THE JOINT ROLE OF *PRATYLENCHUS PENETRANS* AND ASSOCIATED ABIOTIC AND BIOTIC STRESS FACTORS ON THE ONTOGENY OF *SOLANUM TUBEROSUM*

By

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ABSTRACT

THE JOINT ROLE OF PRATYLENCHUS PENETRANS
AND ASSOCIATED ABIOTIC AND BIOTIC STRESS FACTORS
ON THE ONTOGENY OF SOLANUM TUBEROSUM

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The interaction between a migratory root parasitic nematode (Pratylenchus penetrans), a defoliating insect (Leptinotarsa decemlineata), and their host (Solanum tuberosum) were evaluated under varying pesticide and fertilization regimes. The objective was to study the plant, its pests and nutrient requirements as a system so as to define levels of plant response occurring during the growth and development of the plant.

The importance of P. penetrans, L. decemlineata and fertilizers associated with S. tuberosum was identified using two analytical techniques, Analysis of Variance and Path Coefficient Analysis. P. penetrans' most important affect on S. tuberosum occurred during the tuber initiation phase, reducing tuber set. Control of P. penetrans increased tuber set and then nitrogen (N), phosphorus (P), or L. decemlineata limited yield. With an increase in N or P, small tubers increased in size. The most important influence of L. decemlineata occurred during the tuber bulking phase, with late-season defoliation reducing tuber size.

Defoliation of S. tuberosum by L. decemlineata reduced population densities of P. penetrans by influencing the size and possible nutritional quality of the root system.

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A wise woman once wrote:

> I am but the product of my environment. They have come from many sides, but all have shared in the creation of the person that is me.
>
> Time cannot wash it away.

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INTRODUCTION

Solanum tuberosum L. (potato) is a widely cultivated and very significant food crop of worldwide distribution. Potatoes grown in Michigan are subject to attack by many pests that affect plant growth, development and yield. Leptinotarsa decemlineata Say (Colorado potato beetle) and Pratylenchus penetrans (Cobb) (Filipjev & Schuurmans-Stekhoven 1941) (root-lesion nematode) are pests of prime importance. They can be dichotomized into foliar and root feeders.

L. decemlineata feeds by chewing the leaves and terminal growth of S. tuberosum. If defoliation is severe, the plant will die. In less severe cases, the development of tuber production is inhibited and final yield is greatly reduced. P. penetrans is a migratory endoparasite that attacks unsuberized roots and other underground parts of the plant. Small cortical lesions caused by the nematode-infected plants are poor absorbers of water and nutrients essential for normal plant growth. The shoot systems of severely affected plants are stunted, chlorotic and wilt rapidly. These symptoms are a gradual decline or lack of plant vigor rather than the rapid, striking changes that occur from defoliation of potato plants by L. decemlineata. The susceptibility to P. penetrans is variable among potato cultivars.

Plants undergoing nutritional stress do not respond to root and foliar feeding pests in the same manner as healthy plants. It is well documented that the growth, development and yield of S. tuberosum can be greatly increased by the use of fertilizers. Differences in the supply of nitrogen and phosphorus can have marked effects on the growth of the crop and can produce significant changes in the yield of the plant. Fertilizers, by affecting growth rates and

plant longevity, can determine when and how much plant material is available for plant pests such as L. decemlineata and P. penetrans. This also determines the food quality of the plant tissue being consumed by the pest.

Much is known about the impact of specific pests and fertilizers on S. tuberosum growth, development and yield. Little or nothing is known about the joint action of defoliators, root parasites and nutrient deficiencies on the growth and development of S. tuberosum. Correspondingly, little is known about the effect interacting plant stresses have on the population dynamics of pests attacking S. tuberosum. Changes mediated through the plant by one stress factor (e.g., L. decemlineata) may indirectly influence the subsequent impact of a second stress factor (e.g., P. penetrans). Information about this interaction is a necessary prerequisite for the description of the current states of S. tuberosum growing in ecosystems housing multiple stress factors. S. tuberosum is not grown in a pest-free vacuum. Plants are continually subjected to a myriad of interacting forces. The abiotic and biotic components of agro-ecosystems are dynamic, and it is essential that an understanding of the joint action of foliar-feeding and root-feeding pests be studied in respect to all components of the system. Under such a variety of conditions, levels of economic damage can be defined only by studying the plant, its pests and nutrient requirements as a system.

The objective of this research is therefore to develop a basic understanding of the interactions among the migratory root-parasitic nematode (P. penetrans), the defoliating insect (L. decemlineata) and their host (S. tuberosum) under varying nitrogen and phosphorus fertilization regimes.

LITERATURE REVIEW

PRATYLENCHUS PENETRANS

Systematics

Root-lesion nematodes were observed first in 1865 (Sher & Allen, 1953). It was not until 1880, however, that Tylenchus pratensis was described by deMan (1880). Six species, including Pratylenchus penetrans, have been synonomized with T. pratensis (Sher & Allen, 1953), and much of the early information pertaining to deMan's description of T. pratensis should be referred to as Pratylenchus spp. In 1917, Cobb (1917) described T. penetrans, a parasite of violet, cotton and potato, from various regions of the U.S.

In 1927, Cobb reported T. penetrans as a probable synonym of T. pratensis. Since Cobb's description of T. penetrans, Goodey (1932) and Steiner (1927) synonomized T. penetrans with T. pratensis. In 1936, Filipjev published the first generic classification of the Tylenchidae and designated P. pratensis as the type species of the genus Pratylenchus. This work included a list of five species of Pratylenchus, with T. penetrans synonomized with P. pratensis. In 1952, Chitwood and Otiefa (1952) constructed a new combination resurrecting the first generic and species name for P. penetrans. Sher and Allen (1953) and Loof (1960) have made comprehensive studies of the taxonomy of the genus. Much of the confusion concerning the taxonomy of root-lesion nematodes was eliminated by these monographs.

Taxonomy

The genus Pratylenchus (Filipjev, 1936) contains more than 40 species. They are difficult to identify because of morphological similarities. The principal characters used to differentiate Pratylenchus spp. include labial morphology, cephalic annulation, shape of the tail, length of the posterior uterine branch and position of the vulva. Comparison of populations of P. penetrans from different geographical locations and type hosts indicate extensive intraspecific morphological variation (Mai et al., 1977). Vulva position and stylet length are the least variable and the most diagnostic characters.

Distribution--Economic Importance

P. penetrans is widely distributed throughout temperate regions of the world. It is common in Europe, Canada and the northern regions of the U.S. (Loof, 1960). The global distribution of P. penetrans may be related to the distribution of susceptible host plants or climatic factors (Mountain & Patrick, 1959; Norton, 1978). Soil type also influences the distribution of P. penetrans (Oostenbrink, 1961; Kable & Mai, 1968a), being more prevalent and causing more damage in sandy soils (Townshend, 1972; Kable & Mai, 1968b).

P. penetrans is widely distributed in Michigan (Knierim, 1963). It was recovered from more than half of the fields sampled in two recent surveys (Bernard & Laughlin, 1976; Elliot, 1980). It is the most frequently encountered phytopathogenic nematode species in Michigan potato fields (Bernard & Laughlin, 1976), and commonly occurs at economically damaging levels. It is the most economically important plant-parasitic nematode species in the northeastern U.S. (Mai et al., 1977).

Host range studies indicate that more than 350 different plant species are hosts of P. penetrans (Mai et al., 1977). These include many economically important food and fiber crops as well as many weed species. It is a major pest of fruit (Pitcher et al., 1960; Mountain & Patrick, 1959) and vegetable crops (Dickerson et al., 1964; Olthop & Potter, 1973; Barker & Olthop, 1976; Hastings & Bosher 1938), causing extensive losses annually within Michigan (Bird, 1980a). Townshend and Davidson (1960) demonstrated the potential importance of various weed hosts that serve as reservoirs for this nematode.

Biology

The life cycle of P. penetrans consists of the egg, four larval stages and adult males and females. Reproduction is by amphixis, requiring both males and females (Thistlewayte, 1970). Females deposit eggs singly in soil or roots. Hung and Jenkins (1969) and Thistlewayte (1970) studied the processes of oogenesis and embryogenesis. After fertilization, eggs are deposited at a rate of 0.8 to 1.2 eggs per day (Mamiya, 1971). Hastings (1939) reported that the largest number of eggs laid by a single female was 16. Christie (1959) found that the optimum soil temperature for reproduction was 21.1 C. Reproduction decreased as temperature increased above 21.1 C. Kable and Mai (1968a) demonstrated that soil moisture also influences reproduction.

First-stage larvae are formed with the completion of embryogenesis, usually 4 or 5 days following egg deposition. The first molt occurs in the egg. Second-stage larvae hatch in 8 or 9 days at 25 C (Mamiya, 1971). Hatching takes place as a result of continued stylet thrusting which mechanically ruptures the egg and provides an emergence pathway for second-stage larvae. P. penetrans molt three more times, between intervals of feeding, and become

adult males or females. The life cycle takes 30 to 86 days, depending on temperature and host. It is shortest at 30 C, although fewer eggs are laid at this temperature than at 20 C or 24 C (Mamiya, 1971).

Movement

P. penetrans is an obligate parasite of higher plants. It must locate a suitable host plant and successfully penetrate host tissue to establish a parasitic relationship. As a soil-borne pathogen, it is dependent on a number of biotic and abiotic factors that directly influence these processes and nematode survival. Plant roots and gaseous exudates attract P. penetrans. This results in directed orientation (Klinger, 1972). The attraction of P. penetrans to roots is complex. It is caused by behavioral responses to different combinations of factors, including gradients of CO_2, heat and various other substances associated with root metabolism.

In laboratory experiments, Klinger (1972) demonstrated that P. penetrans obtains directional cues by tracking concentration gradients of CO_2 diffusing from plant roots or fungi. The response of P. penetrans to temperature gradients spread over relatively short distances was shown in laboratory experiments by El-Sherif and Mai (1968). These results indicate that P. penetrans is attracted to heat sources, including the metabolically produced heat emanating from root tissue and germinating seeds. Directional movement of P. penetrans is also affected by biochemical substances from plant roots or associated microorganisms (Chang & Rohde, 1969; Edmunds & Mai, 1966; Lavalle & Rohde, 1962). Lavalle and Rohde (1962) observed that initial migration of P. penetrans is significantly greater in the direction of host seedlings. This happens even when roots were removed from the soil, indicating

that diffusible biochemical substances coming from the roots were responsible for the attraction. Attraction was also directly related to the linear growth of roots, with decreasing attractiveness when root growth was slow or did not occur. While some biochemical substances attract nematodes, other plant-produced compounds have a repellent effect. In one case, the repellent activity was related to phenols commonly found in necrotic tissue inhabited by P. penetrans (Chang and Rohde, 1969). Klinger (1972) suggested that within the temperature range of nematode activity, the combined effect of both chemical and thermal stimuli was probably more effective in the localization of potential host plants than the effect of any single stimulus.

Many studies dealing with the influence of environmental factors on P. penetrans indicate that soil moisture, temperature and soil type are important factors in movement and survival. Differences in movement and survival of P. penetrans are directly related to soil particle size distribution, moisture retention, aeration and pore size (Townshend & Webber, 1971). Kable and Mai (1968a) demonstrated how specific soil types, soil moisture and soil temperature affect the survival and movement in soil and penetration of plant roots by P. penetrans. Survival and movement in soil decreases with increasing moisture tension from pF 0.0 (field saturation) to pF 4.2, and increasing soil temperature from 0 C to 37 C. Differential survival in the various soils may explain why P. penetrans appears to be more severe a problem in sand and sandy loam than clay or silt loam soils. Survival is lowest in very dry or very wet soil (Kable & Mai, 1968a; Townshend & Webber, 1971; Kable & Mai, 1968b).

Wallace (1964) reported that the movement of nematodes in soils is dependent on the geometrical relationship between nematode diameter, pore size and the distribution of water. Townshend and Webber (1971) showed that

movement by P. penetrans in three water-saturated Ontario soils was negligible. Movement, however, was maximum when 8-12% of the total pore space was occupied by air. Differences in P. penetrans migration is due to various soil pore sizes.

Penetration

Once a plant root is located, environmental parameters influence root penetration by P. penetrans. These include host age (Wallace, 1964), variety (Bernard & Laughlin, 1976; Bird, 1977), presence or absence of phenolic compounds (Chang & Rohde, 1969), soil temperature (Townshend, 1978) and soil moisture (Townshend, 1972; Kable & Mai, 1968a). Ease of penetration is influenced by plant species. The life stage of the nematode also influences the invasion of roots. Most stages of P. penetrans are able to penetrate roots (Townshend, 1972; Oyekan et al., 1972; Townshend, 1978). The capabilities of the various stages to invade roots, however, are not the same. Kable and Mai (1968a) observed that only the fourth-stage juveniles and adult stages penetrated alfalfa seedlings. Townshend (1978) reported a greater infective capacity of the females, which penetrated corn roots earlier, faster and over a wider temperature range than males or larval stages. He suggested that the larger size of the posterior subventral lobe of the females, which is involved in feeding and penetration, may account for the females' greater infectivity.

Edaphic factors such as temperature and moisture affect penetration. Optimum temperature for penetration of corn roots by P. penetrans is 20 C (Townshend, 1972). Females penetrated alfalfa roots at temperatures from 5 to 35 C, with maximum penetration between 10 and 30 C (Townshend, 1978). Male and juvenile stages have a narrower temperature range, 10-30 C, with maximum

penetration at 20 C. Oyekan et al. (1972) observed that all stages of P. penetrans entered roots of pea, usually requiring a minimum of 12 hours. He observed that the track left in agar by invading stages was often followed by other nematodes, providing a pathway to a previous infection court. The implication is that the superior infectivity of females at wider temperature ranges may increase the likelihood of survival of the species during adverse environmental conditions when females are in close proximity to host roots.

Differential penetration by P. penetrans occurs when host plants are grown in different soil types or in the presence of soil microorganisms. Morsink (1963) found that P. penetrans failed to enter roots of potato seedlings under axenic conditions unless the medium was contaminated with fungi. Townshend (1972) demonstrated that greater numbers of P. penetrans penetrate roots in sandy loam soils than in silt or clay loam soils. This may be attributable to greater nematode movement and greater localization of roots in coarse-textured soils than in fine-textured soils. Penetration is also determined by a complex of interacting biotic and abiotic factors.

Pathogenicity

Pratylenchus spp. cause the formation of root-lesions, usually on feeder roots and occasionally on other underground parts of plants such as potato tubers. These species are primarily parasites of the root cortex, although other components of the root may be invaded. Primary plant symptoms commonly associated with high population densities of P. penetrans include cortical necrosis and cellular discoloration of the inner cortex and adjoining endodermal cells. Secondary symptoms of P. penetrans injury is usually seen in the above ground part of plants, which are stunted and chlorotic, with early death of older

leaves and greatly diminished root systems. Secondary symptoms can, in many cases, be easily confused with other unrelated non-specific factors such as nutrient deficiency, and are not always apparent in plants even if infected with P. penetrans. Plant response to nematode feeding is variable and dependent to a large degree on severity of nematode infestation, inherent genetic characteristics of the host and the prevailing environmental conditions.

Feeding by P. penetrans injures the roots by rupturing and disorganizing cortex cells. Apple roots react in two distinct ways to invasion by P. penetrans (Pitcher et al., 1960). First, and soon after penetration, a discoloration in the invaded epidermal cells occurs. Then, 3 to 4 weeks after feeding on the cortical cells, a dark streak or lesion can be obseved in the underlying vascular tissue of the stele. This type of hypersensitive plant reaction to P. penetrans inhibits the growth and development of the root system, severely infected root systems generally being greatly diminished with fewer, poorly developed feeder roots (Taylor et al., 1971). Cellular damage within the cortical tissue also inhibits the absorption of water and nutrients essential for the development of healthy plants. Kimpinski (1979) showed that the amount of water moving through the stems of potato plants infected with P. penetrans is generally less than in nematode-free plants.

Root lesions form as a result of enzymatic reactions associated with the plant's response to the mechanical influence of nematode migration (cell wall damage) and to the substances nematodes introduce into the plant. Plant reactions to these compounds vary with plant susceptibility. The type and extent of the injury caused by P. penetrans depends in part on the presence or absence and relative concentrations of phenolic substances within the plant. Phenols, in combination with nematode-produced enzymes, give rise to products

that are toxic to parasitized and adjacent root cells (Pitcher et al., 1960). In both apple and peach roots, the tissues that show the most rapid discoloration in the presence of P. penetrans are the tissues that contain the highest levels of phenolic substances. Tuber infections, like root infections, are characterized by discolored, slightly elevated roundish lesions (Cobb, 1917). Formation of root or tuber lesions is not always as prominent as demonstrated in Wisconsin field studies by Dickerson et al. (1964). If infestation of P. penetrans is severe, lesions may coalesce to form larger areas of necrotic tissue causing a further overall increase in plant damage (Filipjev & Schuurmans-Stekhoven, 1941).

Roots with dark brown lesions of varying sizes are present on both primary and secondary roots with the largest lesions usually on the oldest roots (Filipjev & Schuurmans-Stekhoven, 1941). Damage to rhizomes by P. penetrans is usually much less extensive than damage to roots. In general, young plants suffer most from the attacks of P. penetrans (Jaffee & Mai, 1979). This is due to the fact that P. penetrans heavily infects the younger feeder roots of plants (Taylor et al., 1971). As the roots age and suberize, the nutritional status of the root may change and the nematodes migrate into the soil. Age-related pathological responses have also been observed for Pratylenchus spp. attacking a number of other host plants (Wallace, 1973).

