GMs of nematode numbers in relation to soil - N interaction. Adjusted means from COVAR in brackets.

	N treatments ppm			
Soil	0	200	400	600
Clay	521(530)	495(273)	346(172)	316(210)
Sand	128(300)	325(402)	295(389)	309(444)

mainly on bacteria and minute particles or organic debris.

The most striking difference between tylenchids and dorylaimids is size, with dorylaimids often 50 times heavier than tylenchids (Nielsen, 1949). This size difference initiated the separate analysis of the number of dorylaimids (see Table Xl).

The number of dorylaimids was similar in clay and sand, and decreased progressively as N treatments were increased from 0 ppm to 600 ppm (see Table Xll). Both the ANOVAR and COVAR indicated that changes in dorylaimid numbers in relation to N content in the soil were significant.

The number of dorylaimids in clay decreased sharply when the N treatment was increased from 0 to 200 ppm, and levels of 400 ppm and 600 ppm in clay were associated with further decreases in dorylaimid numbers. In sand, dorylaimid numbers changed little when treatment was increased from 0 ppm to 200 ppm, but further increases in N treatment were correlated with sharp decreases in the number of dorylaimids (see Table Xlll). The ANOVAR and COVAR indicated that changes in dorylaimid numbers in relation to soil - N interaction were significant.

Numbers of dorylaimids were highest at 0 ppm N with 40/400 ppm P/K ratio, and at 200 ppm N with 20/200 ppm P/K. At 600 ppm N all levels of the P/K ratio treatment were associated with low dorylaimid populations (see Table XlV). The ANOVAR and COVAR indicated that the difference in dorylaimid

TABLE XI

ANOVAR and COVAR of dorylaimid numbers.

Source	ANOVAR DF	ANOVAR SS	ANOVAR F	ANOVAR Sig.	COVAR DF	COVAR SS	COVAR F	COVAR Sig.
Replication	2	2.772	----	---	---	----	---	---
Soil	1	0.089	0.26	ns	1	0.172	0.45	ns
N	3	27.791	26.70	.01	3	24.054	20.80	.01
P/K	3	0.339	0.33	ns	3	0.379	0.33	ns
Soil-N	3	4.907	4.71	.01	3	4.869	4.21	.01
Soil-P/K	3	0.920	0.88	ns	3	0.896	0.77	ns
N-P/K	9	9.687	3.10	.01	9	9.777	2.82	.01
Soil-N-P/K	9	6.002	1.92	ns	9	6.096	1.76	ns
Error	62	21.512	---	---	63	24.285	---	---
Total	95	74.019			94	74.014		

TABLE XII

GMs of dorylaimid numbers in relation to N treatments. Adjusted means from COVAR in brackets.

N treatments ppm.			
0	200	400	600
52(29)	21(28)	7(9)	2(2)

TABLE XIII

GMs of dorylaimid numbers in relation to soil - N interaction. Adjusted means from COVAR in brackets.

Soil	N treatments ppm.			
	0	200	400	600
Clay	59(59)	8 (6)	8(6)	3(2)
Sand	46(64)	56(60)	6(6)	1(2)

TABLE XIV

GMsof dorylaimid numbers in relation to N-P/K interaction. Adjusted means from COVAR in brackets.

N ppm	P/K treatments ppm			
	0/0	20/200	40/400	60/600
000	41(40)	30 (29)	141(135)	42(40)
200	11(11)	99(100)	14 (15)	13(14)
400	33(33)	3 (3)	7 (8)	4 (4)
600	1 (1)	2 (2)	2 (2)	3 (3)

numbers in relation to different N - P/K levels of interaction were significant.

Analysis of Total Numbers of Tylenchid Nematodes: The purpose for analyzing the number of tylenchids was discussed in the subsection on the analysis of the total number of dorylaimids. The ANOVAR and COVAR are shown in Table XV.

More numbers of tylenchids were recovered from clay than from sand. The GM of tylenchid numbers from the ANOVAR was 133 in clay and only 17 in sand. The GM (adjusted for the covariate, vegetative cover) of tylenchids from the COVAR was 56 in clay and 40 in sand. Both statistical tests indicated that the difference in number of tylenchids was significant between clay and sand.

The GMs from the ANOVAR show that the number of tylenchids increased as N levels increased (see Table XVl). However, the COVAR indicated that the difference in tylenchid numbers in relation to different N levels was not significant. Perhaps the additions of N caused vegetative growth to increase, which then influenced the number of tylenchids.

The number of tylenchids tended to decrease as N treatments in clay were increased. The opposite was true in sand, where increased numbers of tylenchids were associated with increased N levels (Table XVll). The ANOVAR and COVAR indicated that the difference in tylenchid numbers associated with different soil - N interactions was significant.

TABLE XV

ANOVAR and COVAR of tylenchid numbers.

Source	ANOVAR				COVAR			
	DF	SS	F	Sig.	DF	SS	F	Sig.
Replication	2	1.592	---	---	---	---	---	---
Soil	1	19.458	84.03	.01	1	2.467	9.74	.01
N	3	2.451	3.53	.05	3	0.572	0.75	ns
P/K	3	0.509	0.73	ns	3	0.533	0.70	ns
Soil-N	3	7.006	10.09	.01	3	7.046	9.27	.01
Soil-P/K	3	1.067	1.54	ns	3	1.279	1.68	ns
N-P/K	9	2.545	1.22	ns	9	2.284	1.00	ns
Soil-N-P/K	9	3.936	1.89	ns	9	4.061	1.78	ns
Error	62	14.357	---	---	63	15.958	---	---
Total	95	52.922			94	53.020		

TABLE XVI

GMs of tylenchid numbers in relation to N treatments. No adjusted means as COVAR showed no significance.

N treatments ppm			
0	200	400	600
25	52	66	57

TABLE XVII

GMs of tylenchid numbers in relation to soil-N interaction. Adjusted means from COVAR in brackets.

Soil	N treatments ppm.			
	0	200	400	600
Clay	166(168)	186(133)	148(99)	68(54)
Sand	4 (6)	15 (17)	29(34)	47(58)

Analysis of Total Numbers of Non-Stylet Bearing Nematodes; Non-stylet bearing (NSB) nematodes have different feeding habits (see Lit. Rev. P.23) from the dorylaimids and tylenchids, and were analyzed separately from the other groups of nematodes (Table XVlll).

The NSB nematodes were found in approximately equal numbers in clay and sand, and the ANOVAR indicated no difference in numbers between clay and sand. However, the GMs from the COVAR for NSB nematodes were 148 in clay and 181 in sand. The interpretation is that increased vegetative growth in clay may have influenced the number of NSB nematodes, and if vegetative growth had been equal in both soil types, the NSB population would have been greater in sand.

The number of NSB nematodes was higher in soil treated with 200 ppm, 400 ppm and 600 ppm, than in soil with 0 ppm N. The GMs (Table XlX) show this trend, and the ANOVAR indicated that the difference in NSB nematodes in relation to N treatment was significant. The COVAR indicated that the increase in numbers of NSB nematodes in relation to N treatments was no longer significant, and that perhaps increased vegetative growth influenced NSB populations.

The number of NSB nematodes did not show any definite trends when clay soil was treated with various levels of N. However, the number of NSB nematodes recovered from sand increased steadily as N levels increased (Table XX). The ANOVAR and COVAR indicated a significant relationship between the

TABLE XVIII

ANOVAR and COVAR of number of non-stylet nematodes.

Source	ANOVAR				COVAR			
	DF	SS	F	Sig.	DF	SS	F	Sig.
Replication	2	0.172	---	---	---	---	---	---
Soil	1	0.111	0.94	ns	1	0.867	7.24	.01
N	3	1.579	4.47	.01	3	0.504	1.40	ns
P/K	3	0.410	1.16	ns	3	0.358	1.00	ns
Soil-N	3	1.176	3.33	.05	3	1.410	3.92	.05
Soil-P/K	3	0.194	0.55	ns	3	0.275	0.76	ns
N-P/K	9	0.578	0.55	ns	9	0.758	0.70	ns
Soil-N-P/K	9	1.195	1.13	ns	9	1.446	1.34	ns
Error	62	7.296	---	---	63	7.546	---	---
Total	95	12.710			94	12.801		

TABLE XIX

GMs of number of non-stylet nematodes in relation to N. No adjusted means because COVAR indicated no significance.

N treatments ppm.			
0	200	400	600
101	207	164	207

TABLE XX

GMs of number of non-stylet nematodes in relation to soil-N interaction. Adjusted means from COVAR in brackets.

Soil	N treatments ppm.			
	0	200	400	600
Clay	163(166)	227(111)	134 (58)	195(129)
Sand	62(171)	189(243)	200(278)	221(344)

number of NSB nematodes and various levels of N in clay and sand.

The Total Biomass of Nematodes

The biomass of nematodes was greater in clay than in sand soil (Table XX1). The GM of the biomass was 0.217 mgm. in clay and 0.159 mgm. in sand (based on 50g. soil samples). The ANOVAR indicated that this difference in biomass between clay and sand was significant. The COVAR showed no significant difference in biomass between the two soils, indicating that the difference in biomass may be due to the difference of vegetative content in the two soils.

Nematode biomass decreased in association with increased application of N to the soil. Both the ANOVAR and COVAR tests showed that differences in biomass in relation to different N treatments were significant (Table XX11).

When sand was treated with 200 ppm N the biomass was greatest, but applications of 400 ppm N and 600 ppm N were accompanied by a decrease in biomass. In clay the biomass was greatest at 0 ppm N and decreased steadily as N treatments were increased (Table XX111). Differences in biomass in relation to different N levels interacting with clay or sand were significant in both the ANOVAR and COVAR tests.

The greatest nematode biomass was found at levels of 200 ppm N with 20/200 ppm P/K, and 0 ppm N with 40/400 ppm

TABLE XXI

ANOVAR and COVAR of nematode biomass.

Source	ANOVAR				COVAR			
	DF	SS	F	Sig.	DF	SS	F	Sig.
Replication	2	0.300	---	---	---	---	---	---
Soil	1	0.441	6.04	.05	1	0.288	3.76	ns
N	3	1.691	7.17	.01	3	2.504	10.90	.01
P/K	3	0.076	0.35	ns	3	0.104	0.45	ns
Soil-N	3	0.971	4.43	.01	3	1.019	4.44	.01
Soil-P/K	3	0.109	0.50	ns	3	0.290	1.26	ns
N-P/K	9	1.619	2.46	.05	9	1.946	2.82	.01
Soil-N-P/K	9	0.496	0.76	ns	9	0.679	0.99	ns
Error	62	4.531	---	---	63	4.826	---	---
Total	95	10.235			94	10.248		

TABLE XXII

GMs of nematode biomass (mgms.) in relation to N treatment. Adjusted means from COVAR in brackets.

N treatments ppm.			
0	200	400	600
.246(.266)	.252(.243)	.158(.152)	.122(.122)

TABLE XXIII

GMs of nematode biomass (mgms.) in relation to soil-N interaction. Adjusted means from COVAR in brackets.

Soil	N treatments ppm.			
	0	200	400	600
Clay	.404(.410)	.218(.123)	.171(.087)	.149(.101)
Sand	.150(.337)	.291(.357)	.146(.190)	.101(.149)

P/K. The level of 600 ppm N with all levels of the P/K ratio usually were associated with the smallest biomass (Table XXlV). The ANOVAR and COVAR tests both indicated a significant difference in nematode biomass in relation to different levels of the N - P/K interaction.

TABLE XXIV

GMsof nematode biomass (mgms.) in relation to N-P/K interaction. Adjusted means from COVAR in brackets.

N ppm	P/K ratio ppm.			
	0	20/200	40/400	60/600
000	.185(.243)	.193(.258)	.412(.612)	.249(.355)
200	.199(.179)	.415(.360)	.222(.199)	.220(.175)
400	.243(.227)	.152(.132)	.142(.116)	.119(.094)
600	.164(.157)	.132(.131)	.068(.068)	.150(.149)

DISCUSSION

SURVEY

This survey was classed as a restricted general survey (see Lit. Rev. P. 4) because only three prairie soils (tall grass) were sampled in a small geographical area in southern Manitoba. The sites lie within the northern Great Plains whose southern and northern limits were defined as 40°N and 50°N (Thorne and Malek, 1968). Fifty-one genera of nematodes encompassing 8 orders were recovered. Sixteen genera belonged to the order Tylenchida, sixteen genera to the order Dorylaimida, and nine genera to Rhabditida. Bulterius spp., Leptonchus spp., and Pseudhalenchus spp. were newly recorded in Canada.

Orr and Dickerson (1966) recovered 80 genera and seven orders of soil nematodes from a prairie pasture in Kansas (about 40°N). The orders of nematodes were the same in Manitoba and Kansas, except that Orr et al. found no representatives of the order Teratocephalida. Forty-two genera were common to both the Manitoba and Kansas surveys. The majority of genera from Kansas were in the orders Tylenchida, Rhabditida and Dorylaimida, as was the case here. Orr et al. recovered more genera than this survey, probably because they also sampled soil under shrubs and trees along the banks of a creek that ran through the sampling area. Also, Kansas has a higher mean air

temperature in January (29°F) than southern Manitoba (-2.2°F mean, 1874-1968. Annual Meteorological Summary, Winnipeg, Manitoba, 1968), which may account for the greater variety of nematode genera. Burkhalter (1928) found that colder environments (in his case, high altitude) produced an abundance of individuals, but few genera. Orr et al. did not estimate total populations of nematodes, so no comparison is possible between total numbers recovered in southern Manitoba and Kansas.

Pepper (1963) recovered 23 genera of soil nematodes from North Dakota (46° - 49°N). Twelve genera were in the order Tylenchida, six genera were in Dorylaimida, and five genera were in Rhabditida. Samples were taken from barley, wheat, grass and fallow fields. Fifteen genera were common to both the Manitoba and North Dakota surveys.

Meloidogyne spp. and Heterodera spp. were not recovered in Manitoba. This may have been due to the fact that the Fenwick Washer (Goodey, 1963) was not used for extraction. Its use is generally considered for recovery of Heterodera spp. cysts. Most Meloidogyne spp. are not known to survive the rigors of winter temperatures in the northern Great Plains (Thorne and Malek, 1968). Orr et al. found no individuals of Heteroderidae, though their samples were processed specifically for Heterodera spp. and Meloidogyne spp. Pepper found representatives of Heterodera spp., but no Meloidogyne spp., except for a few specimens in a greenhouse that he felt were

imports from outside of North Dakota.

Sixteen genera of nematodes in the order Tylenchida were recovered in this survey, while 36 genera (including Heterodera spp.) of Tylenchida were recovered by Thorne and Malek (1968). Their survey listed tylenchids only, and covered the entire northern Great Plains, which probably accounted for the greater variety of tylenchids.