The pathogenic effects of P. penetrans toward various species of plants has been extensively studied. Cobb (1917) in 1917 reported damage to potato, violet and cotton by P. penetrans. Necrotic lesions on roots and tubers and reduction in the number of tubers was observed. Hastings and Bosher (1938) were first to show that P. penetrans, in the absence of other microorganisms, reduced plant growth 50-75% of seven agriculturally important plants. In potato pathogenicity studies, Oostenbrink (1954, 1958) found that P. penetrans

caused a 50% reduction in plant weight and a 20-50% reduction in tuber yield. Bernard and Laughlin (1976) examined the effects of varying potato cultivars and initial population densities of P. penetrans on tuber yields. Yield reductions were related to the tolerance of the plant to nematode colonization rather than to a specific resistance factor operating in the plant. Wide differences in the damage caused by P. penetrans to apple trees growing on different rootstocks in New York was observed by Parker and Mai (1974). Dickerson et al. (1964) showed marked reductions in potato yields associated with high populations of P. penetrans. Oostenbrink (1966) reported a linear relationship between the initial population densities of P. penetrans and tuber yield. This was confirmed in 1973 by Olthof et al. (1973) and Olthof and Potter (1973). Seinhorst (1950) reported that the initial population density tolerance limit for P. penetrans at 1.0 per gram of soil and by Oostenbrink (1966) as 0.4 to 1.0 per gram in sandy soil and 0.7 to 2.0 per gram in loam or organic soil. Olthof and Potter (1973) established an economic threshold of 2.0 per gram of soil which was used in 1976 by Barker and Olthof (1976) in a report of nematode tolerance limits for a number of crops.

The pathogenic relationships between nematodes and hosts varies with different environmental conditions. Factors that restrict or inhibit plant growth, such as the cellular damage to feeder roots caused by P. penetrans, may inhibit growth by reducing the flow of water and nutrients (Kimpinski, 1979). In years with average or below average rainfall, plant growth and yield losses may be moe severe if high population of P. penetrans interferes with water and nutrient absorption. These effects may be partially offset by common irrigation practices, which may provide the plant with adequate water. Host plants grown in unfavorable conditions, i.e., in soils deficient in potassium,

nitrogen or calcium or at low light levels or following defoliation, are more susceptible and more severely damaged by P. penetrans than vigorous crops (Dolliver, 1961).

The pathogenic effect of P. penetrans on various host plants may be enhanced by interacting with other plant pests operating in the soil or on aerial portions of the plant. Burbee and Bloom (1978) found that an early season increase in the incidence and severity of Verticillium wilt of potato was indicative of a nematode-fungal interaction. Morsink and Rich (1968) obtained similar results, suggesting that root damage by P. penetrans increased the incidence of Verticillium wilt. Using a split-root technique, Conroy et al. (1972) showed that the disease caused by both P. penetrans and Verticillium albo-atrum was usually more severe as the number of nematodes or level of fungal inoculum increased. In most studies of nematode-fungal disease complexes, nematodes increased the severity of fungal diseases. P. penetrans can cause a breakdown in the resistance of pea to Fusarium wilt (Oyekan & Mitchell, 1971). It was suggested that P. penetrans induced biochemical or physiological changes within the plant which were conducive to wilt development.

Ecology

Many factors determine the rate of increase and final density of root and soil populations of P. penetrans. Studies dealing with the influence of the environment on population dynamics of nematodes under field conditions show that soil moisture and temperature are important. Soil type, soil pH, weeds, cropping history, plant host and chemicals introduced by man (pesticides, herbicides, fertilizers) all exert some effect on nematode populations.

Plant species and the physiological status of the plant have a marked effect on the subsequent population changes of P. penetrans in the soil and roots. Dolliver (1961) showed that changes in population levels of P. penetrans are related to the degree of stress to which the plant and nematode are subjected. Populations of P. penetrans in root systems of Wando peas increased significantly when plants were stressed by defoliation, nutrient deficiencies or abnormal light intensity. Treatments which severely restricted root growth significantly reduced numbers of P. penetrans. When plant growth was severely restricted by early defoliation, root population densities significantly decreased, but increased when defoliation occurred later. Conditions inhibiting plant growth cause changes in the physiological processes of the plant, and influence host plant suitability for nematode colonization and susceptibility of the plant to nematode injury.

Dickerson et al. (1964) demonstrated that population increases of P. penetrans were influenced by soil temperature, soil type and previous cropping history. Their results indicate that the optimum temperature for population increase of P. penetrans varies with the host and did not necessarily coincide with optimum temperatures required for root or plant growth. Populations of P. penetrans were shown to increase faster on corn than on potatoes with greatest population increases at 24 and 16 C, respectively. The study indicated that crop rotations in Wisconsin, in which corn was growing in rotation with potatoes, increased the severity of damage caused by P. penetrans to both hosts. Ferris and Bernard (1961) reported similar results, with corn and soybean rotations increasing population levels of P. penetrans. Greenhouse tests by Wong and Ferris (1968) showed that root populations of P. penetrans increased more rapidly in potato and peppermint than in onion roots. Bernard and

Laughlin (1976) showed in a test of four potato cultivars that up to four times as many P. penetrans in final harvest populations were produced on susceptible varieties.

Work by a number of investigators indicates that population levels of P. penetrans oscillate markedly throughout the year. Many of these studies show that the seasonal population fluctuations commonly associated with periods of plant growth follow a characteristic pattern (DiEdwardo, 1961; Ferris & Bernard, 1961; Ferris, 1967). Based on similar soil volumes, P. penetrans populations increased in the spring and early summer, before growth of the crop became extensive, followed by a decrease in soil populations at mid-season when root growth is usually at a maximum. The mid-season decline is then followed by a marked increase in soil population densities of P. penetrans during harvest. Bird (1977) observed that changes in the soil population densities of P. penetrans may be the result of migration patterns into and out of potato roots which result in significant changes in root and soil population densities of P. penetrans during the season. Other causes of population fluctuations may be due to seasonal changes in soil temperature (Mai et al., 1977), or soil moisture (Kable & Mai, 1968a). Seasonal population fluctuations were observed by Dickerson et al. (1964) in Wisconsin potato fields where populations of P. penetrans increased from spring planting to vine kill and natural root senescence in August, followed by a decrease in soil populations from September to February.

Initial soil population densities of P. penetrans are directly related to the final soil populations from the previous crop and in northern climates to overwintering survival. Dunn (1972) demonstrated the importance of soil depth and host roots in overwintering of P. penetrans. Kable and Mai (1968b) showed

the importance of soil depth and soil type on overwintering survival of P. penetrans. Greater numbers of P. penetrans were observed in the top 30 cm of soil than at lower depths, suggesting that overwintering survival decreased with increased soil depth. It was speculated that overwintering survival was related to the permeability of soils to oxygen when water-saturated during the winter months.

The vertical distribution of nematodes in soil is influenced by many biotic and abiotic factors. Population size and distribution in the soil is directly related to the relative size and extensiveness of plant root systems. Wallace (1964) suggested that distribution of plant roots in the soil is the chief factor determining the vertical distribution of nematodes, and that physical factors usually play an important but secondary role. Root distribution, height of water table, soil moisture, soil temperature and soil texture also greatly affect vertical distribution.

Control

Plant-parasitic nematodes can be controlled to varying degrees by land management and cultural control practices. These include exclusion, plant resistance, various cultural control practices such as fallowing, crop rotation, cover crops, time of planting, trap and antagonistic crops, field sanitation and organic amendments. These methods, unlike the rapid efficacy of most nematicides, tend to reduce nematode population densities gradually through time. Their primary importance lies in the realm of pest management and integrated control. Combinations of the exclusion, plant resistance and population reduction control techniques, coupled with the judicious use of chemical nematicides, may reduce population levels of nematodes to

economically acceptable levels.

Not all land management and cultural control practices are equally effective in controlling nematodes. For crop rotation to be effective against P. penetrans, crops unsuitable for growth, reproduction or infectivity must be introduced into the rotation sequence. P. penetrans has a wide host range and thus limits the number and type of crops which are both feasible and economically profitable for the grower. With energy and environmental costs increasing and registration of new materials decreasing, these considerations may need to be re-examined within a new framework of pest control.

Many agricultural production practices such as introducing inorganic and organic compounds into the soil have reduced population levels of P. penetrans. In many cases, population reductions following treatment have been due either to the production of chemical compounds toxic to nematodes or to an increase in the activity of predaceous microorganisms in the soil (Walker, 1969).

More research emphasis has been placed on the influence of nutrients on nematode reproduction than on the joint influence of nutrients and nematodes on plant ontogeny. In 1961, Dolliver (1961) found that moderately reduced NPK fertilization of Wando peas resulted in increased population densities of P. penetrans. Nitrogen was reported to have two effects on nematode populations. Application can result in an increase of nematodes presumably by providing more feeding sites through stimulation of root growth; however, most reports indicate that the addition of nitrogen results in lower nematode numbers (Kimpinski et al., 1976; Patterson & Bergeson, 1967). It has been suggested that ammonia was responsible for this phenomenon (Oteifa, 1955; Eno et al., 1955). Oteifa (1955) speculated that ammonium ions were inhibitory to egg hatching.

Several forms of nitrogen have been studied and not all were equally

effective in their influence on nematode populations. Walker (1971) found that nitrate was least effective in reducing numbers of P. penetrans. Heald and Burton (1968) reported that organic nitrogen in the form of activated sewage sludge reduced nematode populations more than inorganic nitrogen. Unless phytotoxic levels were used, nematode population densities decreased with increasing amounts of nitrogen. Huber and Watson (1974) reported that the form of nitrogen was very important for the control of many plant diseases; however, Workman et al. (1977) was unable to find any differences in soil ammonium or nitrate and found varying levels of nitrate in potato petioles between fumigated and non-fumigated plots. Evidently, other factors were operating directly on the nematode, or indirectly through the host. Nematodes in Manitoba soils generally decreased in clay with increasing nitrogen, but numbers increased in sand with increased nitrogen, indicating that soil factors might be important (Kimpinski & Welch, 1971).

Reductions in population levels of plant-parasitic nematodes has also been achieved with the application of chemical nematicides. Nematicide usage in the U.S. has increased dramatically since the discovery of 1,3-D (mixtures of 1,3-dichloropropane and 1,2-dichloropropenes plus other C_3 hydrocarbons) in 1943. Use of soil fumigant nematicides is becoming increasing cost-prohibitive and is restricted in most cases to use in high value crops. Many are phytotoxic to plants and must be applied several weeks before crops are planted.

Many factors influence the efficacy of nematicides. Goring (1962, 1967) has reviewed the physical and biological factors involved in soil fumigation. Munnecke and VanGundy (1979) have reviewed the movement of fumigants in soil, dosage responses and differential effects. The important factors influencing the movement of soil fumigants are the chemical adsorptive

characteristics of the toxicant, temperature, moisture, organic matter, soil texture and soil profile variability.

Most nematicides, to be effective, must be dissolved in the soil solutions or adsorbed into plant tissue to come in contact with the target organism. Concentration and contact time are also important in the efficacy of nematicides. Not only are there considerable differences between organisms in their response to various concentrations and contact times, but there are differences between stages of the same organism (Munnecke & VanGundy, 1979). Many nematicides are lethal to nematodes because they directly interfere with vital metabolic life processes. Other nematode functions including hatching, movement, feeding behavior, orientation and development may be impaired or inhibited at low nematicide concentrations.

LEPTINOTARSA DECEMLINEATA

The Colorado Potato Beetle (CPB), Leptinotarsa decemlineata Say, is a major foliar feeding pest of many important agricultural crops, including potatoes, tomatoes, peppers and eggplant. Both adults and larvae feed by chewing the leaves and terminal growth of the plant. If defoliation is severe, the plants will die and development of tubers is prevented or yields greatly reduced.

L. decemlineata is indigenous to the central U.S., where it was originally observed feeding on various Solanaceous plants. With the introduction of the cultivated potato into these areas by early settlers, L. decemlineata became a serious pest of potato. It migrated eastward across the U.S. into new potato-producing areas, often reaching epidemic proportions. It was introduced into Europe in the 1920's, where it is now a widespread, serious pest of potatoes.

Life History

L. decemlineata is a multivoltine pest with 1-3 generations per year, depending on the climate and local weather conditions. It overwinters as an adult in the soil. In the spring, adults emerge and begin the primary life cycle, ovipositing almost immediately. Eggs are laid in clusters on the underside of leaves usually after a brief feeding period. CPB has four larval stages. The fourth stage burrows 2-6 inches into the soil and pupates. After a short pupation period ranging from 7-21 days (Olsen et al., 1980), it emerges as an adult and soon mates, repeating the cycle. The number of generations is largely a function of temperature. The life cycle can be completed in 30 days, depending primarily on temperature.

Biology

Many of the biological and physiological processes governing the growth, development and survival of L. decemlineata are environmentally determined. These include overwintering, spring emergence, egg laying, hatching, larval development and pupation.

Overwintering. During the hibernation phase, CPB survives best in a moderately dry soil with temperatures above -8 C (Hurst, 1975). The depth below the soil at which beetles hibernate depends on three factors: soil type, moisture and temperature. These are important in determining overwintering survival and spring emergence. Hurst (1975) reported that depth of penetration is shallow in clay soils and deeper in sandy soils. Burrowing to greater depths in sandy soil provides greater protection from environmental extremes and decreases the rate of overwintering mortality. Different soils have different heating and moisture retention characteristics and affect not only overwintering survival rates, but also emergence of spring adults.

Spring emergence is directly related to soil temperature and depth of hibernation. Soil temperatures of 9-14 C is the temperature threshold for spring emergence (Olsen et al., 1980; Hurst, 1975). First emergence is from shallow overwintering sites. This affects the spring emergence distribution pattern because threshold temperatures are not reached or maintained uniformly through the entire soil profile or between soil types. Wegorek (1959) studied the emergence rate in relation to temperature. He reported that total emergence spans about 30 days with the largest percentage occurring during a 10-day period when soil temperatures reach 20 C.

After spring emergence, beetles begin searching for feeding and oviposition sites. This may require a short dispersal phase. Wind velocity and

direction dictate the location of host and suitable oviposition sites by weak flying adult beetles (Hurst, 1975). Although not essential, beetles usually feed for a short period before mating and egg laying (Gibson et al., 1925). Copulation may not be necessary for females because some inseminated the previous year remain fertile through the winter.

Oviposition. Eggs are laid during the day, singly or in clusters on the undersides of leaves. The greatest number of egg masses are deposited on the largest leaves, usually on or near the 3 terminal leaflets of the compound potato leaf (Gibson et al., 1925). The eggs are cemented to the leaf undersurface, an egg mass consisting on the average of about 30 eggs. Much larger and smaller egg masses have been reported (Kowalska, 1969). Gibson et al. (1925) reported that the number of eggs per mass varies between 6 and 129. The total number of eggs a female oviposits varies from 200 to 800 (Hurst, 1975; Kowalska, 1969). After depositing the first egg mass, the female usually rests for one or more days. Egg laying may continue over an extended period of time.

Photoperiod directly affects oviposition rates, especially of first and second generation females. Eggs are laid by females which have emerged only during times of sufficiently long photoperiods. Short daylengths (< 15 h) cause females to cease oviposition and begin diapause (Kowalska, 1969). This results in a decrease in overwintering mortality and an increase in post-hibernation fecundity.

Temperature also affects fecundity. Wegorek (1959) gives the threshold temperature for oviposition at 18 C while Alfaro (1949, cited in Olsen et al., 1980) reports a threshold of 16.5 C. Kowalska (1969) reported that the highest

rate of oviposition occurs at 28.7 C, but 21.7 C is optimum for maximum fecundity. This increase in the total number of eggs is due to the increased life span of the female at the lower temperature.

Food quality is an important factor affecting fecundity (Kowalska, 1969). Females feeding on leaves of mature plants and on lower leaves reduces ovogenesis and oviposition and accelerates the onset of diapause. Maximum fecundity is realized only when beetles feed on young potato plants (Kowalska, 1969). Plant and varietal difference also influence oviposition (Ting & Fraenkel, 1968).

Egg Development and Hatching. The length of the egg stage varies with environmental conditions. Temperature is the most important factor. The threshold for egg development is 12-13 C, with maximum developmental rates reported at 30.5 C and 24.4 C (Hurst, 1975). Under field conditions, Chlodny (1975) reported developmental times ranging from 4 to 10 days in warm climates, and 5 to 21 days in cold areas.

Larval Development. Temperature is by far the most important climatic factor governing the rate and duration of larval development. The threshold for larval development is circa 12-13 C, if other conditions are ideal (Hurst, 1975). The upper threshold is 33 C. DeWilde (1950, cited in Hurst, 1975) considers a field threshold temperature as 17 C for first and second larval instars.

Under field conditions, Larczenko (1958) reports a range of 21-43 days for total larval development. Karg and Trojan (1968) give the average duration per stage as L_1-3 days, L_2-5 days, L_3-9 days and L_4-15 days. Johnson (1916) reports total larval developmental times of 14-19 days in Washington, D.C.

Pupal Development. Pupal development occurs at 15-16 C and above with the time ranging from 7-21 days (Olsen et al., 1980).

Mortality

Many factors affect CPB mortality. Temperature is the most important climatic parameter. Other factors such as precipitation, soil moisture, soil type, humidity, food quality and food quantity have also been shown to influence CPB survival.