Examination of grass roots under a stereomicroscope revealed no damage from endoparasitic and ectoparasitic nematodes. Twenty genera of suspected plant-parasitic nematodes were recovered in Manitoba. Orr et al. recovered 23 genera of suspected plant-parasitic nematodes, but gave no data concerning the possible economic importance of this group in prairie pastures. Pepper recovered 15 genera of suspected plant-parasitic nematodes. He found root damage, but was not sure if nematodes, fungi, or both were responsible.

PHYSICAL AND CHEMICAL FACTORS IN THE SOIL ENVIRONMENT OF NEMATODES

Soil Moisture

Moisture content in the field plots increased gradually from July to November 1968. Plot A had a moisture reading in July of 33.6% and 44.1% in November, while plot B increased from 12.4% in July to 17.2% in November (see Methods P. 35 for explanation of calculations). The normal moisture range of

agricultural soils is 10 to 50% (Russell, 1961).

Increase in moisture content during the season in all plots was probably associated with the progressive decrease in air temperature. The lower temperatures would decrease water evaporation from soil and transpiration from plants.

No relationship was found between the moisture content of the three plots and the kinds of nematodes that were extracted. Forty-three genera were recovered from clay plot A, thirty-seven genera from sand plot B, and thirty-six genera from clay plot C. The genera recovered from plot B that were not found in the clay plots were Chronogaster spp., Discolaimus spp. and Leptonchus spp.

Monthly readings revealed that moisture content was similar in both clay plots, but lower in the sand plot. Soils of fine texture and high colloidicity, such as clays, hold more water than coarse granuled soil (Lyon et al., 1952). The number of nematodes in the two clay plots was different, though each plot contained similar amounts of moisture. Plot B harbored the least number of nematodes. Lower moisture content in B may have decreased the number of plants and microorganisms, and nematode populations also decreased.

Moisture content measurements were based on the amount of hygroscopic and capillary water in the soil. Hygroscopic water content is greater in clays than sand soils, but is unavailable for normal biological activities because it is usually in non-liquid form. Therefore, the difference in the

amount of capillary water between sand and clay would not be as great as indicated by the percent moisture contents in the results, but it is higher in clays.

The clay and sand soils in the laboratory were watered every second day. The moisture content in the soil immediately after watering was estimated at, or slightly above field capacity. The direct influence of moisture on nematodes (a medium or water film for nematodes to swim in) was thought to be similar in both soils. The wet soil probably encouraged bacterial development with subsequent increases in bacteria-feeding NSB nematodes, which were the most numerous group.

Since pF ranges were not established for the laboratory or field soils, caution was necessary in interpreting the influence of the soil moisture contents on nematode populations.

Previous workers dealt mainly with the influence of moisture on individual species, usually in the genera Heterodera or Meloidogyne (Godfrey and Hoshino, 1933; Wallace, 1956; Dropkin et al., 1958). As this project studied a mixed population, and did not recover Heterodera spp. or Meloidogyne spp., it is difficult to compare results. Also, this project dealt with moderate moisture levels in which most soil nematodes thrive, while other workers studied levels (high or low) of soil moisture which limited nematode activity, survival or reproduction.

Soil Temperature

Soil temperatures in the three field plots were similar during each monthly reading, and decreased steadily with the onset of winter. Diurnal fluctuations (as in the laboratory) probably occurred, but their effects on nematode populations are unknown. Soil temperature extremes during a growing season seldom kill bacterial or fungi populations (Lyon et al., 1952), and soil nematodes may be likewise affected. Soil temperatures in the field and laboratory during the sampling period never reached the extremes (either low or high) that are considered either lethal, or inhibiting.

The generic identification of nematodes prevented comparison of Manitoba species with those recovered from lower latitudes. Detailed examination of specimens from Manitoba and, for example Texas, might indicate that certain nematode species follow Bergmann's principle, with larger specimens being recovered from Manitoba.

The mean atmospheric (near surface) temperature in January in Kansas is 29°F (Orr and Dickerson, 1966), and -2.2° F in southern Manitoba. Neither Orr et al., Pepper, nor I obtained data on soil temperatures in winter, but long cold winters in Manitoba probably hinder development of certain genera such as Meloidogyne spp. Orr et al. and Pepper also did not find Meloidogyne spp. in Kansas or North Dakota soils.

Soil Type

The greatest number of nematodes and genera (43) were found in clay plot A. Clay plot C contained the second greatest number of nematodes, and 36 genera. Sand plot B contained the least number of nematodes, and 37 genera.

The COVAR for the three Manitoba plots indicated that differences were correlated to some of the five covariates examined (N, P, K, pH and soil conductivity), and not to soil type. Nitrogen, potassium and soil conductivity had the highest correlation with nematode numbers.

The laboratory experiment revealed that the total number of nematodes, total biomass, and total number of tylenchid nematodes were greater in clay soil. The number of dorylaimids and NSB nematodes were similar in clay and sand. Increase in total number of nematodes and biomass in clay was probably due to the greater vegetation. Mean dry weight of top vegetation per pot from clay was 3.95g. and 1.91g. from sand. The amount of top growth from the different fertilizer treatments and soils is given in Appendix Vll. Tylenchid nematodes showed an affinity to clay, out of proportion to increased vegetation content. Clay soil may have certain properties, chemical or physical, that make it a better habitat than sand for tylenchid nematodes.

Few authors gave mechanical analysis of their soils, so that comparisons with Manitoba soil is difficult. Orr *et*

al., Pepper, and Thorne and Malek gave little information on the mechanical analysis. Orr et al. described soil sampled in Kansas as ranging from heavy clay to fine loam. Thames (1959) in Florida sampled a soil (91.1% sand, 6.7% silt, 2.2% clay) covered with pine and sedges.

General statements occur in the literature dealing with suitability of "sand" or "clay" soil as habitats for nematodes. Seinhorst (1956) found Ditylenchus dipsaci more abundant in clay soils. Wallace (1963) stated that most plant-parasitic nematodes cause greater plant damage in sand soils than in clay soils. Nielsen (1949) found the same nematode species occurring in clay or sand soil, and that numbers were also the same in the two soils.

Inorganic Materials in the Soil

Effects of N, P and K on nematode populations are not clear. Some authors noted increases in populations while others observed decreases. Most studies were on specific plant-parasites.

Clay plot A contained 13 ppm N and 1360 ppm K, clay plot C contained 1.5 ppm N and 411 ppm K, and sand plot B contained 1.0 ppm N and 74 ppm K. Plot A harbored the most soil nematodes followed by plot C, and plot B, respectively. The COVAR indicated that N and K influenced nematode populations, but P did not. The greater amounts of N and K in plot A probably

increased the plant and microbial content of plot A, which supported a large nematode population.

The ANOVAR in the laboratory experiment indicated that N influenced total biomass, and the total number of dorylaimids, tylenchids, and NSB nematodes. None of the categories were influenced by P/K ratio treatments. Why K was unimportant in the laboratory is not clear. Perhaps high values of K relative to N made K the deciding factor in the field. In the laboratory, however, while K was still high, the much increased N content (600 ppm treatments) may have overshadowed K. Also, P combined with K may have obscured the effects of K.

Interactions of Soil Factors: Many soil interactions exist but only those that were analyzed statistically will be discussed. The laboratory experiment studied soil - N (soil type based on mechanical analysis interacting with the nitrogen in nitrate ions in the soil solution), soil - P/K, N - P/K and soil - N - P/K interactions. The soil - P/K and soil - N - P/K interactions showed no significance for any category (total numbers, biomass, etc.).

The N - P/K interaction was significant for nematode biomass and dorylaimid numbers. The N - P/K interaction of 200 ppm N with 20/200 ppm P/K and 0 ppm N with 40/400 ppm P/K were associated with the greatest biomass and highest number of dorylaimids. The 600 ppm N levels with any P/K ratio were correlated with low numbers of dorylaimids.

Perhaps certain interactions were optimum for maximum nematode biomass and dorylaimid numbers, while higher levels of N had the opposite effect. Interactions could affect microorganisms, plants and nematodes directly or indirectly.

The soil - N interaction was significant for all categories. Nematode numbers in clay tended to differ from numbers in sand when treated with comparable amounts of N.

The total number of nematodes and nematode biomass decreased in clay with increased N, while sand showed an initial increase with increased N and then levelled off. The explanation may be that the original sand soil contained less than 1 ppm N and the addition of N increased the microbial and nematode populations, but more than 200 ppm N was limiting. The original clay soil contained about 4 ppm N which probably was sufficient for the normal biotic potential, but increases of 200 ppm N or more, limited the nematodes, or microorganisms that were food for nematodes.

Dorylaimid numbers showed sharp declines in clay when N content was 200 ppm or more, while in sand the decline began at 400 ppm N. High N content in both soil types probably was detrimental directly to dorylaimids, or indirectly, to soil fungi, believed to be their main food. Perhaps, high amounts of N caused large increases in soil bacteria which competed with and thus reduced the number of fungi.

Tylenchid nematode numbers declined in clay with increased N content and increased in sand with increased N content.

In clay the added N may have increased bacteria to the detriment of fungi. Fungi are believed the main food of many free-living tylenchids. By-products such as gums and mucilages, that bacteria excrete into soil reduce the size of soil pores, which can be undesirable in fine textured soils. Perhaps the elimination of pore canals in clay hindered tylenchids, as well as dorylaimids.

In sand the competition between fungi and bacteria would still exist, but additional N would tend to increase plant growth. Increased plant growth would encourage some fungal increase and tylenchids would increase in number, because the original sand soil harbored few tylenchid nematodes.

One must remember that 600 ppm in clay, the level least favorable for tylenchids, harbored more tylenchids than at 600 ppm N in sand, the level most favourable for tylenchids. Clay had the greatest capacity for tylenchids and optimum conditions were observed in untreated clay with 4 ppm N. The optimum in clay may have been 20 or 40 ppm N, but no observations were made at these levels.

The NSB nematodes showed no significant changes in numbers with increased N content in clay, but in sand, added N was associated with greater numbers of NSB nematodes. Addition of N to clay probably increased the bacterial content and the NSB nematodes should have increased correspondingly, but the fine textured clay may have become inhospitable if bacterial by-products clogged soil pores. The original sand

soil contained little N and a small population of bacterial feeding nematodes. Increased N content would increase Nitrosomonas spp., Nitrobacter spp. and other nitrifying bacteria (Russell, 1961). The nematodes feeding on bacteria would increase, even though some of the higher levels of N might be harmful to nematodes.

Tylenchids, dorylaimids and NSB nematodes may have interacted with each other. The design of the laboratory experiment did not permit the examination of the interactions, and observations on nematode types should be viewed with caution.

The COVAR introduced the covariate of vegetation into the laboratory experiment, and some of the significant associations derived from the ANOVAR were altered. This is discussed under "plants".

Other workers, such as Wallace (1963) stated that soil interactions are important to soil nematodes, but little work has been done in this area. To my knowledge, no one has statistically analyzed the effects of interactions of soil factors on nematodes.

Osmotic Pressure and Soil Conductivity: The soluble salts in the soil solution influence osmotic pressure. Soil conductivity is a measure of the amount of soluble salts in solution. If the value of soil conductivity is high, the amount of soluble salts in the soil solution is also high,

and indicates that plant rootlets may have difficulty in obtaining water and nutrients from the soil against the osmotic potential. Russell (1961) stated that if soil conductivity is less than 4.0 (4 millimhos per cm.), plants will suffer no ill effects.

The average conductivity in each of the field plots was under 1.5, indicating the low concentration of soluble salts in the soil solution. At this level grass vegetation would not suffer from salt damage.

The COVAR indicated that changes in conductivity in the field plots were correlated with changes in the number of nematodes. The conductivity in plot A was 1.1, 1.4 in plot C and 0.5 in plot B. Perhaps the dilute salt solution in sand caused excess water to move into, and salts to move out of the nematodes by osmosis.

The conductivity in the laboratory was 0.4 for sand and 1.2 for clay before treatments. Conductivity changed with the addition of N, P and K (see Appendix VI). These values were not analyzed statistically, but the effect on nematodes may have been similar to that postulated in the field soil.

Osmotic pressure changes also affect microorganisms, so that the influence on nematodes may be indirect.

Hydrogen Ion Concentration (pH)

The pH in the field for all plots ranged from 6.5 to 7.7 for the July 1968 samples. The COVAR indicated that soil pH in the plots had no effect on nematode populations.

Both the laboratory soils had a pH of about 7.5 at the start of the experiment, and 7.2 at the end. The influence of pH on nematodes in the laboratory was not analyzed, but it was assumed to be similar to the field.

Banage and Visser (1965) found that a pH range of 6.5 to 8.0 was optimum for most soil nematodes. They believed that soil pH is important in combination with other factors.

Soil Atmosphere

Measurements on soil aeration and atmosphere in the field or laboratory were not obtained. Aeration was probably greatest in sand plot B because of the coarse granules, and the least amount of moisture. But soil from plot B was moist on all the sample dates and indicated high capillary water content. The laboratory soils were kept damp and soil aeration probably was low.

BIOLOGICAL FACTORS IN THE NEMATODE ENVIRONMENT

Biological factors in the soil such as bacteria, fungi,

predacious nematodes, and plants influence nematode populations.

Predacious and Free-Living Fungi

No precise observations were made in the field or laboratory on the effects of predacious fungi on nematodes. A few dead nematodes were filled with fungal hyphae. The wet slightly alkaline soils in the laboratory favoured bacterial development. Fungi were observed on the soil surface early in the experiment but later disappeared. Free-living fungi are thought to be a major food source of many soil nematodes.

Bacteria

Most literature dealing with soil nematodes and bacteria emphasize their roles in plant diseases. No bacterial diseases were observed on the grass plants in the field or laboratory. The stress in my study is on the importance of bacteria as food for nematodes. Russell (1961) stated that bacteria are probably the most common microoganism in soil, and that they are a major food source for soil nematodes.

No direct observations were made on bacterial content, but wet and slightly alkaline soils in the laboratory would favour development of bacteria over fungi. The influence of various physical soil factors on bacteria and fungi were discussed in previous sections.

Plants and Plant Roots

Plant roots are a major environmental factor affecting soil nematodes. They act directly as a food supply, and indirectly by carrying large concentrations of microorganisms on their surface. The uptake of ions and liberation of carbon dioxide produce changes in the pH of the soil solution, which in turn produce changes in numbers and kinds of microorganisms around plant roots. Concentrations of microflora around plant roots encourages development of protozoa and nematodes which feed on this population.

Field measurements were made on basal plant density, as it was impractical to determine root content and weight. Basal vegetation measurements were not included as another covariate in the COVAR because they were obtained in random fashion for each entire plot, and not within subplots or replicates. The vegetative density of plot A was 0.47 (47% of ground surface was covered with basal vegetation), 0.30 for plot C, and 0.22 for plot B. The geometric means of the numbers of nematodes recovered from 50g. samples was 863 in A, 562 in C, and 353 in B (July 3,1968 samples). This was not proof of more vegetation yielding more nematodes, but the correlation exists for these data.

The vegetative cover was removed from the laboratory pots and weighed after oven drying. The weight of vegetative cover (or measurement of basal vegetation) is not directly

related to root growth, but increased top growth indicates greater root growth.