Temperature exerts a primary influence on CPB mortality, depending on the stage of development. Adult beetles can withstand temperatures to 58-60 C and temperatures as low as -10 C (Hurst, 1975). Soil temperatures of -12 C are lethal to hibernating CPBs (Chittenden, 1907). Larvae are destroyed at 35 C and temperatures below 0 C, as are the eggs. Gibson et al. (1925) observed that other temperature-related processes are operating which affect mortality of CPB life stages. Egg cannibalism by CPB larvae is temperature-dependent, frequently occurring during periods of cold stress.

Rainfall is the second most important environmental influence affecting survival of L. decemlineata. First and second instar are especially vulnerable to heavy rainfall. During periods of heavy downpours, small larvae are washed off the plant and perish in pools of soil water beneath the plant.

Excess soil water also affects overwintering mortality. Death occurs as a direct result of submersion, indirectly by creating optimum conditions for the development of disease pathogens and by limiting the beetles to the surface layers of soil where they die of frost during harsh winters (Hurst, 1975).

Excess soil moisture can cause pupal mortality as high as 80%, compared to 30-40% in moderately moist soil (Olsen et al., 1980). Other factors such as the influence of rainfall and snow cover protect hibernating CPBs from cold temperature extremes (Hurst, 1975). Winters with little snow permit frost to penetrate deeply into the soil and increase overwintering mortality. Harcourt

(1971) reported that frost mortality may be as high as 70% during Ontario winters.

Starvation is an important mortality factor. Due to the aggregated spatial distribution of larvae, food shortages may occur in very small areas of the field. As the food supply diminishes, larvae begin dispersing in search of food. When the limit of food supply is reached, the larvae starve, resulting in late season population decreases.

Food Consumption

Feeding by L. decemlineata adults begins soon after emergence of spring adults. They feed between periods of egg deposition on newly emerging potato seedlings. This continues until the end of the oviposition phase and death of the adult.

After emerging from the egg, first instar larvae often feed on the egg shell and frequently on other unhatched eggs before migrating to the top of the plant. Small quantities of leaf tissue may be consumed before the first molt. After the first molt, second instar larvae feed on newly expanding leaf tissue, preferring the more succulent, interveinal portions of the leaf (Gibson et al., 1925). After the second molt, leaf feeding continues, which now includes the midribs and larger veins of the leaf. Most feeding and, correspondingly, most plant damage occurs after the third molt. If fourth stage larvae are numerous, rapid defoliation can occur, resulting in both the death of the plant and reduced potato yield. In the absence of leaf tissue, CPB larvae may feed on the main stems of the plant or, because of overcrowded conditions, may begin dispersing away from the plant in search of a new food source. Feeding continues at a lower rate through the night. Heaviest feeding occurs 2-4 hours before twilight

(Chlodny, 1975). Feeding continues to within a few hours of pupation. Consumption by adults may be very damaging, especially to very young plants and especially later in the season when adults are abundant.

Rates of food consumption by L. decemlineata is dependent on the quality and quantity of food available. Wegorek (1959) showed lower nutrient and dry matter content of leaves grown in diffuse light which significantly affected the subsequent feeding habits of L. decemlineata. Food consumption by adults begins at 13 C and peaks at 25 C, almost doubling between 21 C and 25 C (Chlodny, 1975). Trojan (1968b) reported that female beetles consume 15.5 cal/day at 20 C, whereas males consume 17.4 cal/day. Grison (1950, cited in Hurst, 1975) related food intake to temperature and reported maximum food consumption at about 25 C. Above this temperature, most food was consumed nocturnally. Below 25 C, most food was consumed during the day.

Wegorek (1959) reported similar values for larval consumption patterns. At 20 C, food consumption by larval stages was 0.2, 1.5, 5.2 and 23.0 cm^2, respectively, of which more than 75% of the total 29.9 cm^2 was consumed by the fourth stage larvae. Chlodny (1967) reports the percent total consumption for larval stages as: L_1-2.8%, L_2-6.3%, L_3-20.8% and L_4-70%. Gibson (1925) reported similar findings of larvae consuming 28.0 cm^2 of potato leaf within a developmental period of 16 days. Hurst (1975) found that certain temperature levels are essential for larval food consumption, with a lower temperature threshold of 12 C.

Population Dynamics

Seasonal population fluctuations of L. decemlineata are dependent on the survival of each life stage. Many of the mortality factors previously described

are important in determining population trends during the season. Reductions in the potential population size begin with overwintering mortality of adults in the soil. This is partially determined by the activity of the adult beetles before the onset of diapause. Females which begin egg laying before hibernating decrease their chances of survival by depleting the critical body fat reserves necessary to endure the winter. If they do survive the winter, fecundity rates are lower. This contributes to between-season population fluctuations of CPB. The effects of adverse weather conditions (i.e., rainfall, subnormal temperatures) increase the mortality of newly emerged adults and prevent the laying of a full complement of eggs.

The reduction in egg population is due mainly to the cannibalistic nature of adults and newly emerged larvae (Trojan, 1968a). Karg and Trojan (1968) determined the reduction in the total number of eggs from cannibalism to be between 5 and 18%.

During the first and second instars, the principal mortality factor contributing to seasonal population fluctuations is rainfall. During heavy downpours, small larvae are washed from the plant to the ground where they perish in pools of surface water. Mortality caused by natural enemies can be significant during these initial larval stages. Overall mortality during these stages may be as high as 30-72% (Karg and Trojan, 1968).

Food quantity is a major factor determining the survival of third and fourth larval instars. CPB larvae hatching from eggs laid late in the season by adult females may not have enough foliage available to sustain normal growth and development through the larval stages. As the food supply diminishes, larvae begin migrating both within and between potato plants. When the limit of food supply is reached, CPB search for food. Even if food is available, larvae

may not have enough developmental time to complete metamorphosis before perishing during vine kill or harvesting. The number of larvae dying from starvation is density-dependent. As larval numbers increase, available resources decrease and mortality due to starvation increases.

Once the food supply is exhausted, larvae starve and the adults emigrate in search of other food resources. Harcourt (1971) showed that population trends are largely controlled by summer adult survival. Emigration, resulting from limited food supply, is regarded as the principal density-dependent factor responsible for numerical change in the population from generation to generation.

Harcourt (1971) reported that there are no natural control agents effective in preventing the CPB from overpopulating its food supply in Ontario. Karg and Trojan (1968) also reported that the natural enemy complex played an insignificant part in reducing population levels of CPB and their impact on plant defoliation and yield. This included many of the general predators such as ground beetles and lady beetles on eggs and other larval stages.

Hurst (1975) reported that two natural enemies in England, Podisus maculiventis and Lebia grandis, have not been successful in controlling L. decemlineata because both had higher temperature and humidity requirements for survival. Perillus bioculatus and Doryphorophaga dorophorae may be effective in controlling endemic populations of CPB (Harcourt, 1971). Mention is made of an entomophogus fungi (Beaveria effusa) and a bacterial pathogen (Cocobacillus leptinotarsae) contributing to CPB mortality (Hurst, 1975).

Parasitism and predation rates are influenced by many factors, including changes in the spatial structure of the population. During the early season, populations of CPB are characterized by a significant degree of aggregation

(Karg and Trojan, 1968). As the season progresses, the population distribution changes from an aggregational one to a random one with gradual dispersion of CPB aggregates. This distribution changes with a simultaneous increase in the density of CPB larvae, causing an increase in the number of contacts CPB larvae have with natural enemies. CPB mortality due to natural enemies increases with time and dispersal of larvae and adult beetles.

SOLANUM TUBEROSUM

Solanum tuberosum (Fig. 1) is a widely cultivated tuber-bearing food crop of worldwide distribution. It is indigenous to the Peruvian and Bolivian Andes of South America as S. tuberosum spp. andigena (Harris, 1978). It was introduced into Europe from the New World in 1570 by returning Spanish conquistadores. From this Spanish source, the potato spread throughout Europe and the Mediterranean and finally into North America in 1621.

Originally, S. tuberosum spp. andigena was unsuited to the long summer days and cold nights of Europe. Yields were poor with unsightly, misshapen tubers. Selections for earliness resulted in new varieties adapted for the European and North American climates. This eventually precipitated its widespread cultivation and consumption among the peasants of Europe and pioneers of the New World. Today potatoes are a major food staple.

The genus Solanum contains over 2000 species. In addition to S. tuberosum, seven other cultivated species and 154 wild species of potato are recognized. Through the efforts of plant geneticists, numerous potato cultivars have been developed with adaptations to various environmental conditions, consumer demands and production strategies.

Since the Irish potato famine of 1845, which killed or displaced an estimated two million people, much emphasis has been placed on the study of the potato crop. Numerous studies have examined the influence of various biotic and abiotic factors on plant growth, development and yield.

Life History

Potatoes are generally best adapted to cool temperate regions. They are usually grown from vegetative seedpieces; however, propagation from seed is

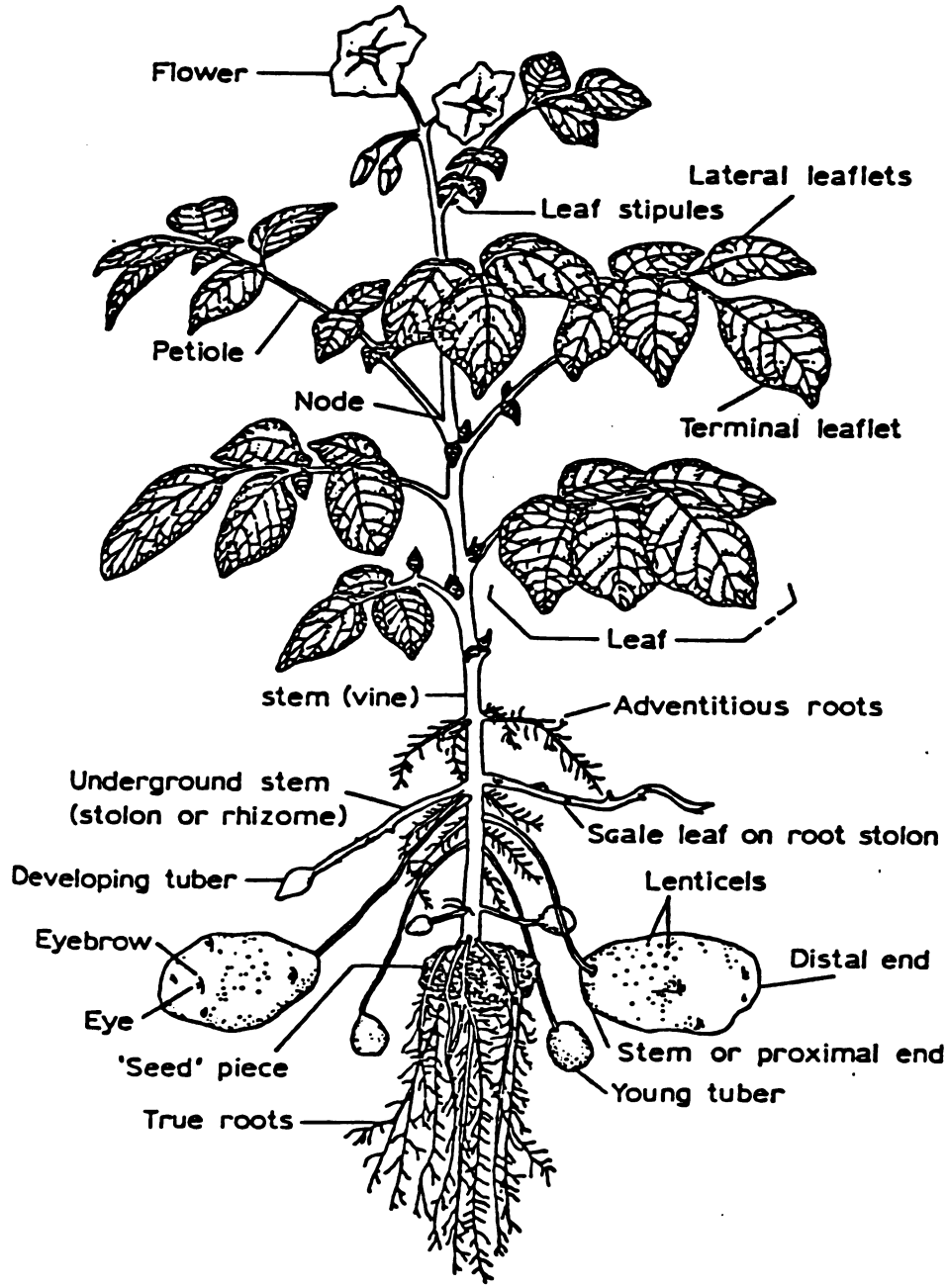

Figure 1. Diagrammatic sketch of a single stem potato plant (after Workman et al., 1979).

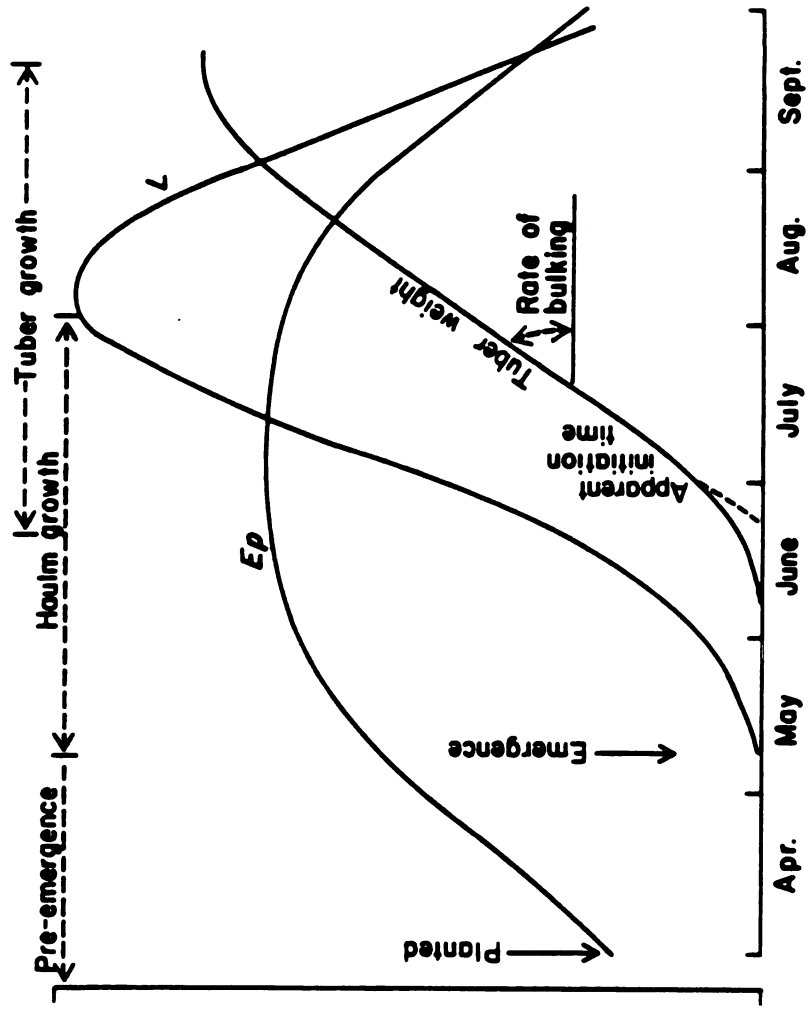

Figure 2. Relationships of main components of potato growth (after Milthorpe and Moorby, 1960).
L = leaf area index, E_p = potential rate of net assimilation

possible. Sprouts initiated from the mother tuber produce the daughter plant and the subsequent crop. Until sprout emergence and leaf expansion, the young potato seedling is dependent on the carbohydrate reserves of the mother tuber. This sets a lower limit on the seed tuber size (Ivins & Milthorpe, 1963), with final tuber yield increasing with increasing seedpiece size (Harris, 1978).

Ivins and Milthorpe (1963) have divided the seasonal life history of the potato plant into three phases (Fig. 2). The first phase of growth is pre-emergence. This involves the initial development of roots and sprouts from stored carbohydrates in the mother tuber. Developmental rates are dictated primarily by soil temperature and seedpiece size (Ivins & Milthorpe, 1963). The second phase is the haulm growth phase. After sprout emergence, the plants become photosynthetically active. Growth accelerates and the leaves, stems and roots increase rapidly in size, number and weight. Growth during this phase is dictated by environmental conditions, such as nutrient availability and the presence of pest organisms. The tuber growth phase is the final growth stage, being closely interrelated with and overlapping the haulm growth phase. It begins with tuber initiation and concludes at harvest. Tuber weight is the final result of the growth rate of leaves and stems, the production and distribution of assimilates, the time of tuber initiation and the time of senescence of the foliage.

Environmental Influences

Weather is the most important single factor influencing the growth, development and yield of potatoes. It is extremely complex and cannot be defined as simply a combination of light, temperature and soil moisture, but must be considered in terms of a number of interacting forces impacting on the plant.

Temperature. The potato is a cool weather crop. It is ideally suited for areas where the mean annual temperature is 5-10 C and where the mean temperature of July is not over 21 C (Hardenburg, 1949). Temperature affects plant respiration and transpiration. The optimum temperature for vegetative growth is 20-25 C, depending on the variety tested (Borah et al., 1960; Borah & Milthorpe, 1962). The potato plant cannot survive extended periods of frost, with extensive damage caused by a disruption of cellular membranes, loss of cytoplasmic water and leakage of ions (Harris, 1978).