When COVAR is used, it is important that the independent variable (dry weight of grass cover) is not influenced by the dependent variable (nematode numbers, biomass, etc.). No proven plant-parasitic nematodes were found in the laboratory soil and it was assumed that the COVAR was valid. Nematodes may affect the vegetation indirectly by feeding on microorganisms in symbiosis with plant roots, and caution was necessary in the interpretation of data (Steel and Torrie, 1960).

More nematodes were recovered from clay than sand in the laboratory, and the difference was significant according to the ANOVAR. The COVAR with the covariate of vegetative cover found soil had no effect. Clay soil contained more plant rootlets, and probably harbored more microorganisms and nematodes. The COVAR indicated that nematode numbers should have been similar if plant growth had been the same in clay and sand.

The number of dorylaimids was similar in clay and sand, and decreased progressively as N treatments were increased from 0 ppm to 600 ppm. Different levels of N - P/K interaction were associated with changes in the number of dorylaimids. The ANOVAR showed that differences in the dorylaimid numbers in relation to various N treatments, and N - P/K interactions were significant. The COVAR indicated that the influence of

changes in vegetative growth did not significantly alter the number of dorylaimids.

The number of tylenchid nematodes was higher in clay than in sand. The COVAR indicated that if plant growth in clay and sand had been similar, more tylenchids would still have occupied clay. Different levels of N were associated with changes in tylenchid numbers, and the ANOVAR indicated that the changes were significant. According to the COVAR, different N levels did not influence tylenchid numbers. If plant growth had been similar in both soils, tylenchid numbers would not have responded to different N treatments.

The number of bacterial feeding non-stylet bearing (NSB) nematodes was similar in both soils, but the COVAR indicated that soil influenced the number of NSB nematodes. These might have been more numerous in sand if similar quantities of vegetation were present in both soils; according to the COVAR. The literature states that nematodes with open buccal capsules and well developed lip regions generally are more numerous in coarse soils.

Nitrogen influenced NSB nematodes in the ANOVAR test, but not in the COVAR. According to the COVAR, if vegetative growth had been similar in both soils, different N treatments would not have influenced NSB nematodes.

Changes in biomass of nematodes were correlated to soil, N, soil - N interaction, and N - P/K interaction. The ANOVAR indicated that these correlations were significant.

The COVAR indicated that the covariate of vegetative content did not alter these correlations.

Previous workers agree that vegetation influences nematode populations. Increased vegetation in soil is associated with greater numbers of nematodes, and vice versa.

Predacious Nematodes and Other Soil Organisms

The genera Tripyla, Mylonchulus, Butlerius and Discolaimus were observed infrequently in the field and laboratory. Their effect on other nematodes was not determined.

Insect remains, tardigrades, rotifers, protozoans, mites, and enchytreaid worms were observed occassionally in the field samples. No attempt was made to identify these soil animals.

The laboratory soil was sterilized before the inoculation of nematodes, which drastically reduced the number of common soil inhabitants. A few soil animals were introduced with the nematode inoculant. Spider mites that had crawled into the pots from the greenhouse were observed regularly, but infrequently.

DISTRIBUTION OF SOIL NEMATODES

The field plots were sampled at 0 to 6 inch and 6 to 12 inch levels in 1967. Nematodes in the 0 to 6 inch levels were 5 to 10 times as numerous as in 6 to 12 inch levels, and

were congregated around grass roots which grow mostly in the upper levels of the soil.

Peters (1953) found that soil nematodes were most numerous vertically in the top 2 inches and horizontally in the region of the roots, especially in grasses. Nielsen (1949) found that soil nematodes were most numerous in the upper 2 or 3 cm. of the soil.

Seasonal Fluctuations of Nematode Populations

The seasonal fluctuations in total numbers of nematodes in plot A differed in 1967 and 1968. The same applied to plot B (see Table 11, Field Results P. 41). This indicates the hazard of assuming that an equal rise and fall of nematode numbers in one year will occur in ensuing years.

The reasons for the different fluctuations in 1967 and 1968 are unknown, but annual changes in climatic conditions may be the cause.

Annual differences in winter and summer temperatures, and lack of adequate snow cover in winter may damage plant roots and other soil organisms. Changes from year to year in precipitation may cause populations to fluctuate. The mean rainfall for this area is 15.47 inches. In 1967 the rainfall was 13.66 inches, and 23.09 inches in 1968 (Annual Meteorological summary, Winnipeg, 1968). Nematode populations may have cyclic periods of increase and decrease in numbers,

independent of normal annual weather conditions.

Ecological Succession: Populations of nematode species may fluctuate over periods of time. The number of NSB nematodes in the laboratory may have changed if samples had been taken in March 1969, instead of January 1969. The same applies to the other groups. The only way to determine the fluctuations would be to sample every few days, or at least every month. This was not done in the laboratory because it was outside the objective of the experiment. The nematode groups did fluctuate in the field. The greatest range was in plot B where dorylaimids made up 36% of the total population in September 1968, and only 8% in November 1968.

Statistical Analyses

In a medium as complicated as soil, it is difficult to consider all the factors that may influence nematode populations. The COVAR in the field study did not include moisture content or pF ranges in the soil, nor different vegetative contents of the plots. Variations in soluble salt content in the laboratory soils, caused by additions of chemicals were not included in the ANOVAR or COVAR.

These are the dangers of statistical analyses, and specifically covariance analysis, where missing parameters may be highly correlated with included parameters.

CONCLUSIONS

The survey in three prairie soils in southern Manitoba recovered 51 genera of soil nematodes. Sixteen genera were in the order Tylenchida, 16 in Dorylaimida, 9 in Rhabditida, and the remaining 10 in five other orders. Forty-three genera were recovered from clay plot A, 37 from sand plot B, and 36 from clay plot C. Helicotylenchus spp., Tylenchorhynchus spp., Tylenchus spp., Mesorhabditis spp., Panagrolaimus spp., and Eudorylaimus spp. were the most numerous, and were recovered from all plots. Butlerius spp., Leptonchus spp., and Pseudhalenchus spp. were newly recorded in Canada. Heterodera spp. and Meloidogyne spp. were not encountered. The genera were similar in number and kind to genera recorded from other areas, and especially to the work of Orr and Dickerson (1966) in Kansas.

The hypothesis, or prediction, that density, and quantity of vegetative cover influence nematode populations was confirmed by observations from both the field and laboratory.

Plot A (clay) had the greatest vegetation density and the highest number of nematodes, while plot B (sand) had the least vegetation and the lowest number of nematodes. The clay soil in the laboratory contained more vegetation than sand soil, and also harbored the highest number of nematodes and greatest nematode biomass.

The hypothesis that nitrogen, phosphorus and potassium

influence nematode populations was accepted for nitrogen. The results for K were contradictory, and the prediction for P was rejected. Nitrogen and potassium influenced nematode populations in the field. Plot A had the greatest amount of N (13.5 ppm) and K, followed in order by plot C and B. Plot A also harbored the most nematodes. Phosphorus and K did not affect nematode populations in the laboratory but N did. Increased N (up to 600 ppm) levels in the laboratory clay soil were associated with lower total numbers of nematodes, lower numbers of dorylaimids and tylenchids, and with lower values of biomass. Higher N levels in sand were correlated with higher total numbers of nematodes, lower numbers of dorylaimids, higher numbers of tylenchids, and more NSB nematodes.