Low temperatures retard vegetative growth and tuber initiation (Borah et al., 1960; Borah & Milthorpe, 1962). High temperatures delay tuber induction and decrease the rate of tuber development (Werner, 1934). Yamaguchi et al. (1964) reported that the optimum temperature for tuber formation of Russet Burbank potatoes is 15-25 C. At temperatures above 26 C, stolons are short with tubers misshapen, forming sessile to the plant near the soil surface. Borah et al. (1960) showed that high temperatures favor emergence and delay tuber initiation. The earliest tuber initiation and the greatest number of tubers were encouraged by low temperatures. After tuber initiation, tuber growth was reported to be fastest at a temperature of 15-20 C. Bushnell (1925) reported that tuber yields decreased with increasing temperature from 20-29 C, with no tubers forming at 29 C. The delay in tuber initiation and decrease in the rate of tuber growth at high and low temperature extremes is due to the balance between carbohydrate metabolism and plant maintenance.

Light. Light intensity influences the rate of photosynthesis which directly affects growth and development through the production and distribution of assimilates (Ivins & Milthorpe, 1963). Photosynthesis increases with increasing light intensity until an optimum level is reached. Chapman and Loomis (1953)

demonstrated that maximum rates of photosynthesis occurred when light intensities of 80,000 lux were reached. Light saturation levels occur only when water and CO_2 are limiting (Ivins & Milthorpe, 1963). Tuber weights are higher at higher light intensities because of the influence of light intensity on photosynthetic rate (Harris, 1978).

In general, growth and development is influenced by light intensity, since tuber formation, maximum stem elongation and plant senescence occur earlier at higher light intensities (Ivins & Milthorpe, 1963). At high light intensities, there is a greater total production of dry matter, and a higher percentage of dry matter is used in tuber production. Early tuber initiation, although favorable for increased tuber growth, may be offset by early plant senescence.

Growth and development is influenced by daylength and considerable differences in plant response to photoperiod exist among potato varieties and developmental stages. Ivins and Milthorpe (1963) reported that most potato varieties require a short daylength (10-14 h) for maximum tuber production. Above a daylength of 14 h, tuber growth is inhibited and excessive development of the foliage occurs. Below a daylength of 10 h, tuber growth is stimulated and top growth inhibited. Early varieties have a high critical daylength (15-17 h), whereas late varieties have a lower requirement (12-14 h). Early varieties grow under short days in the spring, and this short day influence promotes tuber initiation and growth. Tuber formation of the late varieties is inhibited during mid-summer (long days), obtaining maximum tuber growth during the shorter days of late summer and early fall.

Water. Water is an important factor in potato production. S. tuberosum is very sensitive to water stress. For optimum vegetative growth and tuber yield, rainfall or its equivalent, irrigation, needs to be distributed to keep water

deficits small to prevent growth inhibition. Water deficits result in smaller, narrower, spindly-shaped leaflets and decrease yield and quality of tubers (Epstein & Grant, 1973). Haddock et al. (1974) found that the reduction of integrated water potential from -0.6 to -1.5 bars through the season caused a 35% reduction in potato yields growing in Utah.

Large diurnal fluctuations in the water content of leaves inhibit potato growth (Harris, 1978). This is caused by the inability of the plant to absorb water at a rate sufficient to replace the water lost through transpiration. Fluctuations in water content are accompanied by high leaf temperatures during periods of high transpiration and limited soil moisture. When moisture is adequate, transpiration maintains leaf temperatures close to the ambient and prevents wilting. Decreases in the production and translocation of photosynthates and corresponding decreases in plant growth and yield are associated with inadequate soil moisture.

Water is important for nutrient uptake. There is an additional increase in tuber production for every unit of water evapotranspired (Harris, 1978). Vitosh and Warnke (1971) observed that high rainfall or excessive irrigation causes considerable losses of nitrogen in sandy soils. Highly mobile nutrients such as nitrogen were readily leached below the effective rooting depth of the potato plant, thus requiring an additional application of nitrogen. Conversely, low soil moisture levels interfere with the absorption of plant nutrients by decreasing the availability and concentration of various nutrients in soil solution adjacent to potato roots.

Timely applications of water can also modify the effects other environmental factors have on plant growth. Early irrigation during hot, dry conditions lowers the soil temperature and may indirectly produce earlier tuber

set and lead to a more rapid development of tubers than would normally have occurred (Ivins & Milthorpe, 1963). Over-irrigation may result in reduced yield by creating conditions favorable for disease development (Harris, 1978) or by increasing losses from bruising and skinning of tuber during harvest (Hardenburg, 1949).

Plant Nutrients

Optimum production of high quality potatoes requires an adequate supply of the proper nutrients throughout the growth of the plant. Potato soils differ in their ability to provide certain nutrients at critical times during the season. Most mineral nutrients essential for plant growth have general effects on the plant. This can very over a wide range of fertilization rates and from season to season. Many of the mineral elements have specific biochemical roles and relatively small effects on growth within a narrow range of supply. Other nutrients, such as the macronutrients (Nitogen (N), Phosphorus (P), Potassium (K)), have much broader effects over wider ranges of supply.

Nitrogen. Nitrogen is absorbed by plants primarily in the form of nitrates in the soil rhizosphere. Once absorbed by the plant, the nitrate is reduced to ammonium and combined with carbon molecules to form amino acids. The amino acids are linked to form enzymes which control the metabolic processes of the plant. In addition to this role, nitrogen is also an integral part of the chlorophyll molecule.

Phosphorus. Absorption of phosphorus by potato roots occurs primarily as inorganic monovalent or divalent phosphate ions. Phosphorus is relatively immobile in soils, being tightly bound to soil particles. Phosphorus, like nitrogen, is an extremely important structural component of many compounds

synthesized within the plant, and performs an invaluable role in energy metabolism (Tisdale & Nelson, 1975). The hydrosis of high energy phosphate bonds is almost exclusively used to drive chemical reactions.

Nutrient absorption is a complex process involving the movement of mineral nutrients, primarily from the soil, into the roots of the plant. From the roots they are distributed to the various parts of the plant, where they are utilized in various metabolic processes. During the early stages of growth, the mother tuber provides the ready source of organic and inorganic nutrients necessary to sustain growth (Moorby, 1968; Ivins & Milthorpe, 1963). With the development of the root system, the plant begins extracting nutrients from the soil. The rate at which these nutrients are incorporated into the plant is then dependent on a number of complex environmental, physiological and edaphic factors.

Uptake of plant nutrients into the plant is directly related to the nutrient status of the soil. Increases in nutrient supply, through fertilizer application, invariably show increases in total nutrient uptake and percent nutrient content in dry matter yield (Werner, 1934; McCollum, 1968a; Mukherjee et al., 1966). In some cases, uptake has been so extensive that nutrient concentrations in tubers have approached human toxicity levels (Kirkham et al., 1974).

Water is also important in nutrient uptake. Roots come in contact with more nutrients when growing in moist soil than when growing in a drier one because growth is more extensive. Decreases in uptake rates have been shown to coincide with periods when soil moisture deficiencies were increasing (Tisdale & Nelson, 1975). Short-term fluctuations do not appear to affect the plant, but can have a significant impact on the plant if soil moisture stress and decreased nutrient absorption continue for an extended period of time (Munns &

Pearson, 1974). Nutrient absorption is a very complex process depending primarily on soil moisture, the concentration adjacent to the potato root, soil temperature, total absorptive surface of the root and the rate of metabolic processes occurring at various developmental stages of the plant (Harris, 1978).

Effects on Growth, Development and Yield. Changes in nutrient supply affect growth, development and yield, primarily by influencing the net amount of photosynthesis in the plant. Differences in N and P supply are directly related to the temporal changes in size and efficiency of leaves, and to the changes in the ontogeny of the plant (McCollum, 1968b).

Temporal changes in plant ontogeny have been studied by examining what affect various nutrient levels have on the growth and senescence of leaves and the initiation and bulking of tubers. In general, it has been observed that high levels of N and P delay tuber initiation and correspondingly the onset of the tuber bulking phase (Ivins & Bremmer, 1965, cited in Harris, 1978; Kable & Mai, 1968a). This is apparently caused by an increase in the growth and development of leaf tissue by diverting assimilates to leaves which could be used for initial tuber growth. The influence that high levels of N and P have on delaying tuber initiation and bulking and, ultimately, tuber yield, is partially offset by the affect these nutrients have on the development and maintenance of leaf area.

Leaf area of a plant depends on the number and size of leaves. Net photosynthesis is a function of total leaf area, net assimilation rate (E) and the longevity of leaves or leaf area duration (D). Increases in the levels of N or P greatly increase leaf area (Harris, 1978; Lorenz, 1947; Dainty et al., 1959; Ivins & Milthorpe, 1963). Increases in leaf area increase tuber bulking rates, and increases in N and P supply cause apical meristems on the plant to develop,

accounting for much of the increase in leaf area. N also causes increases in leaf area through leaf production and expansion of existing leaves throughout the season. P has the same influence but the effects appear earlier and are less persistent than the effects of N. Ivins and Bremmer (1965, cited in Harris, 1978) showed that tuber bulking rates increased with increasing leaf area.

Dyson and Watson (1971, cited in Harris 1978) reported that potato yield is closely related to leaf area duration (D) and leaf area index (LAI) during the growth period of the crop. Tuber yields depend in part on the total leaf area (estimated by LAI) produced and the interval of time between tuber initiation and leaf senescence. It has been repeatedly shown that high levels of N prolong the life of the leaves while P has the opposite effect of shortening it (Harris, 1978). Tuber yields are thus increased because application of high levels of N or P increase net photosynthesis by either increasing the size of the leaf system or by prolonging the life of leaves or both.

ROLE OF SOIL NUTRIENTS AND NEMATICIDES ON S. TUBEROSUM AND P. PENETRANS

In 1978 and 1979, studies were conducted to examine the influence of selected production management inputs on the growth, development and yield of S. tuberosum and the population dynamics of P. penetrans. Each experiment during both years consisted of three fertilizer levels and three insecticides and nematicide treatments. In 1978, S. tuberosum (cv Superior) were used to evaluate the interaction of three nitrogen levels and three nematicide treatments. A second experiment in 1978 examined two nitrogen levels and five nematicide treatments (Appendix A). In 1979, S. tuberosum (cv Superior and Russet Burbank) were used to evaluate the interaction of three phosphorus levels and three nematicide treatments.

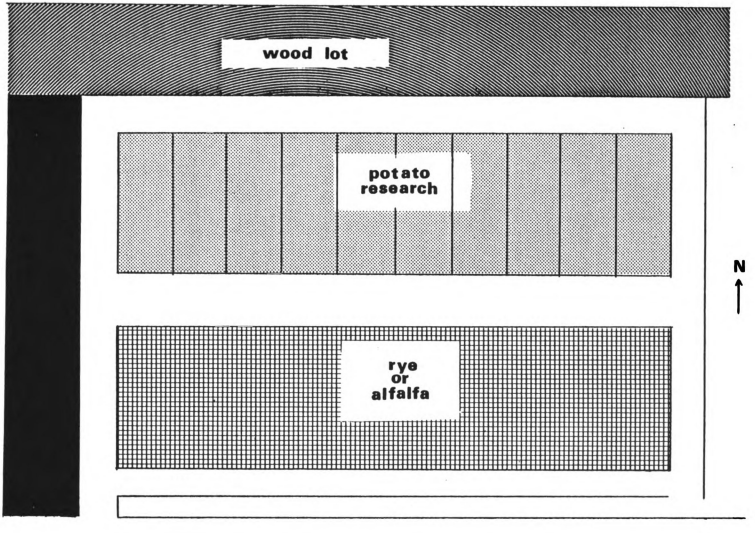

Figure 3. Plot design of the Montcalm Potato Research Farm, Entrican, Michigan.

MATERIALS AND METHODS

Field experiments were conducted in 1978 and 1979 to evaluate the role of soil nutrients and nematicides on the growth of S. tuberosum and the population dynamics of P. penetrans. Two potato cultivars (Superior and Russet Burbank) were grown on a McBride sandy loam soil (alfic fragiothods) at the Montcalm Potato Research Farm in Entrican, Michigan. The farm is separated into two large north-south rectangular blocks (Fig. 3). During any year, one block is utilized for current experimental research while the other block is spring planted to rye or alfalfa. The following spring it is planted. Blocks are rotated every other year to enhance soil organic content and to reduce populations of soil borne organisms and insects detrimental to S. tuberosum.

Planting Procedure

Each year, seed beds were prepared by disking the field plots to break the soil and to cut the rye or alfalfa. The field was then plowed and planted with a 2-row Lockwood potato planter. Seedpieces (whole certified seed, $\geq$ 5 cm diameter) were planted on May 22 and 23, 1978, and May 16 and 17, 1979. Each plot consisted of four rows 0.86 m wide and 15.24 m long. Seed spacing was 20 cm for Superior and 30 cm for Russet Burbank. All plots were irrigated with a solid set sprinkler system according to need determined by measurements of evapotranspiration.

Sampling Procedure

Plant growth and development was measured at various intervals during 1978 and 1979. The experimental area was first divided into 5 blocks of equal

size to compare sampling variation within and between treatments. In sampling foliage, two plants were randomly selected from the outside rows of each plot. The soil immediately below each plant was carefully removed to a depth of ca. 0.35 m. In 1978, the soil directly below each plant sample was hand-sifted for roots and tubers. In 1979, it was sifted through a series of sieves in a hand-driven mechanical shaker. Soil and plant material was first passed through a 0.95 cm hardware cloth and then through 0.31 cm hardware cloth. Roots and tubers removed from both screens were bagged and returned to the laboratory with the foliage and a representative soil sample of 1000 cm^3. Tuber numbers were also determined at this time for each treatment and sampling period.

Soil and root populations of P. penetrans were estimated from samples taken at these times. Nematode extraction techniques for both soil and roots were the same for both 1978 and 1979. Soil samples for nematode analysis were taken by core sampling (15-20 cores) the two outside rows of each plot and later, after plant germination, by removing the soil adjacent to the roots of the plant. Root samples were derived from plants returned to the laboratory for plant growth analysis. Soil and root populations of P. penetrans were determined using the centrifugation-flotation technique (Jenkins, 1964) and shaker technique (Bird, 1971), respectively. Estimates of soil and root nematode population densities were based on 10 cm^3 of soil and 0.1 gram of root in 1978, and 100 cm^3 of soil and one gram of root in 1979. The quantitative differences in the quantities of soil and root material used for estimating population densities of P. penetrans in each of the two years were determined by economic and time constraints. In 1978 the time and labor required to process nematode samples was not available and estimates were based on the smaller root and soil samples. At various intervals during the 1978

season, both the 10 and 100 cm^3 and 0.1 and 1.0 gram soil and root samples were processed to compare the efficiency and reliability of the estimates achieved by both methods. This was achieved first by agitating the 10 ml vial of nematode suspension and extracting 1.0 ml with a 1.0 ml syringe. Nematodes were counted in a circular petri dish under a 15X dissecting microscope. Immediately afterward, the remaining 9.0 ml of nematode suspension was counted and recorded.

Harvesting Procedure

Tuber yields were calculated from the harvest of the two center rows of each plot with a self-propelled potato harvester specifically developed for field research (Chase et al., 1978). Tubers from each plot were graded, weighed and bulk lots brought to the laboratory for specific gravity determinations. Specific gravity was determined after weighing the bulk samples in air and then in water and applying these data to the equation:

S.G. = (wt. in air) / (wt. in air - wt. in water)

A completely random block-two factorial design was used, with each treatment replicated five times. The data were subjected to an analysis of variance to statistically examine differences in plant growth, development, yield and nematode control.

Nitrogen

Two experiments were established in 1978 to examine nitrogen levels and their interactions with selected insect and nematode control programs, and to monitor growth, development and yield.

In the first experiment (Table 1), cv Superior was evaluated at three

nitrogen rates (84, 168 and 336 kg/ha) and three pesticide treatments (control, aldicarb (Temik 15G), and 1,3-D + MIC (Vorlex)). All plots received 84 kg/ha of N, P_2O_5 and K_2O (15-15-15) as a starter fertilizer banded 5 cm to the side and below the seed piece. The plots to receive an added nitrogen treatment were side-dressed with urea (45% N) at an application rate of 112 kg/ha on June 13, 1978, and either 84 kg/ha or 140 kg/ha on June 22, 1978.

Phosphorus

Two experiments were established in 1979 to examine varying phosphorus levels and their interactions with selected insect and nematode control programs and to monitor growth, development and yield. In the first experiment, seed pieces (cv Superior) were planted in plots treated with three levels of phosphorus (0, 56 and 168 kg/ha) and three pesticides (control, aldicarb and 1,3-D + MIC). In the second experiment, seed pieces (cv Russet Burbank) were planted in plots receiving treatments identical to those in experiment one. In each experiment, those plots to receive phosphorus were supplied with either 56 or 168 kg/ha P_2O_5 at planting. The rows in each plot were hilled and side-dressed at a rate of 162 kg/ha urea (45% N) on June 20, 1979.

The controls in each experiment, during both years, received no soil pesticides; however, the foliar insecticide Methamidophos (Monitor 10G) was used as needed throughout the entire experiment to minimize the impact of foliar-feeding insects. The soil-applied pesticides, except 1,3-D + MIC, were applied at planting in the fertilizer furrow at a rate of 3.4 kg/ha active ingredient. The 1,3-D + MIC was injected on a broadcast basis to a soil depth of 20 cm at the rate of 93.5 kg/ha on May 3, 1978, and on May 1, 1979.

RESULTS

Nitrogen

Both nitrogen and nematicides influence final tuber yields of S. tuberosum (Table 1). In the absence of a nematicide, the higher two rates of nitrogen had no significant (P=0.5) influence on tuber yield. In the presence of 1,3-D & MIC or aldicarb, increasing rates of nitrogen resulted in significant (P=0.05) increases in final tuber yield. Total yield from plots treated with either aldicarb or 1,3-D & MIC were significantly (P=0.05) higher than that of the controls. Highest total yields were observed in the 336 kg/ha nitrogen plots with aldicarb and 1,3-D & MIC.