The hypothesis that soil type influences nematode populations was rejected in the field study, but was accepted for tylenchid and NSB nematodes in the laboratory. The field study indicated that soil type did not regulate nematode numbers, but that N, K and soil conductivity were important. The analysis of variance indicated that soil type influenced the total number of nematodes, the total number of tylenchids, and the nematode biomass in the laboratory. But, the analysis of covariance indicated that differences in total numbers and biomass were due to the different vegetative content of the two soils and not to soil type. The tylenchids had an affinity for clay soil in the laboratory.

The analysis of covariance also indicated that NSB nematodes were more numerous in sand soil.

There was no evidence that soil temperature, moisture, and pH values that were recorded in the field and laboratory influenced the distribution and abundance of nematodes directly. These properties are known to affect plants and microorganisms that are food sources for nematodes.

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APPENDIX I

CLASSIFICATION OF RECENT SURVEYS.

TABLE I

Large scale general surveys.

Author	Date	Location
Altherr	1960	French Cameroons
Andrassy	1959	Rumania
Andrassy	1959	Yugoslavia
Andrassy	1963	South Argentina
Andrassy	1964	Mongolia
Colbran	1964	Queens., Aust.
Gateva	1961	Bulgaria
Heynes	1962	South Africa
Loof	1964	Venezuela
Luc	1960	West Africa
Luc	1964	Central African Rep.and Congo
Mai	1960	North East U.S.A.
Martin	1961	Rhodesia and Nyasaland
Maslennikova	1966	Uzbek S.S.R.
Mulvey	1961	Canada
Mulvey	1963	Canadian Arctic and Alaska
Mulvey	1967	Nigeria
Oteifa	1962	Egypt
Rossen	1962	Sweden and Lapland
Sasser	1962	Peru
Stoyanov	1961	Bulgaria
Thorne	1964	Puerto Rico
Thorne	1967	Puerto Rico
Thorne	1968	Northern Great Plains
Timm	1965	Thailand and Philippines

TABLE II

Large scale specific surveys.

Author	Date	Location
Ameen	1960	East Pakistan
Amica	1965	Italy
Caveness	1959	United States
Eis	1961	Poland
Eur. Plant Prot. Org.	Annual	Europe
Faber	1962	Austria
Gotoh	1963	Japan
Inchinohe	1959	Japan
Kiryanova	1958	Antarctica
Luc	1958	Madagascar
Martin	1959	Rhodesia
Nirula	1963	Northern India
Raski	1964	Italy
Rhodesian Min. of Agric.	1961	Rhodesia and Nyasaland
Sandner	1967	Poland
Sandner	1968	Poland
Sethi	1968	Northwest India
Toler	1959	Panama
Whitehead	1960	Kenya
Willis	1967	Maratime Provinces,Canada
Zemlayanskaya	1957	Uzbek S.S.R.

TABLE III

Small scale (restricted) general surveys

Author	Date	Location
Altherr	1963	Lorraine, France
Andrassy	1961	Tanganyika
Andrassy	1964	East Africa
Balbaeva	1962	Alma-Ata, U.S.S.R.
Banage	1962	Westmorland, Eng.
Bassus	1960	Germany
Bingefors	1960	Sweden
Brzeski	1962	Poland
Brzeski	1962	Poland
Chapman	1957	Kentucky, U.S.A.
Decker	1960	Sudan
Diker	1960	Turkey
Eliava	1958	Tbilisi, Georgian S.S.R.
Eliava	1966	Georgian S.S.R.
Esser	1964	Florida, U.S.A.
Griffin	1964	Wisconsin, U.S.A.
Guevara	1963	Granada, Spain
Guiran	1962	Canary Islands
Hu	1959	Formosa
Hutchinson	1961	New Jersey, U.S.A.
Hutchinson	1963	Ceylon
Jensen	1961	Oregon, U.S.A.
Khakimov	1966	Golodnaya, U.S.S.R.
Kopvillem	1958	Kirov, U.S.S.R.
Luc	1960	Togoland
Maeseneer	1963	West Germany
Malo	1961	Florida, U.S.A.
Mastauskis	1958	Lithuania
McGlohon	1961	North Carolina, U.S.A.
Miller	1962	New York, U.S.A.
Milne	1961	South Africa
Minz	1961	Isreal
Mountain	1961	Ontario, Canada
Nickle	1960	Idaho, U.S.A.
Orr	1966	Kansas
Pepper	1963	North Dakota, U.S.A.
Perry	1959	Wisconsin, U.S.A.

TABLE III continued

Small scale (restricted) general surveys

Author	Date	Location
Perry	1963	Bermuda
Pineda	1958	Cuba
Prasad	1965	India
Rebois	1968	Alabama, U.S.A.
Ritter	1959	Tunisia
Scotto la Massese	1965	Algeria
Shlepetene	1961	Lithuania
Somasekhar	1959	India
Swamy	1966	Mysore, India
Tarjan	1964	Puerto Rico
Tarjan	1967	Panama
Thames	1959	Florida, U.S.A.
Ustinov	1961	Western Ukraine
Waseem	1962	Nova Scotia, Canada
Weischer	1960	Germany
Witkowski	1958	Torun, Poland
Yuen	1966	Broadbalk Wilderness, England
Zuckerman	1960	Mass., U.S.A.

TABLE IV

Small scale (restricted) specific surveys

Author	Date	Location
Birchfield	1961	Louisiana, U.S.A.
Chamberlain	1961	Canary Islands
Davies	1962	North Wales
El-Haidari	1966	Saida, Lebanon
Fisher	1963	South Dak., U.S.A.
Holtzmann	1963	Hawaii, U.S.A.
Hutchinson	1959	New Jersey, U.S.A.
Irish Min. of Agriculture	1967	Ireland
Kemper	1958	Germany
Koski	1957	Florida, U.S.A.
Lordello	1960	Brazil
Mai	1961	New York, U.S.A.
Norton	1963	Iowa, U.S.A.
Olsen	1962	Nfld., Canada
Orchard	1965	Vanc. Isle., Canada
Pender	1957	North Carol., U.S.A.
Roivainen	1962	Finland
Salisbury	1961	Sask., Canada
Savary	1957	Switzerland
Sayre	1960	Ontario, Canada
Scheiber	1961	Gautemala
Sen	1960	Bihar, India
Wickens	1960	Uganda

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APPENDIX II

LIST OF VEGETATION FROM 1968 FIELD WORK.

Dominant Vegetation

Bromus inermis Leyss - Awnless Bromegrass
Poa compressa L. - Wiregrass

Other Vegetation

Equisetum hyemale L. - Common Scouring - Rush
Equisetum scirpoides Michx. - Dwarf Scouring - Rush
Galium boreale L. - Northern Bed Straw
Trifolium repens L. - White Clover
Taraxacum officinale Weber - Dandelion
Artemisia absinthium L. - Absinthe or Wormwood
Sonchus uliginosus Bieb. - Smooth Perennial Sow-Thistle
Potentilla anserina L. - Silverweed
Plantago major L. - Common Plantain
Aster canescens Pursh - Canescent Aster
Achillea lanulosa Nutt. - Woolly Yarrow
Hordeum jubatum L. - Wild Barley
Agropyron repens (L.) Beauv. - Quack Grass

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APPENDIX III

EXTRACTION OF NEMATODES FROM SOIL

The extraction efficiencies of a modified Baermann Funnel and a modified sugar flotation (SF) technique were compared. The SF technique recovered a higher percentage of nematodes from sand or clay than did the BF technique.

	SF technique	BF technique
Clay	42.2 ± 3.4*	25.3 ± 2.9
Sand	37.5 ± 3.5	25.8 ± 3.9

* Standard error.