Medium size A tuber (5-8 cm diameter) yield showed similar results to that of total yield (Table 1). Aldicarb and 1,3-D & MIC with nitrogen rates above 168 kg/ha significantly (P=0.05) increased the yield of A size tubers. Both aldicarb and 1,3-D & MIC at the 84 kg/ha nitrogen significantly (P=0.05) increased the small B size tuber (> 5 cm diameter) yield compared to the 1,3-D & MIC treatments at the 336 kg/ha and 168 kg/ha nitrogen rates. Aldicarb at the highest nitrogen rate resulted in the greatest yield of large tubers (> 8 cm diameter (Table 1)). This was significantly (P=0.05) greater than any treatment at the 84 kg/ha nitrogen rate.

Nitrogen fertilizer had no detectable effect on nematode population dynamics (Tables 2, 3). There were no significant (P=0.05) differences in soil population densities of P. penetrans among the plots until the August 1, 1978, sample (Table 2). From August 1, 1978, to harvest on August 21, 1978, soil population densities of P. penetrans were significantly (P=0.05) lower in the aldicarb-treated plots. Based on P. penetrans recovered from root tissue, both

Table 1. TUBER YIELD - Influence of selected management inputs on the yield and grade of S. tuberosum (cv Superior).

Treatment		Tuber yield (quintal/ha)			
Nitrogen (kg/ha)	Pesticide	5-8 cm	<5 cm	>8 cm	Total
84	Check	266.1 a[1]	10.5 ab	5.4 a	285.4 a
84	Aldicarb[2]	332.1 bc	13.6 b	5.2 a	335.2 bc
84	1,3-D & MIC[3]	316.4 c	13.1 b	5.5 a	349.3 c
168	Check	295.0 ab	8.6 a	9.1 ab	309.7 abc
168	Aldicarb	358.1 d	11.8 ab	12.8 ab	381.8 d
168	1,3-D & MIC	379.8 d	9.0 a	12.1 ab	398.7 d
336	Check	281.8 ab	10.0 ab	7.3 a	300.1 ab
336	Aldicarb	378.0 d	10.5 ab	28.2 b	416.1 d
336	1,3-D & MIC	375.8 d	8.0 a	26.0 ab	409.6 d

[1]Column means followed by the same letter are not significantly different (P=0.05) according to the Student-Newman-Keuls Multiple Range Test.

[2]Applied at planting in the fertilizer furrow at a rate of 3.4 kg a.i./ha.

[3]Injected on a broadcast basis to a soil depth of 20 cm at the rate of 93.5 l/ha on May 1, 1978.

Table 2. SOIL POPULATION - Influence of selected management inputs on soil populations of P. penetrans on S. tuberosum (cv Superior).

Treatment		P. penetrans per 10 cm^3 soil[4]					
Nitrogen (kg/ha)	Pesticide	139.2	241.2	373.5	543.8	768.0	983.3
84	Check	1.4 a[1]	0.6 a	1.2 a	2.0 a	4.4 d	1.6 abc
84	Aldicarb[2]	0.6 a	0.4 a	0.8 a	0.0 a	0.0 a	0.4 ab
84	1,3-D & MIC[3]	1.0 a	0.2 a	1.4 a	2.4 a	0.4 ab	1.8 ab
168	Check	2.4 a	0.6 a	0.8 a	3.4 a	2.0 bc	6.8 c
168	Aldicarb	1.2 a	0.4 a	0.4 a	0.4 a	0.0 a	0.0 a
168	1.3-D & MIC	2.4 a	0.0 a	0.4 a	0.6 a	0.4 ab	1.0 ab
336	Check	2.2 a	0.8 a	1.0 a	2.0 a	3.2 cd	3.8 bc
336	Aldicarb	2.4 a	0.2 a	0.0 a	0.6 a	0.0 a	0.2 a
336	1.3-D & MIC	1.2 a	0.0 a	0.4 a	0.2 a	0.6 ab	2.6 abc

[1]Column means followed by the same letter are not significantly different (P=0.05) according to the Student-Newman-Keuls Multiple Range Test.

[2]Applied at planting in the fertilizer furrow at a rate of 3.4 kg a.i./ha.

[3]Injected on a broadcast basis to a soil depth of 20 cm at the rate of 93.5 l/ha on May 1, 1978.

[4]Degree day accumulation base 10 C.

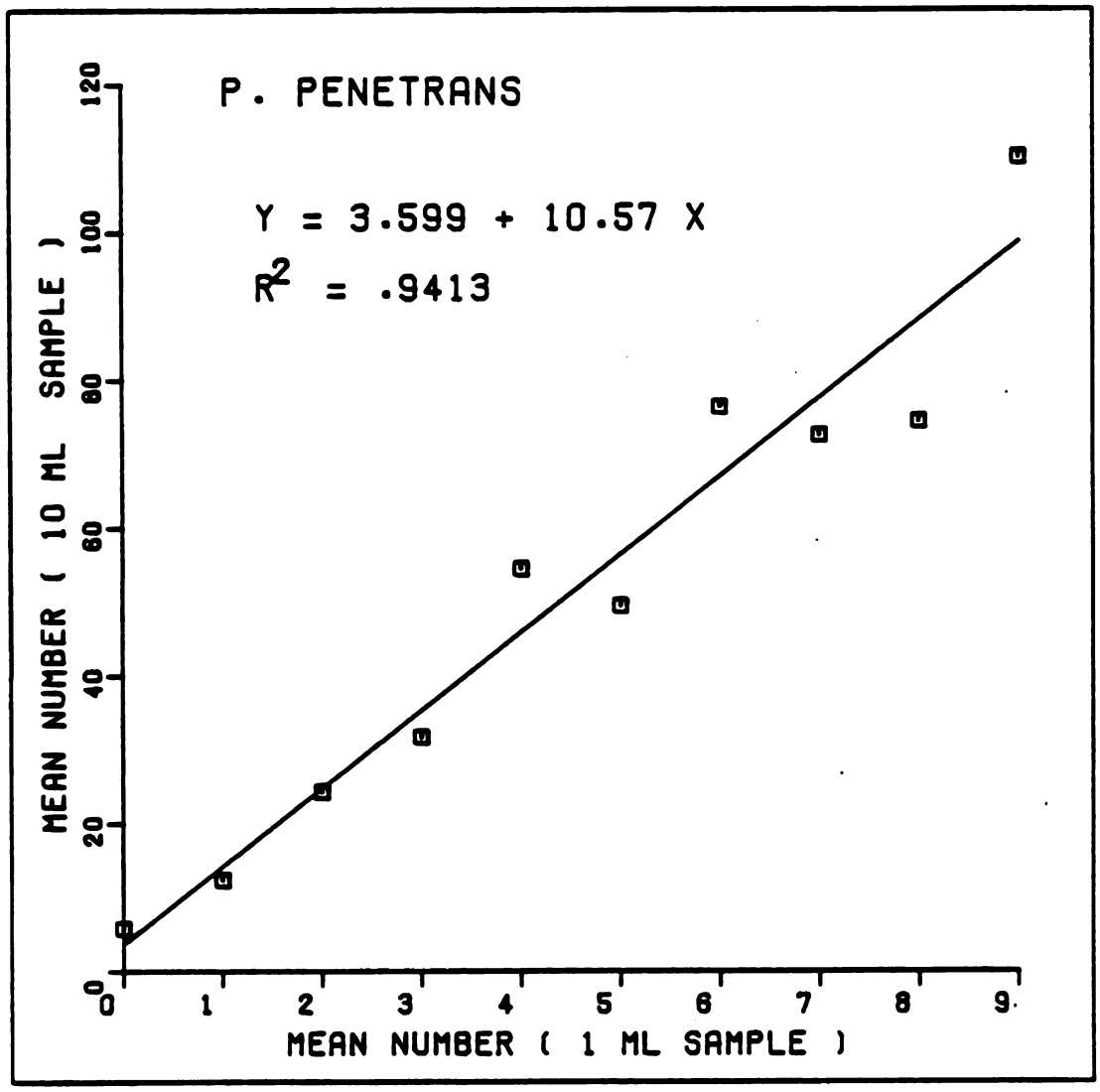

Figure 4. Relationship between the number of P. penetrans observed in 10.0 ml post-extraction sample and a corresponding 1.0 ml subsample.

aldicarb and 1,3-D & MIC reduced population densities of P. penetrans (Table 3). Aldicarb resulted in the best season-long nematode control.

Least squares linear regression analysis was performed on the mean population density estimates obtained from the 1.0 ml subsample and the corresponding 10.0 ml samples. The following significant relationship was obtained.

$$Y = 3.599 + 10.57 X$$

$$r^2 = 0.9413$$

where: Y = mean number of P. penetrans per 10.0 ml sample

X = mean number of P. penetrans per 1.0 ml sample

A plot of these data (Fig. 4) shows a highly significant (P=0.01) positive linear correlation of 0.9702. As the mean number of P. penetrans increased in the 1.0 ml subsample, so did the corresponding mean number of P. penetrans observed in the 10.0 ml sample.

When the data are examined within sample dates, few significant (P=0.05) differences were detected in root, tuber, foliage or total plant fresh weights (Appendix B). Plant fresh weight, however, generally increased with increasing nitrogen and in combination with nematicides. Assuming additive treatment effects, significant (P=0.05) differences were observed for foliage, tuber and total plant fresh weights averaged over the entire sample period for the respective plant parameter. In the presence of 1,3-D & MIC or aldicarb, increasing rates of nitrogen resulted in significant (P=0.05) increases in average seasonal foliage fresh weight (Table 4). These same trends were also observed in the average seasonal tuber and total plant fresh weights (Table 4). No significant (P=0.05) differences in average seasonal root fresh weight were detected (Table 4).

Table 3. ROOT POPULATION - Influence of selected management inputs or root populations of *P. penetrans* on *S. tuberosum* (cv Superior).

Treatment		*P. penetrans* per 0.1 g root tissue[4]			
Nitrogen (kg/ha)	Pesticide	373.5	543.8	768.0	983.3
84	Check	6.8 c[1]	8.8 ab	10.0 cd	3.0 bc
84	Aldicarb[2]	0.0 a	0.0 a	0.0 a	0.6 abc
84	1,3-D & MIC[3]	1.2 a	1.0 a	1.6 ab	3.4 abc
168	Check	6.2 bc	7.0 b	15.8 d	3.2 abc
168	Aldicarb	0.8 a	0.2 a	0.0 a	0.4 ab
168	1.3-D & MIC	1.6 ab	1.8 a	3.6 bc	2.0 abc
336	Check	5.8 bc	10.2 b	10.0 cd	4.2 c
336	Aldicarb	1.6 a	0.4 a	4.8 ab	0.0 a
336	1,3-D & MIC	0.8 a	1.2 a	4.0 bc	1.0 abc

[1]Column means followed by the same letter are not significantly different (P=0.05) according to the Student-Newman-Keuls Multiple Range Test.

[2]Applied at planting in the fertilizer furrow at a rate of 3.4 kg a.i./ha.

[3]Injected on a broadcast basis to a soil depth of 20 cm at the rate of 93.5 l/ha on May 1, 1978.

[4]Degree day accumulation base 10 C.

Table 4. Influence of nitrogen fertilizer and nematicide on average seasonal root, foliage, tuber and plant fresh weight of S. tuberosum (cv Superior).

Treatment		Average Seasonal Fresh Wt. (Grams)			
Nitrogen (kg/ha)	Pesticide	Root	Foliage	Tuber	Plant
84	Check	7.3 a[1]	260.1 a	383.5 ab	666.0 ab
84	Aldicarb[2]	7.0 a	335.6 a	392.9 ab	738.4 abc
84	1.3-D & MIC[3]	6.9 a	365.1 bc	468.5 bc	827.2 cd
168	Check	7.0 a	294.7 ab	419.4 abc	700.4 abc
168	Aldicarb	6.9 a	360.2 bc	387.7 ab	799.1 bcd
168	1,3-D & MIC	6.8 a	389.1 bc	437.1 abc	794.1 bcd
336	Check	7.8 a	261.7 a	345.5 a	625.1 a
336	Aldicarb	7.5 a	369.3 bc	386.3 ab	793.0 bcd
336	1,3-D & MIC	7.7 a	424.8 c	480.0 c	889.5 d

[1]Column means followed by the same letter are not significantly different (P=0.05) according to the Student-Newman-Keuls Multiple Range Test.

[2]Applied at planting in the fertilizer furrow at a rate of 3.4 kg a.i./ha.

[3]Injected on a broadcast basis to a soil depth of 20 cm at the rate of 93.5 l/ha on May 1, 1978.

Phosphorus

In the phosphorus experiment with cv Superior, application rate and nematicide treatment significantly (P=0.05) increased final yield (Table 5). Regardless of the pesticide used, yields were higher at the higher phosphorus rate (Table 5). Within each phosphorus level, total yields increased consistently from the controls, to the aldicarb and 1,3-D & MIC treated plots, respectively. The total yield of plots treated with 1,3-D & MIC were significantly (P=0.05) higher than the controls at the 0 kg/ha and 56 kg/ha phosphorus rates. Highest total yields were observed in the 168 kg/ha phosphorus plots with aldicarb and 1,3-D & MIC. Yields of medium size A potatoes (5-8 cm diameter) showed similar results to that of total yield (Table 5). No significant differences in yields of B size tubers (< 5 cm diameter) were observed. Yields of the oversize 'Jumbo' grade potatoes (> 8 cm diameter) increased with increasing phosphorus rate in the controls and aldicarb-treated plots. Both aldicarb at the 168 kg/ha phosphorus rate and 1,3-D & MIC at the 56 kg/ha and 168 kg/ha phosphorus rates significantly (P=0.05) increased yields over the controls and the 0 kg/ha phosphorus plots. The control at the 168 kg/ha phosphorus rate and 1,3-D & MIC at the two highest phosphorus rates significantly (P=0.05) increased the specific gravity of potatoes over the aldicarb plots at the 56 kg/ha phosphorus rate (Table 6).

Phosphorus fertilization had no detectable affect on nematode population dynamics. There were no significant (P=0.05) differences in soil population densities of P. penetrans among the plots except for the sample of June 26, 1979 (DD_{10C}=442.7)(Table 7). Aldicarb significantly (P=0.05) reduced the soil population density of P. penetrans over the controls and 1,3-D & MIC treatments in the 0 kg/ha phosphorus plots. There were no significant (P=0.05)

Table 5. TUBER YIELD - Influence of selected management inputs on the yield of Solanum tuberosum (cv Superior).

Treatment		Tuber yield (quintal/ha)			
Phosphorus (kg/ha)	Pesticide	5-8 cm	< 5 cm	> 8 cm	Total
0	Check	240.8 a[1]	12.2 a	11.7 a	265.1 a
0	Aldicarb[2]	277.2 ab	14.7 a	22.4 ab	314.3 ab
0	1,3-D & MIC[3]	310.8 bc	16.6 a	25.3 abc	352.6 bc
56	Check	277.4 ab	11.8 a	16.8 ab	306.1 ab
56	Aldicarb	310.0 bc	12.5 a	32.1 bcd	354.7 bc
56	1,3-D & MIC	333.9 c	14.2 a	42.7 d	390.8 c
168	Check	316.6 bc	13.0 a	21.7 ab	351.3 bc
168	Aldicarb	353.6 c	13.3 a	40.8 cd	407.8 c
168	1,3-D & MIC	363.6 c	13.8 a	33.5 bcd	410.7 c

[1]Column means followed by the same letter are not significantly different (P=0.05) according to the Student-Newman-Keuls Multiple Range Test.

[2]Applied at planting in the fertilizer furrow at a rate of 3.4 kg a.i./ha.

[3]Injected on a broadcast basis to a soil depth of 20 cm at the rate of 93.5 l/ha on May 1, 1979.

Table 6. SPECIFIC GRAVITY - Influence of selected management inputs on specific gravity of Solanum tuberosum.

Treatment			
Phosphorus (kg/ha)	Pesticide	Russet Burbank	Superior
0	Check	1.068 a[1]	1.066 ab
0	Aldicarb[2]	1.070 a	1.066 ab
0	1,3-D & MIC[3]	1.072 a	1.067 ab
56	Check	1.069 a	1.066 ab
56	Aldicarb	1.070 a	1.065 a
56	1,3-d & MIC	1.072 a	1.068 b
168	Check	1.072 a	1.068 b
168	Aldicarb	1.072 a	1.066 ab
168	1,3-D & MIC	1.077 b	1.068 b

[1]Column means followed by the same letter are not significantly different (P=0.05) according to the Student-Newman-Keuls Multiple Range Test.

[2]Applied at planting in the fertilizer furrow at a rate of 3.4 kg a.i./ha.

[3]Injected on a broadcast basis to a soil depth of 20 cm at the rate of 93.5 l/ha on May 1, 1979.

Table 7. Influence of selected management inputs on soil population densities of P. penetrans on S. tuberosum (cv Superior).

Treatment		P. penetrans per 100 cm^3 soil[4]					
Phosphorus (kg/ha)	Pesticide)	46.6	212.3	233.7	442.7	723.2	995.5
0	Check	28.2 a[1]	41.0 a	20.6 a	19.6 b	78.2 a	39.0 a
0	Aldicarb	30.4 a	36.0 a	17.4 a	2.0 a	85.0 a	2.6 a
0	1,3-d & MIC	34.8 a	30.3 a	16.2 a	15.6 b	79.0 a	39.0 a
56	Check	42.4 a	39.2 a	20.2 a	12.4 ab	120.8 a	55.6 a
56	Aldicarb	23.0 a	24.0 a	9.6 a	3.0 a	23.6 a	4.2 a
56	1,3-D & MIC	29.6 a	16.0 a	18.4 a	8.2 ab	12.6 a	53.2 a
168	Check	54.6 a	50.0 a	19.4 a	20.6 b	80.4 a	40.6 a
168	Aldicarb	42.0 a	36.8 a	12.0 a	2.8 a	25.8 a	8.4 a
168	1,3-D & MIC	32.0 a	13.8 a	14.8 a	10.6 ab	119.8 a	41.0 a

[1]Column means followed by the same letter are not significantly different (P=0.05) according to the Student-Newman-Keuls Multiple Range Test.

[2]Applied at planting in the fertilizer furrow at a rate of 3.4 kg a.i./ha.

[3]Injected on a broadcast basis to a soil depth of 20 cm at the rate of 93.5 l/ha on May 1, 1979.

[4]Degree day accumulation base 10 C.

differences in root population densities of P. penetrans among the plots season-long (Table 8). Based on P. penetrans recovered from root tissue in this test, aldicarb resulted in the best nematode control.

There were no significant (P=0.05) differences in root, tuber or total plant fresh weight or tuber number among the treatments season-long (Appendix C). Foliage fresh weights were generally higher within the 1,3-D & MIC or aldicarb treatments at the two highest phosphorus rates. When the fresh weights are averaged over the entire sampling season, no significant (P=0.05) differences in root, foliage, tuber or total plant fresh weights were detected between treatments (Table 9).

In the phosphorus experiment with cv Russet Burbank, application rate and nematicide treatment contributed significantly (P=0.05) to final yield (Table 10). Regardless of the pesticide used, yields were generally higher at the phosphorus rate. The 1,3-D & MIC at the two highest phosphorus rates significantly (P=0.05) increased total yield when compared to the controls at the 0 kg/ha and 56 kg/ha phosphorus rate and the 0 kg/ha aldicarb plots. Yield of large size potatoes (> 8 cm diameter) increased with increasing phosphorus, and was highest in the 1,3-D & MIC treated plots (Table 10). Within each phosphorus level, yields increased consistently from the controls to the aldicarb and 1,3-D & MIC treated plots, respectively. The 1,3-D & MIC at the 168 kg/ha phosphorus level significantly (P=0.05) increased the yield of large size tubers. The yield of small B size tubers (> 5 cm diameter) was significantly (P=0.05) greater in the 56 kg/ha phosphorus control plots than in the control plots than in the control treatments at the lower phosphorus level. Regardless of the phosphorus rate, yield of A size potatoes (5-8 cm diameter) was highest in the 1,3-D & MIC treated plots (Table 10). Yield of A size potatoes was

Table 8. Influence of selected management inputs on root population densities of P. penetrans on S. tuberosum (cv Superior).

Treatment		P. penetrans per gram root tissue[4]			
Phosphorus (kg/ha)	Pesticide	233.7	442.7	723.2	995.5
0	Check	19.2 a[1]	56.2 a	178.2 a	94.6 a
0	Aldicarb[2]	2.6 a	11.0 a	6.4 a	6.0 a
0	1,3-D & MIC[3]	15.4 a	20.0 a	206.0 a	74.0 a
56	Check	18.6 a	24.2 a	205.2 a	181.6 a
56	Aldicarb	7.0 a	14.0 a	5.6 a	25.2 a
56	1,3-D & MIC	16.2 a	17.0 a	149.4 a	150.6 a
168	Check	24.6 a	36.0 a	175.0 a	213.8 a
168	Aldicarb	2.8 a	10.8 a	9.0 a	5.6 a
168	1,3-D & MIC	8.8 a	19.2 a	173.2 a	148.2 a

[1]Column means followed by the same letter are not significantly different (P=0.05) according to the Student-Newman-Keuls Multiple Range Test.

[2]Applied at planting in the fertilizer furrow at a rate of 3.4 kg a.i./ha.

[3]Injected on a broadcast basis to a soil depth of 20 cm at the rate of 93.5 l/ha on May 1, 1979.

[4]Degree day accumulation base 10 C.

Table 9. Influence of phosphorus fertilizer and nematicide on average seasonal root, foliage, tuber and plant fresh weight of S. tuberosum (cv Superior).

Treatment		Average seasonal fresh wt. (Grams)			
Phosphorus (kg/ha)	Pesticide	Root	Foliage	Tuber	Plant
0	Check	10.8 a	77.5 a	305.4 a	414.3 a
0	Aldicarb	11.0 a	107.6 a	344.6 a	482.8 a
0	1,3-D & MIC	10.5 a	84.7 a	367.7 a	484.3 a
56	Check	12.5 a	85.1 a	329.8 a	448.5 a
56	Aldicarb	10.3 a	79.5 a	381.9 a	493.5 a
56	1,3-D & MIC	10.4 a	115.3 a	411.8 a	556.4 a
168	Check	10.3 a	92.4 a	358.2 a	481.7 a
168	Aldicarb	10.7 a	123.6 a	400.4 a	558.3 a
168	1,3-D & MIC	10.4 a	120.6 a	443.0 a	595.1 a

[1]Columns followed by the same letter are not significantly different (P=0.05) according to the Student-Newman-Keuls Multiple Range Test.

[2]Applied at plant in the fertilizer furrow at a rate of 3.4 kg a.i./ha.

[3]Injected on a broadcast basis to a soil depth of 20 cm at the rate of 93.5 l/ha on May 1, 1979.

Table 10. TUBER YIELD - Influence of selected management inputs on the tuber yield of S. tuberosum (cv Russet Burbank).

Treatment		Tuber yield (quintal/ha)				
Phosphorus (kg/ha)	Pesticide	5-8 cm	< 5 cm	> 8 cm	Misshapen	Total
0	Check	204.9 a[1]	25.2 a	2.5 a	27.2 a	259.7 a
0	Aldicarb[2]	219.7 ab	27.4 ab	3.8 ab	49.6 bc	300.7 ab
0	1,3-D & MIC[3]	278.7 bc	27.1 ab	6.3 ab	34.9 ab	346.9 bc
56	Check	240.2 abc	35.1 b	8.3 ab	29.9 ab	313.5 b
56	Aldicarb	244.1 abc	26.1 ab	8.5 ab	58.5 c	337.1 bc
56	1,3-D & MIC	302.7 c	30.0 ab	13.0 b	42.6 abc	388.3 c
168	Check	284.0 bc	33.4 ab	9.4 ab	34.6 ab	361.3 bc
168	Aldicarb	234.9 ab	28.3 ab	11.7 ab	72.6 d	347.4 bc
168	1,3-D & MIC	299.5 c	28.3 ab	21.2 c	34.6 ab	383.5 c

[1]Columns followed by the same letter are not significantly different (P=0.05) according to the Student-Newman-Keuls Multiple Range Test.

[2]Applied at plant in the fertilizer furrow at a rate of 3.4 kg a.i./ha.

[3]Injected on a broadcast basis to a soil depth of 20 cm at the rate of 93.5 l/ha on May 1, 1979.

significantly (P=0.05) increased with 1,3-D & MIC at phosphorus rates above 56 kg/ha over the control and aldicarb plots at 0 kg/ha. The yield of misshapen grade tubers generally increased with increasing phosphorus and were highest in the aldicarb and 1,3-D & MIC treatments. Yields of misshapen tubers were significantly (P=0.05) increased by aldicarb at the 168 kg/ha phosphorus rate. The 1,3-D & MIC at the 168 kg/ha phosphorus rate significantly (P=0.05) increased the specific gravity of Russet Burbank potatoes (Table 6).

Regardless of the phosphorus level, soil population levels of P. penetrans were consistently lower in the aldicarb plots season-long (Table 11). During the June 26, 1979 (DD_{10C}=442.7) sample, aldicarb significantly (P=0.05) reduced soil population densities of P. penetrans at all phosphorus rates when compared to the control treatments at the 168 kg/ha phosphorus rate. Based on P. penetrans recovered from root tissue in this test, aldicarb resulted in the best nematode control (Table 12).

There were no significant (P=0.05) differences in root or tuber fresh weights or tuber number season-long (Appendix D). Total plant fresh weight was higher in all nematicide-treated plots. Foliage fresh weight was generally higher at the higher phosphorus rate and in combination with either nematicide. Phosphorus and nematicide directly influence average seasonal fresh weights (Table 13). In the presence of 1,3-D & MIC or aldicarb, increasing rates of phosphorus resulted in significant (P=0.05) increases in average seasonal foliage, tuber and total plant fresh weights. No significant (P=0.05) differences in average seasonal root fresh weight were detected (Table 13).

Table 11. Influence of selected management inputs on soil population densities of *P. penetrans* on *S. tuberosum* (cv Russet Burbank).

Treatment		*P. penetrans* per 100 cm^3 soil[4]					
Phosphorus (kg/ha)	Pesticide	46.6	212.3	233.7	442.7	723.2	1155.9
0	Check	16.8 a[1]	39.0 ab	14.6 a	15.6 ab	40.2 a	57.0 bc
0	Aldicarb[2]	21.8 a	42.8 b	5.4 a	5.8 a	6.0 a	2.0 a
0	1,3-D&MIC[3]	23.6 a	18.2 ab	12.8 a	11.4 ab	37.6 a	45.2 abc
56	Check	15.8 a	37.8 ab	12.0 a	13.4 ab	37.0 a	32.8 abc
56	Aldicarb	13.4 a	32.8 ab	4.2 a	5.0 a	23.8 a	1.6 a
56	1,3-D & MIC	17.0 a	11.6 a	9.8 a	12.6 ab	11.8 a	32.8 abc
168	Check	21.2 a	29.2 ab	11.2 a	19.8 b	20.4 a	75.4 c
168	Aldicarb	25.6 a	36.6 ab	5.8 a	4.8 a	10.8 a	9.8 ab
168	1,3-D & MIC	28.6 a	10.8 a	14.0 a	12.8 ab	15.4 a	43.2 abc

[1]Columns followed by the same letter are not significantly different (P=0.05) according to the Student-Newman-Keuls Multiple Range Test.

[2]Applied at plant in the fertilizer furrow at a rate of 3.4 kg a.i./ha.

[3]Injected on a broadcast basis to a soil depth of 20 cm at the rate of 93.5 l/ha on May 1, 1979.

[4]Degree day accumulation base 10 C.

Table 12. Influence of selected management inputs on root population densities of P. penetrans on S. tuberosum (cv Russet Burbank).

Treatment		P. penetrans per gram root tissue[4]			
Phosphorus (kg/ha)	Pesticide	233.7	442.7	723.2	1155.9
0	Check	16.6 a[1]	47.0 ab	59.0 a	96.4 ab
0	Aldicarb[2]	2.2 a	10.6 a	3.0 a	5.0 a
0	1,3-D & MIC[3]	38.0 a	40.4 ab	64.8 a	134.8 b
56	Check	12.6 a	65.4 b	54.4 a	67.0 ab
56	Aldicarb	4.2 a	2.8 a	0.8 a	1.6 a
56	1,3-D & MIC	22.8 a	29.0 ab	49.0 a	94.6 ab
168	Check	18.2 a	22.0 ab	49.6 a	85.4 ab
168	Aldicarb	2.8 a	8.6 a	8.4 a	4.0 a
168	1,3-D & MIC	15.0 a	43.8 ab	58.0 a	109.0 b

[1]Columns followed by the same letter are not significantly different (P=0.05) according to the Student-Newman-Keuls Multiple Range Test.

[2]Applied at plant in the fertilizer furrow at a rate of 3.4 kg a.i./ha.

[3]Injected on a broadcast basis to a soil depth of 20 cm at the rate of 93.5 l/ha on May 1, 1979.

[4]Degree day accumulation base 10 C.

Table 13. Influence of phosphorus fertilizer and nematicide on average seasonal root, foliage, tuber and plant fresh weight of S. tuberosum (cv Russet Burbank).

Treatment		Average seasonal fresh wt. (Grams)			
Phosphorus (kg/ha)	Pesticide	Root	Foliage	Tuber	Plant
0	Check	14.1 a[1]	218.5 a	306.1 a	559.9 a
0	Aldicarb[2]	15.1 a	276.7 ab	355.7 ab	669.8 a
0	1,3-D & MIC[3]	15.3 a	333.7 abc	414.2 ab	787.9 ab
56	Check	14.7 a	284.6 a	356.8 ab	678.1 a
56	Aldicarb	16.1 a	366.5 abcd	363.5 ab	769.6 ab
56	1,3-D & MIC	16.2 a	469.8 cd	484.1 b	999.2 b
168	Check	14.8 a	387.8 bcd	379.4 ab	805.8 ab
168	Aldicarb	16.2 a	411.4 bcd	385.5 ab	836.1 ab
168	1,3-D & MIC	17.3 a	510.8 d	466.5 ab	1025.7 b

[1]Columns followed by the same letter are not significantly different (P=0.05) according to the Student-Newman-Keuls Multiple Range Test.

[2]Applied at plant in the fertilizer furrow at a rate of 3.4 kg a.i./ha.

[3]Injected on a broadcast basis to a soil depth of 20 cm at the rate of 93.5 l/ha on May 1, 1979.

DISCUSSION

The Role of Soil Nutrients and Nematicides on S. tuberosum and P. penetrans

The growth of S. tuberosum is limited by numerous abiotic and biotic factors. Many studies have demonstrated the importance of fertilizers in promoting S. tuberosum growth and optimization of tuber yield. Relatively little, however, is known about the influence of P. penetrans on growth, development and yield of S. tuberosum. Characterization of plant-nematode interactions is dependent on accurate assessment of the influence of various biotic and abiotic factors inherent in the nematode crop ecosystem and associated production management strategies. Knowledge of preplant nematode densities and the associated levels of control achieved with chemical pesticides is needed to understand the relationships governing fertilizer recommendations and plant and yield response. The development of future S. tuberosum production practices is dependent on identifying these relations.

Subtle changes in the growth and development of S. tuberosum associated with N or P fertilizer were directly related to differences in final tuber yield. Observations empirically derived showed that S. tuberosum grown at increased N or P levels accelerated early season foliar growth. This is partially reflected in the higher early season root, plant and foliage fresh weights. Plants at the higher rates of N and P also responded by an earlier abscission of the lower leaves. The leaf canopy developed sooner and, because of an adequate water and nutrient supply and a larger leaf system, were maintained longer and plant senescence delayed. P appeared to delay plant senescence which is contrary to what is commonly reported to occur (Harris, 1978). The change in nutrient

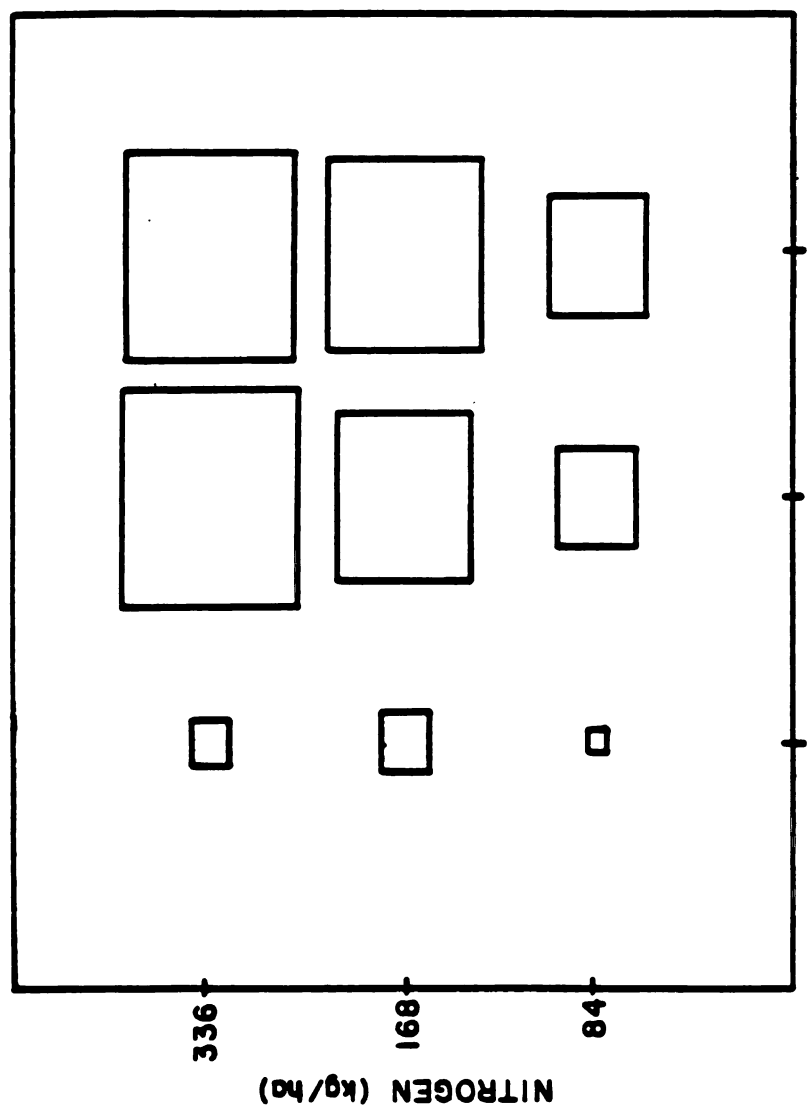

Figure 5. Influence of three rates of nitrogen and two pesticides on the final yield of S. tuberosum (cv Superior).

supply thus had its greatest affect on plant development by influencing leaf area and leaf area duration.