APPENDIX IV

Classification of nematodes recovered from field plots in 1967 and 1968. Symbols indicate the main food source of the individual genera (based on Goodey, 1963): * = bacteria, o = fungi, # = plants, x = predatory on other nematodes, + = unknown.

	Classification	Food Habits	Plots in which nematodes were recovered 1967	1968
Order	TYLENCHIDA (Filipjev, 1934) Thorne, 1949			
Family	TYLENCHIDAE Filipjev, 1934			
Genera	Tylenchus Bastian, 1865	+	ABC	ABC
	Aglenchus Andrassy, 1954	+		A
	Tetylenchus Filipjev, 1936	+		A
	Psilenchus de Man, 1921	+	AC	AC
	Tylenchorhynchus Cobb, 1913	o	ABC	ABC
	Pseudhalenchus Tarjan, 1958	+		A
Family	HOPLOLAIMIDAE (Filipjev, 1934) Wieser, 1953			
Genera	Hoplolaimus Daday, 1905	#		AB
	Rotylenchus Filipjev, 1936	#	A	
	Helicotylenchus Steiner, 1945	#	ABC	ABC
Family	CRICONEMATIDAE (Taylor, 1936) Thorne, 1949			
Genera	Criconemoides Taylor, 1936	#		AB
	Paratylenchus Micoletzky, 1922	#	AC	A
Family	NEOTYLENCHIDAE (Thorne, 1941) Thorne, 1949			
	Hexatylus T. Goodey, 1926	o	A	ABC
	Notholtylenchus Thorne, 1941	o	A	A

APPENDIX IV-continued

	Classification	Food Habits	Plots in which nematodes were recovered 1967	1968
Family	APHELENCHIDAE (Fuchs, 1937) Steiner,1949			
Genus	Aphelenchus Bastian, 1865	o	ABC	ABC
Family	APHELENCHOIDIDAE (Skarbilovich,1947) Paramonov, 1953			
Genus	Aphelenchoides Fischer, 1894	0	ABC	ABC
Family	PARAPHELENCHIDAE (T.Goodey, 1951) J.B. Goodey, 1960			
Genus	Paraphelenchus (Micoletzky, 1922) Micoletzky, 1925	0	ABC	ABC
Order	RHABDITIDA (Oerley,1880) Chitwood, 1933			
Family	DIPLOGASTERIDAE (Micoletzky, 1922) Steiner 1929			
Genus	Butlerius T. Goodey, 1929	X	B	AB
Family	RHABDITIDAE Oerley, 1880			
Genus	Mesorhabditis (Osche, 1952) Dougherty,1953	*	ABC	ABC
Family	PANAGROLAIMIDAE (Thorne, 1937) Paramonov, 1956			
Genus	Panagrolaimus Fuchs, 1930	*	ABC	ABC

APPENDIX IV-continued

	Classification	Food Habits	Plots in which nematodes were recovered 1967	1968
Family	CEPHALOBIDAE (Filipjev, 1934) Chitwood and Chitwood, 1934			
Genera	Cephalobus Bastian, 1865	*	ABC	ABC
	Eucephalobus Steiner, 1936	*	ABC	ABC
	Chiloplacus Thorne, 1937	*	ABC	ABC
	Cervidellus Thorne, 1937	*	B	A
	Acrobeles von Linstow, 1877	*	ABC	ABC
	Acrobeloides (Cobb, 1924) Thorne, 1937	*		A
Order	TERATOCEPHALIDA (Andrassy, 1958) n. grad.			
Genus	Teratocephalus de Man, 1876	o*	BC	B
Order	ARAEOLAIMIDA de Coninck and Schuurmans Stekhoven, 1933 emend.			
Family	PLECTIDAE Oerley, 1880			
Genera	Plectus Bastian, 1865	*	ABC	ABC
	Wilsonema Cobb, 1913	*	B	AB
	Ereptonema Anderson, 1966	+	AC	AB
	Chronogaster Cobb, 1913	*	B	B
Family	AXONOLAIMIDAE Sch. Stek. and de Coninck, 1933			
Genus	Cylindrolaimus de Man, 1880	*	ABC	B
Order	MONHYSTERIDA (Oerley, 1880) Sch. Stek. and de Coninck, 1933 emend.			

APPENDIX IV-continued

	Classification	Food Habits	Plots in which nematodes were recovered 1967	1968
Family	MONHYSTERIDAE Oerley, 1880			
Genera	Monhystera Bastian, 1865	+		AC
	Prismatolaimus de Man, 1880	+	AC	ABC
Order	CHROMADORIDA (Filipjev, 1917) Chitwood,1933			
Family	CYATHOLAIMIDAE (Micoletzky, 1922) de Coninck and Sch. Stek., 1933			
Genus	Achromadora Cobb, 1913	*	C	A
Order	ENOPLIDA (Baird, 1853) Chitwood, 1933			
Family	TRIPYLIDAE Oerley, 1880			
Genus	Tripyla Bastian, 1865	x		C
Order	DORYLAIMIDA (de Man,1876) Pearse,1942			
Family	DORYLAIMIDAE de Man, 1876			
Genera	Dorylaimus Dujardin, 1845	+#	ABC	ABC
	Mesodorylaimus Andrassy, 1959	*	A	AC
	Eudorylaimus Andrassy, 1959	*	ABC	ABC
	Labronema Thorne, 1939	x	A	ABC
	Pungentus Thorne and Swanger, 1936	+	C	ABC
	Discolaimus Cobb. 1913	x	B	B
	Aporcelaimus Thorne and Swanger,1936	x		ABC

APPENDIX IV-continued

	Classification	Food Habits	Plots in which nematodes were recovered 1967	1968
	Tylencholaimus de Man, 1876	+		ABC
	Enchodelus Thorne, 1939	#		C
	Xiphinema Cobb, 1913	#	AC	AC
Family	BELONDIRIDAE Thorne, 1939			
Genera	Axonchium Cobb, 1920	+	A	ABC
	Dorylaimellus Cobb, 1913	+	AC	ABC
Family	LEPTONCHIDAE Thorne, 1935			
Genera	Leptonchus Cobb 1920	+		B
	Tylencholaimellus Cobb, 1915	+	C	B
Family	MONONCHIDAE Chitwood, 1937			
Genus	Mylonchulus (Cobb, 1916) Pennak, 1953	x		BC
Superfamily	ALAIMOIDEA (Micoletzky, 1922) n. grad.			
Genus	Alaimus de Man, 1880	+	A	BC

APPENDIX V

1967 FIELD DATA

TABLE I PLOT A.

0 to 6 inches	No. of nemas recovered from 50g. soil samples			Fertilizer Analysis Aug. 24 only				
				in ppm.				Conductivity mmhos/cm.
Subplot	Aug.24	Sept.27	Nov.1	N	P	K	pH	
1	1300	290	230	6.4	31.3	1000	6.8	0.5
2	1560	740	740	3.5	26.9	1000	6.5	0.6
3	2460	605	435	14.5	22.9	1000	6.5	0.5
4	430	200	160	6.4	47.7	1000	7.0	0.7
5	1140	475	215	8.3	35.5	1150	6.5	0.6
6	920	225	345	3.7	33.2	1150	6.5	0.4
7	700	335	110	7.5	73.8	1500	7.4	0.6
8	550	415	125	4.3	39.9	1150	6.8	0.4
9	1460	195	250	4.2	34.6	1200	6.5	0.4
6 to 12 inches								
1	90	30	85	5.2	21.2	830	7.0	0.5
2	180	90	35	7.0	15.6	765	6.8	0.7
3	100	75	115	6.4	15.9	810	6.8	0.5
4	140	85	30	5.7	72.9	1050	7.2	0.7
5	170	115	40	7.8	29.7	915	6.8	0.7
6	40	55	80	5.4	16.5	870	6.8	0.6
7	190	90	30	16.2	11.8	1250	7.5	0.7
8	120	90	30	5.0	25.0	770	6.8	0.4
9	10	120	15	6.3	28.0	820	6.7	0.4

TABLE II PLOT B.