Vigorous early season foliar growth which occurred at the high levels of N and P did not appear to delay the initiation and development of tubers. Differences in the number and weights of tubers and the attainment of final tuber yield are usually associated with differences in the phenological development of the plant (Harris, 1978; Ivins and Milthorpe, 1963). Fertilizers exert their primary affect on yield by influencing the development and maintenance of leaf area. A delay in plant maturity, which is usually seen in plants which develop a larger leaf system during early developmental stages, usually results in a delay in tuber initiation and development. These observations of deviation from expected plant response to N and P may be attributed to plant variability or sampling error. The lack of a phenological response between N and P levels as they affect tuber development may have resulted from high residual nutrient levels in the soil. Further research needs to be conducted to elucidate these relationships.

The yield of S. tuberosum to increasing rates of nitrogen and edaphic pesticides was significantly increased. Yields increased with increasing levels of nitrogen, attaining higher yields at the greater rates (Fig. 5). Tuber yields also increased regardless of the pesticide used. Analysis of the 1978 data revealed that control of P. penetrans with either 1,3-D & MIC or aldicarb resulted in an increase in tuber set. Nitrogen then appeared to be limiting yield. As the nitrogen rate was increased, the small tubers increased in size. P. penetrans thus had its greatest affect on final yield in the alteration of the nitrogen requirements of the potato plant for maximizing yield.

Due to the Bray P_1 soil test results, little or no crop response was

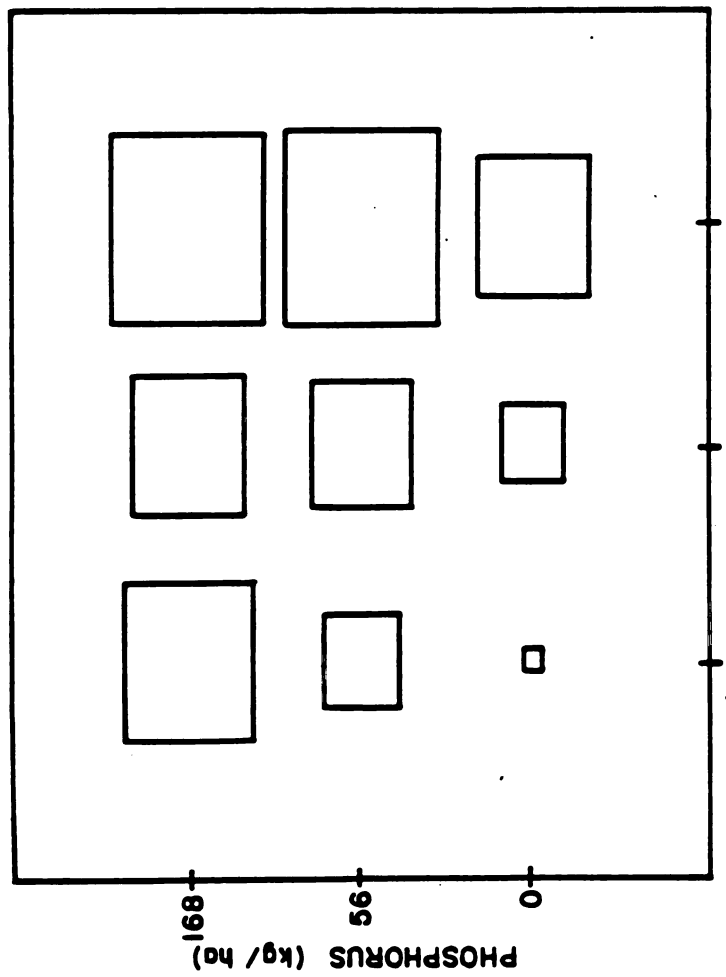

Figure 6. Influence of three rates of phosphorus and two pesticides on the final yield of S. tuberosum (cv Superior).

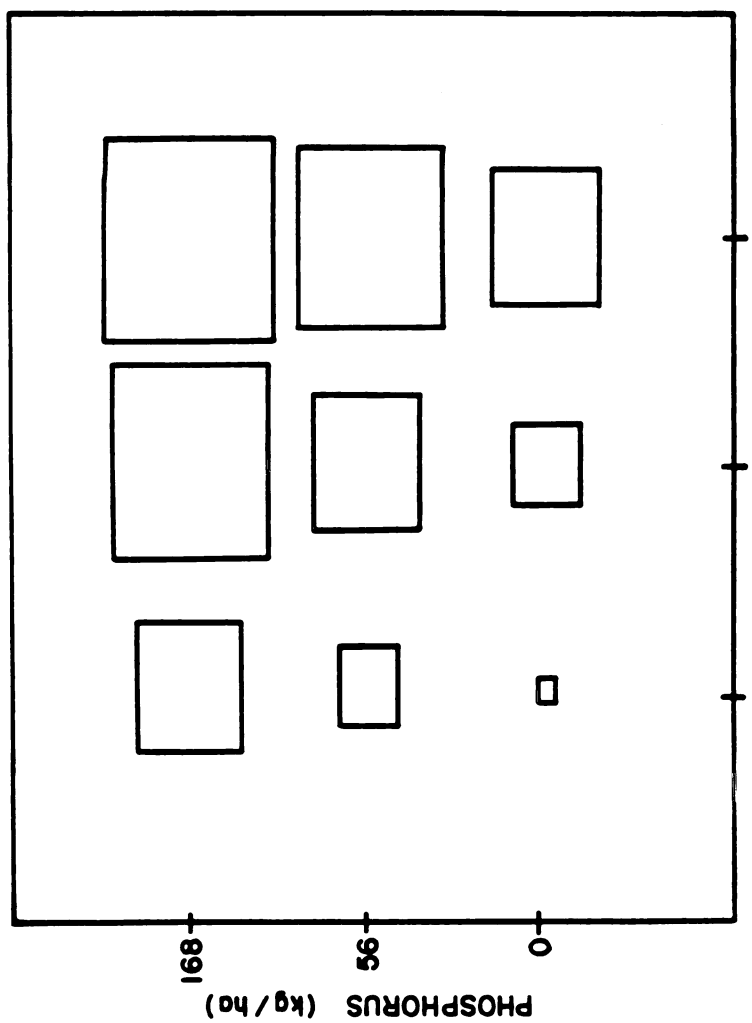

Figure 7. Influence of three rates of phosphorus and two pesticides on the final yield of S. tuberosum (cv Russet Burbank).

expected from soil with such high levels of available phosphorus (over 268 kg Bray soil phosphorus per hectare). Despite the high phosphorus residues in the soil, yield responses were significant from increasing the phosphorus application rate (Figs. 6, 7). Nelson and Hawkins (1947) have also reported significant yield responses from additional phosphorus even on soils high in accumulated phosphorus. It should be noted that other factors than an increase in final tuber yield need to be examined to justify increasing fertilizer recommendations. When cv Russet Burbank yields are examined, yield increases with increasing phosphorus are partially offset by increasing yields of misshapen tubers. A cost function taking into consideration fertilizer expense and an increase in unmarketable tubers must be considered in the economics of future production management practices involving fertilizer use.

Control of P. penetrans in 1979 did not appear to affect tuber set as it did in 1978, although significant yield increases did occur with edaphic pesticide use. The number of smaller tubers were generally higher at the lower P levels and increased in size with increasing P. The influence of P. penetrans on tuber set may need to be examined more closely in relation to pesticide and fertilizer use. Nematode control recommendations based on preplant population densities are dependent on it.

The roles of fungal diseases were not evaluated in these tests. Certain soil fumigants applied at specific rates control root diseases of S. tuberosum caused by fungi and plant parasitic nematodes (Cetas and Harrison, 1963; Miller and Hawkins, 1969). In addition to the fungicidal and nematicidal properties, many edaphic pesticides affect soil nutrient relations (Elliot et al., 1977; Winslow and Willis, 1972). This may explain why yields increased with 1,3-D & MIC even though control of P. penetrans did not appear to be achieved.

Knowledge of the population dynamics of P. penetrans and the associated host response is essential to the understanding of how P. penetrans influences plant growth and development. Assessing plant response and crop losses is dependent on reliable methods of monitoring P. penetrans populations, host plant responses and environmental factors which may modify these relationships. Plant pathogenicity can be measured by examining the deleterious affect of the abiotic or biotic factors on relative growth rate. In other cases, it has been measured in terms of plant growth reductions expressed by plant weight such as differences in root weight. It is questionable whether the techniques employed in these studies are sensitive enough to accurately measure and identify the small differences in plant growth (as expressed by plant weight) occurring between treatments. This may be due to the error involved in measuring plant biomass in units of plant fresh weight. It may also explain why so few significant differences in any of the plant growth parameters were observed during the season. The possibility does exist that insignificant differences in plant growth and development as measured by plant fresh weight can occur during the course of the season, additively culminating with significant differences in tuber yield.

The data collected on the plant and root systems do support the view that P. penetrans causes most of its damage by destroying or inhibiting the normal physiological function of the root system, rather than by significantly reducing root weight. This may explain the significant differences in yield with increasing N and P levels. A healthy nematode-free root system is required for optimal use of these elements and maximization of yield.

Plant response to nematode infection may also result in the formation of new roots to compensate for the roots destroyed. Thus, slow growth early in

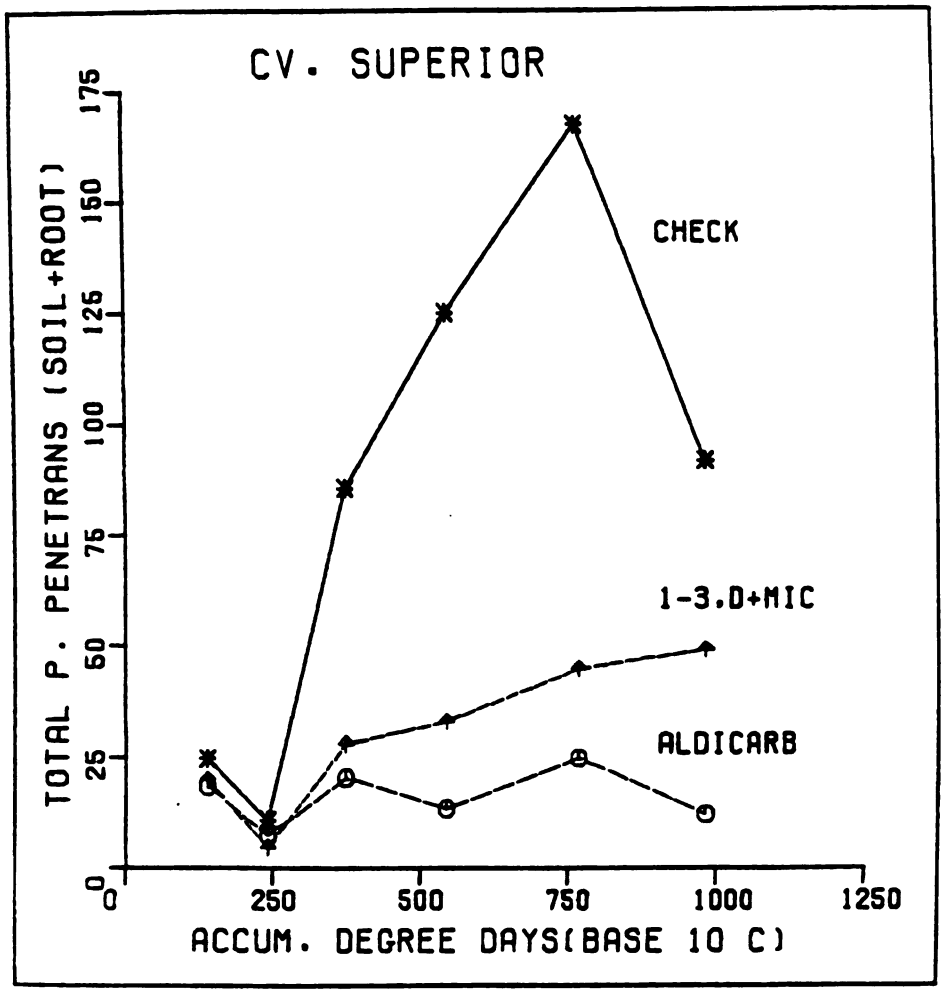

Figure 8. Influence of two edaphic pesticides on total (soil + root) population density of P. penetrans on S. tuberosum (cv Superior) (1978).

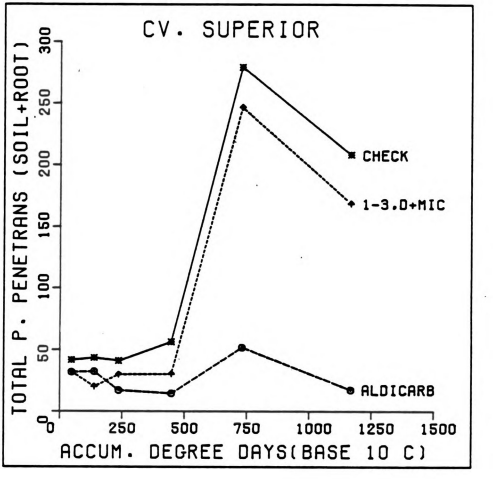

Figure 9. Influence of two edaphic pesticides on total (soil + root) population density of P. penetrans on S. tuberosum (cv Superior) (1979).

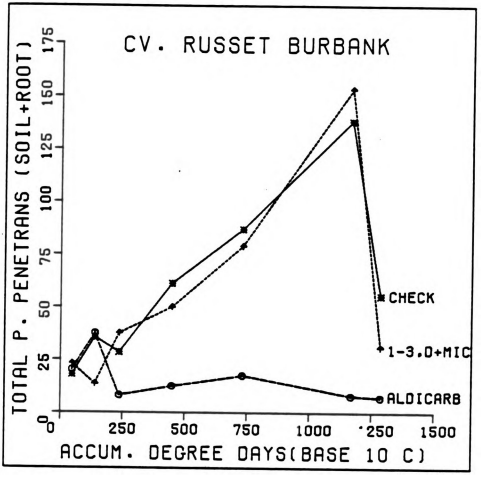

Figure 10. Influence of two edaphic pesticides on the total (soil + root) population density of P. penetrans on S. tuberosum (cv Russet Burbank) (1979).

the season and a delay in plant maturity due to prolonged vegetative growth may be more indicative of P. penetrans pathogenicity. It may also be that the initial soil and root population densities of P. penetrans observed in many of these field studies were at levels that the plant could tolerate and thus caused no detrimental affect on plant or root production. Differences in S. tuberosum susceptibility to P. penetrans has been demonstrated by Bird (1977) and Bernard and Laughlin (1976). Differences in varietal response of S. tuberosum to P. penetrans may need to be examined more closely in relation to other biotic and abiotic factors influencing plant growth, development and yield.

Chemical nematicides are used to reduce soil population densities of nematodes below plant damage thresholds. It is difficult to ascertain whether any of the nematicides used in these studies, with the exception of aldicarb, reduced soil populations of P. penetrans below the damage thresholds established for S. tuberosum in mineral soils. The concept of a universally acceptable damage threshold for S. tuberosum needs to be modified to take into consideration other factors such as Ferris (1980) has suggested. In light of the present studies, the static models of the past need to be examined more closely in relation to the influence of various abiotic and biotic factors on the dynamics of plant damage thresholds.

Significant reductions in population levels of P. penetrans were achieved with some of the edaphic pesticides evaluated in these studies. With the exception of aldicarb, final soil and root population densities of P. penetrans were higher than those observed at the beginning of the season (Figs. 8, 9, 10). In some cases, as with 1,3-D & MIC, a late season resurgence in population densities of P. penetrans was statistically indistinguishable from the controls. Only in the aldicarb-treated plots were final soil and root population levels

reduced below the initial population levels. The possibility of multi-year nematode control with this material is being evaluated by Bird et al. (1980).

The efficacy of edaphic pesticides evaluated in these studies was statistically insignificant in terms of nematode control because of considerable variability in the number of P. penetrans recovered from soil and roots within treatments. Variability in the rate and placement of edaphic pesticides may have contributed significantly to the variability in the number of nematodes observed. This could have contributed to the statistical insignificance declared in the analysis of soil and root population densities of P. penetrans. This was specially evident in the aldicarb treatments where abnormally large population densities of P. penetrans occasionally occurred. Nematode sampling is another source of experimental error that may have contributed to count variability, such as failing to obtain a representative soil or root sample from an underlying aggregated population from the soil or roots. Further research into these areas is therefore needed.

The linear relationship observed between the 1.0 ml subsample and the larger 10.0 ml sample showed that the subsample can be used to accurately and reliably estimate both soil and root population densities of P. penetrans. As the mean number of P. penetrans increased in the 1.0 ml subsample, so did the corresponding P. penetrans density observed in the 10.0 ml sample. The mean population densities of P. penetrans were used to formulate the relationship because seldom is one sample used to accurately estimate field population densities of plant parasitic nematodes.

The economics of nematode sampling prohibit large numbers of samples from being processed to estimate field population densities of most plant parasitic nematodes. Due to the aggregational characteristics of nematode

populations in soil and roots, smaller numbers of samples can result in gross errors of considerable magnitude toward estimating field population densities of nematodes. Conversely, greater numbers of samples will usually provide more accurate estimates of the true mean population density. Using the smaller subsample can allow a greater number of samples to be used to estimate soil and root densities of P. penetrans.

An examination of residuals of the individual observations showed that over 80% of the total variability between density estimates of the 1.0 ml subsample and the 10.0 ml sample occurred when fewer than 3.0 P. penetrans were observed per 1.0 ml subsample. If economic or damage threshold densities are small, as they are reported to be for P. penetrans (< 10 per 10.0 ml sample), the population estimates derived from the smaller 1.0 ml subsample may be of limited value. The relationship is applicable only to economic or damage thresholds where nematode densities are greater than 14 per 10.0 ml sample. At densities below this level, the subsample method cannot distinguish P. penetrans densities from zero. The technique may be more applicable to another commodity or variety where economic or damage thresholds are higher.