0 to 6 inches	No. of nemas recovered from 50g. soil samples			Fertilizer Analysis Aug. 24 only				
				in ppm.				Conductivity mmhos/cm.
Subplot	Aug.24	Sept.27	Nov.1	N	P	K	pH	
1	65	370	90	0.8	7.7	45	7.3	0.2
2	65	250	175	0.2	5.6	60	7.1	0.2
3	140	365	270	0.2	5.0	65	7.3	0.2
4	270	200	220	10.0	3.4	105	7.1	0.3
5	165	295	215	0.5	2.5	55	7.0	0.2
6	205	240	405	0.4	3.4	60	7.0	0.2
7	275	390	150	1.9	2.2	55	7.1	0.2
8	220	325	270	0.6	3.7	60	7.2	0.2
9	330	555	185	0.5	3.4	50	7.2	0.2
6 to 12 inches								
1	20	20	80	0.4	3.6	50	7.2	0.2
2	50	75	45	0.5	4.1	50	7.2	0.2
3	35	85	40	0.6	13.2	50	7.4	0.2
4	10	40	35	3.0	3.0	55	7.3	0.2
5	30	30	25	0.5	3.6	45	7.2	0.2
6	35	20	25	0.4	4.7	40	7.2	0.2
7	30	55	50	1.7	1.6	45	7.3	0.2
8	55	65	40	0.9	1.9	45	7.3	0.2
9	40	15	10	0.6	1.9	45	7.3	0.2

TABLE III PLOT C.

0 to 6 inches	No. of nemas recovered from 50g. soil samples			Fertilizer Analysis Aug. 24 only				
				in ppm.				Conductivity mmhos/cm.
Subplot	Aug.24	Sept.27	Nov.	N	P	K	pH	
1	325	675	530	1.4	5.0	400	7.7	1.0
2	835	565	480	1.1	3.7	395	7.4	1.6
3	235	390	245	2.2	5.9	340	6.8	0.6
4	375	695	860	2.5	3.4	510	7.6	0.8
5	540	300	410	0.9	5.6	335	7.1	1.3
6	280	400	540	1.3	8.2	310	6.6	0.5
7	530	425	470	2.2	4.7	420	7.0	0.5
8	410	650	570	0.4	5.0	455	7.4	0.6
9	700	345	375	1.0	7.0	290	7.0	0.7
6 to 12 inches								
1	45	105	120	4.8	2.2	225	7.9	1.2
2	20	205	215	4.0	2.3	270	7.5	1.9
3	35	60	80	2.6	2.5	240	7.1	0.5
4	50	300	110	3.2	1.9	365	7.7	0.8
5	80	50	50	2.4	2.3	200	7.4	1.5
6	15	50	110	2.1	1.9	200	7.1	0.5
7	85	250	50	1.1	3.1	360	7.2	0.5
8	80	175	160	8.0	2.2	380	7.6	0.8
9	125	140	325	1.9	2.5	180	7.5	0.8

1968 FIELD DATA

TABLE IV PLOT A

0 to 6 inches	No. of nemas recovered from 50g. soil samples					Fertilizer Analysis. July, 3 only				
						in ppm.				Conductivity mmhos/cm.
Subplot	May 24	July 3	Aug. 24	Sept. 24	Nov. 15	N	P	K	pH	
1	440	700	1320	1100	1150	5.3	33.6	930	7.0	1.2
2	780	830	880	1140	--	3.7	23.1	1495	6.8	1.0
3	400	880	1080	1500	--	10.4	30.9	1195	6.7	1.0
4	400	1320	980	730	--	30.7	37.2	1745	6.4	2.2
5	470	1050	800	1720	960	18.9	25.4	1615	6.4	0.9
6	430	1110	630	1020	--	16.0	40.4	1395	6.6	1.1
7	450	690	640	690	--	5.9	38.2	1535	7.1	1.0
8	570	620	600	810	--	10.4	26.9	1315	6.5	0.9
9	530	770	800	690	800	19.7	24.7	1055	6.6	1.0

TABLE V PLOT B

0 to 6 inches	No. of nemas recovered from 50g. soil samples					Fertilizer Analysis July, 3 only				
						in ppm.				Conductivity mmhos/cm.
Subplot	May 24	July, 3	Aug. 24	Sept. 24	Nov. 15	N	P	K	pH	
1	170	380	440	580	570	0.9	1.6	50	7.0	0.5
2	170	370	420	690	-	1.4	1.4	47	6.9	0.5
3	200	450	170	480	-	1.9	1.1	65	6.8	0.4
4	120	390	300	500	-	0.7	0.8	82	7.1	0.4
5	250	230	420	530	620	0.9	0.8	80	7.0	0.5
6	280	400	275	580	-	1.8	0.8	92	7.2	0.5
7	200	230	210	430	-	0.7	1.1	79	7.5	0.5
8	260	300	230	350	-	0.9	0.8	95	7.2	0.4
9	80	550	180	500	500	0.9	0.8	75	7.2	0.4

TABLE VI Plot C

0 to 6 inches	No. of Nemas recovered from 50g. soil samples			Fertilizer Analysis July 3, only				
				in ppm.				Conductivity mmhos/cm.
Subplot	May 24	July 3	Aug. 24	N	P	K	pH	
1	800	1070	635	2.7	4.0	325	7.7	1.7
2	610	530	520	1.7	3.6	519	7.7	1.5
3	700	640	660	1.7	2.8	318	7.1	0.9
4	1120	680	620	1.4	1.9	455	7.7	1.5
5	750	730	540	0.9	4.7	515	7.5	1.8
6	590	440	430	2.1	2.3	226	6.9	1.0
7	770	520	450	1.7	4.4	473	7.6	1.5
8	270	830	400	0.8	1.9	510	7.2	1.6
9	770	170	440	0.7	4.4	354	7.5	1.4

APPENDIX VI

Analyses of laboratory soils prior to treatments, immediately after treatments, and at termination of experiment. N P K levels are in ppm, and conductivity is in mmhos per cm. * not available.

Factors analyzed	Untreated soils		Two representative soil samples immediately after treatments. Brackets indicate same two samples at termination of experiment.	
	Sand	Clay	Sand	Clay
N	0	4	273(150)	262(245)
P	4	10	14 (4)	25 (25)
K	30	533	215(170)	835(670)
pH	7.5	7.5	--*(7.3)	--*(7.1)
Con.	0.4	1.2	--*(0.3)	--*(2.1)

APPENDIX VII

Amount of top growth recovered from laboratory pots at the termination of experiment.

Treatment no.	Treatment levels (ppm).			Top growth. Dry weight in grams.	
	N	P	K	Sand	Clay
1	0	0	0	0.94	3.19
2	0	20	200	0.77	3.24
3	0	40	400	0.88	2.43
4	0	60	600	0.93	2.68
5	200	0	0	2.03	4.48
6	200	20	200	2.52	4.23
7	200	40	400	2.60	3.94
8	200	60	600	2.51	4.81
9	400	0	0	2.02	4.27
10	400	20	200	2.02	4.75
11	400	40	400	2.69	4.42
12	400	60	600	2.31	5.02
13	600	0	0	1.17	4.98
14	600	20	200	2.25	3.67
15	600	40	400	2.50	3.39
16	600	60	600	2.32	3.60