An analysis of variance was conducted on plant data derived from the following equation:

$$Y = \Sigma(X_{ijk}) / N$$

where: X = observed plant fresh weight

i = treatment number from 1 to i

j = block number 1 through j

k = sample period from 1 through k

N = number of sample periods

Y = average season treatment mean

It was assumed that the time in which plant samples were taken from each treatment will dictate to a major extent the quantitative level of the mean seasonal fresh weight. Any random combination of plant samples taken during the course of the season will produce a different mean seasonal fresh weight. Depending on the plant parameter, a greater frequency of plant samples occurring in the early stages of plant growth will bias the estimate and reduce the value of the seasonal mean. In contrast, a greater sample frequency during the later season when some plant parameters (e.g., tuber weight) are developing at maximal rates, will tend to bias the estimate by inflating the seasonal treatment mean. Unless a method is devised for weighting observation times between and within seasons, a comparison between treatment effects is difficult and has interpretational problems associated with it. If plants within treatments are sampled synchronously through the season, comparison of treatment effects can be made.

Temporal changes in the phenological development of S. tuberosum may obscure differences between treatments. If a treatment produces a shift in phenological development, treatment differences in seasonal fresh weight will tend to be small and not significant (P=0.05). Collapsing time within treatments will obscure these phenological relationships and declare insignificance between treatments. If, on the other hand, plant fresh weights between treatments is observed to be consistently higher or lower through time, then treatment differences are maximized in the final analysis and significance (P=0.05) between treatments declared. The significance implied by the analysis suggests that there are either significant shifts in the phenological development of the plant and/or significant treatment responses. By collapsing time, the cause of the differences is indistinguishable.

ROLE OF P. PENETRANS AND L. DECEMLINEATA ON THE GROWTH OF S. TUBEROSUM

The objective of a study in 1979 was to examine the affects of P. penetrans and L. decemlineata on the growth, development and yield of S. tuberosum (cv Superior). An additional objective was to examine how plant defoliation by L. decemlineata, as it is mediated through S. tuberosum, affects the population dynamics of P. penetrans.

MATERIALS AND METHODS

Caged Environment

Seed pieces (cv Superior) wee planted on May 24, 1979, at the Montcalm Potato Research Farm in west central Michigan. Each plot consisted of two rows, 1.83 m in length and 0.86 m apart, with 0.20 m spacings between plants.

Twenty-seven insect cages, measuring 1.83 x 1.83 x 1.83 m, were erected over the plots after planting. Each cage was assigned one of nine different treatments. A treatment consisted of one of three population levels of L. decemlineata and one of three population levels of P. penetrans. L. decemlineata population levels were achieved by stapling leaves with egg masses obtained from adjacent potato fields to the leaves of newly emerged plants within the cages on June 22, 1979. Eggs were allowed to hatch and then larval populations manipulated to plant densities of either 0, 10 or 20 larvae per plant.

The nematode population levels of P. penetrans within the cage plots were achieved by various techniques. Preplant sampling of the cage sites provided estimates of initial soil population densities (P_i) of P. penetrans. Initial soil population densities were then numerically ranked and separated into three groups: low ($2 \leq P_i \leq 4$), medium ($15 \leq P_i \leq 25$) and high ($511 \leq P_i \leq 532$). The cages with the low initial soil population levels were then fumigated with 1,3-D (Telone II, 93.5 l/ha) on May 1, 1979. The medium population levels represent natural field populations. The high population levels of P. penetrans were achieved by complementing the natural field populations with a liquid suspension of P. penetrans obtained from potato roots cultured in the

laboratory. A 10 ml aliquant of the nematode suspension was applied at planting to these treatments and represents an approximate addition of 500 nematodes to the root rhizosphere of the germinating potato plant.

Plant growth and development was monitored every 2-4 weeks throughout the season. Plants were randomly selected from one specific row of each plot during the season. After removal, plants were returned to the laboratory for analysis. In the laboratory, root weight, stem weight, leaf weight, tuber weight and tuber number were recorded for each sampling date. Plant dry weights were then determined after drying at 35 C in a plant drying oven. Total leaf area of each plant was calculated with a Lambda leaf area meter (Model LI 3000).

Soil and root populations of P. penetrans were estimated by techniques previously described. On September 14, 1979, the remaining row within each cage plot was harvested. Individual tubers from each cage plot were separated into ten different tuber size categories (1-10 cm). The number of tubers in each size class were counted and weighed. During the season, plants were maintained under normal commercial irrigation and disease control practices.

Path Coefficient Analysis

Path coefficient analysis was used as a conceptual framework and a guide for data collection as well as a method for analyzing the results. It is a technique, first proposed by Wright (1921, 1934), to deal with the interrelationships among linearly related variables. Statistical applications of the path coefficient method have been demonstrated by Li (1977), Duncan (1966), Grafius (1978) and Tai (1975). Its application to the investigation of plant stress caused by insect and nematode pests is unique.

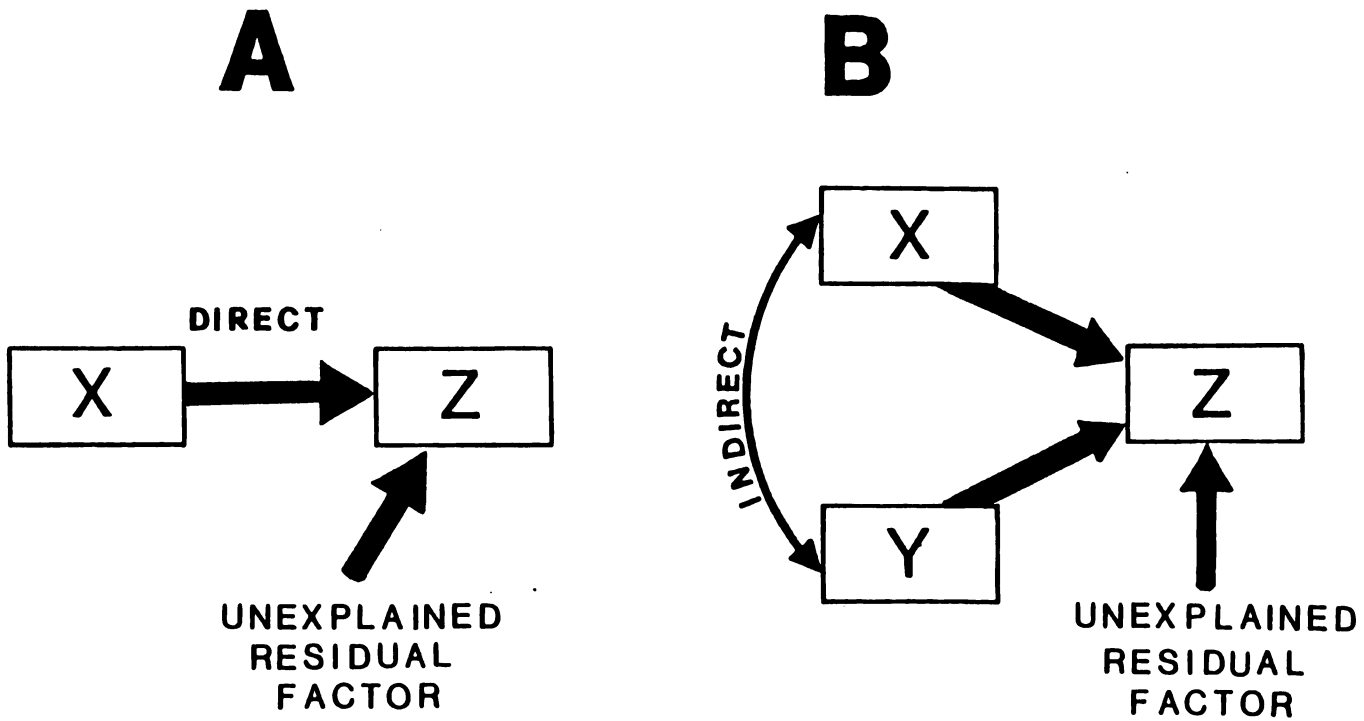

Figure 11. Relationship between independent and dependent variables and an unexplained residual factor in determining the outcome of another variable.

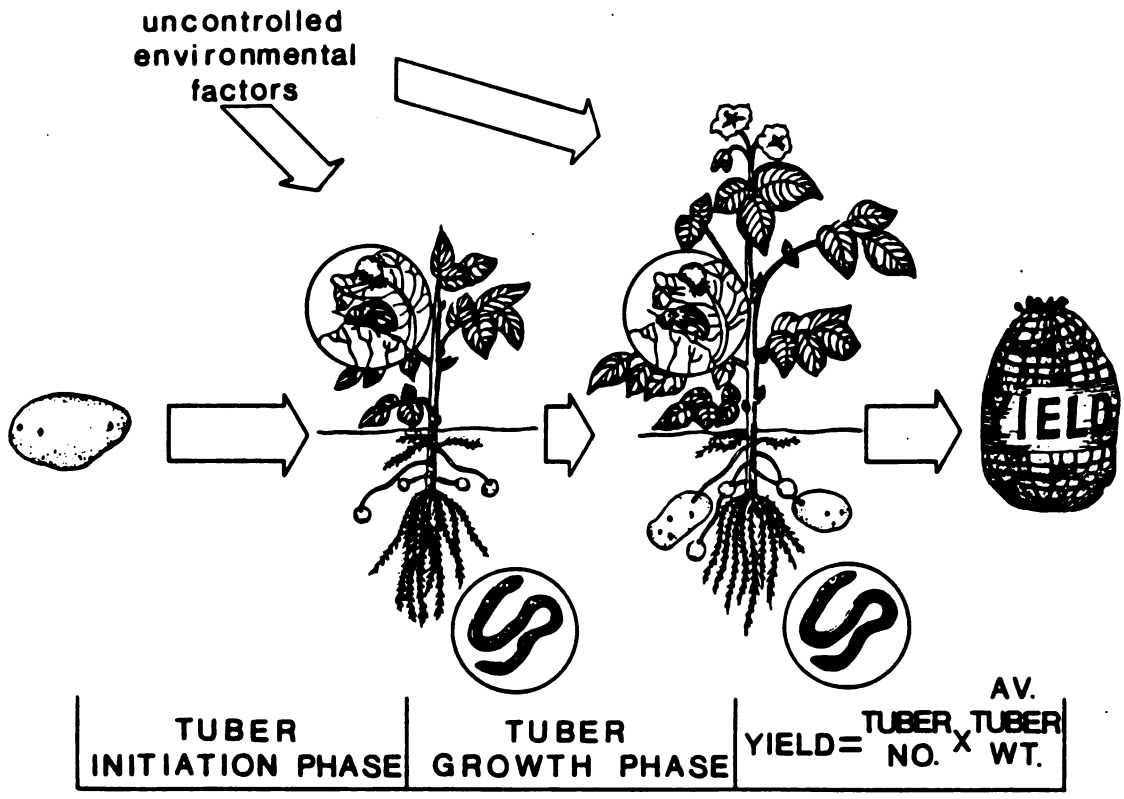

Figure 12. Conceptual diagram illustrating sequential effects of abiotic and biotic factors on yield components of S. tuberosum.

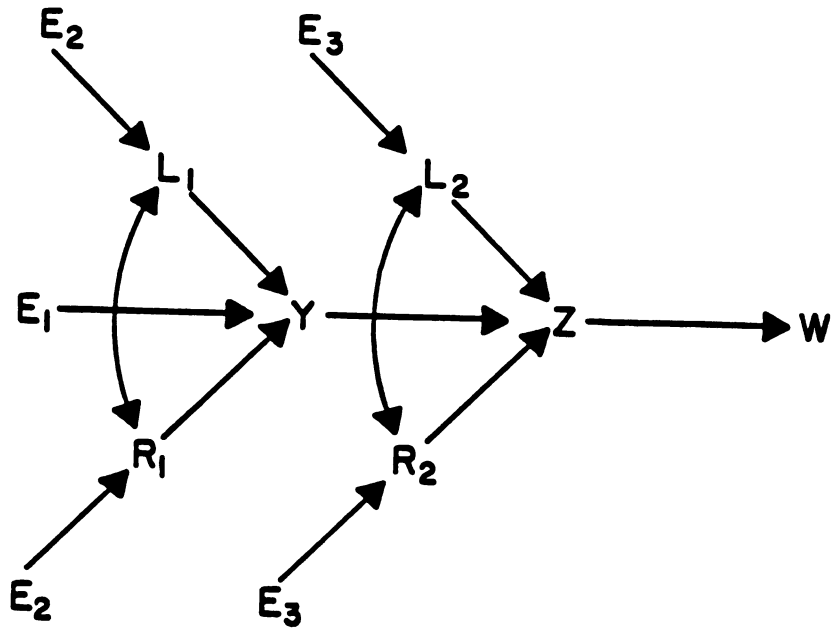

Figure 13. Path diagram of path coefficient analysis for S. tuberosum ontogeny.

Path coefficient analysis is a form of structural linear regression analysis with respect to standardized variables in a closed system. Unlike multiple regression, the path method is not concerned with the best or closest prediction of Y based on the information contained in the X variables. It is concerned with the proposal of a plausible interpretation of the interrelationships between variables. It is based on the construction of a qualitative diagram in which every component of the system is represented either as being completely determined by individual components within the system as is A (Fig. 11) or by combinations of individual components as in B. The variables are arranged in a proposed causal order to indicate their interrelationships. Directions are assigned via arrows to indicate the influence each variable has on another. A double-headed arrow is used to denote a mutual association between variables. In this way, the direct and indirect influences certain causal components have in producing changes in other components can be illustrated.

The path diagram is based on the sequential development of the yield components of the potato plant (Fig. 12). Final yield in the diagram is determined by the sequential affects the various abiotic and biotic factors have on the yield components at their respective developmental stages. For example, the development of the first yield component, number of tubers per plant, is completely determined by the resources available to the plant during the early stages of growth and the number and frequency of pests attacking it. Another yield component, average tuber weight per plant, whose development occurs after tubers are initiated, is not only influenced by the resources available to it during its growth phase but also by the initiation and development of tubers which occurred earlier. Within this sequential arrangement, final yield is the multiplicative product of average tuber number

per plant and the average tuber weight per plant.

The plant environment has been separated into two independent components. First, a biotic component which includes a foliar feeding component in L. decemlineata and root-feeding component in P. penetrans. All the other environmental factors affecting the plant during its ontogeny are pooled together to form the uncontrolled environmental components, U_1 through U_7. These would include such factors as genetic variability, undetected environmental and pathological factors and experimental error. These also represent the residual effect of the variation that has been left unexplained by changes in the causal variables on the effect variable.

A path coefficient analysis of the causal diagram was used to determine the interrelationships between biotic factors, yield components and yield (Fig. 12). Each path in the diagram not only has a direction but also has a quantitative value to measure the importance of a given path of influence. The value assigned to the path is the path coefficient P_{ij} (e.g., P_{XY} is the path from X to Y). Each path coefficient deals with the relationships between standardized variables. Standardized variables are those variables measured from their mean values in units of their own standard deviation. The process of standardization makes all variables equal in mean (zero) and equal in variance (unity).

The path coefficient measures the importance of a given path of influence from the cause to the effect variable. It is defined as the proportion of the variability explained by the causal variable when all other factors are held constant except the one in question, the variability of which is kept unchanged to the total variability. Variability is measured by the standard deviation. Each path coefficient is calculated according to the specified structure of the

Where:

$r_{12} = P_{12}$

$r_{2X} = P_{2X} + P_{3X}r_{23}$

$r_{3X} = P_{3X} + P_{2X}r_{23}$

$r_{43} = P_{43}$

$r_{56} = P_{56}$

$r_{6Y} = P_{6Y} + P_{7Y}r_{76}$ ---where $r_{6X}=r_{7X}= 0$

$r_{7Y} = P_{7Y} + P_{6Y}r_{76}$ ---where $r_{6X}=r_{7X}= 0$

$r_{87} = P_{87}$

$r_{XY} = P_{XY}$ --where $r_{6X}=r_{7X}= 0$

$r_{YW} = P_{YW}$

$r_{1W} = P_{1W} + P_{1Y}P_{YW} + P_{1X}P_{XW} + P_{3W}r_{23}P_{12} + P_{12}P_{2X}P_{XY}P_{YW}$

$r_{2W} = P_{2W} + P_{2X}P_{XW} + P_{3W}r_{23} + P_{2X}P_{XY}P_{YW}$

$r_{XW} = P_{XW} + P_{XY}P_{YW}$

$r_{3W} = P_{3W} + P_{3Y}P_{YW} + P_{3X}P_{XW} + P_{2W}r_{23} + P_{3X}P_{XY}P_{YW}$

$r_{4W} = P_{4W} + P_{4Y}P_{YW} + P_{4X}P_{XW} + P_{43}r_{23}P_{2W} + P_{43}P_{3X}P_{XY}P_{YW}$

$r_{5W} = P_{5W} + P_{5Y}P_{YW} + P_{56}P_{6Y}P_{YW} + P_{56}r_{76}P_{7W}$

$r_{6W} = P_{6W} + P_{6Y}P_{YW} + P_{7W}r_{76}$

$r_{7W} = P_{7W} + P_{7Y}P_{YW} + P_{6W}r_{76}$

$r_{8W} = P_{8W} + P_{8Y}P_{YW} + P_{87}P_{7Y}P_{YW} + P_{87}r_{76}P_{6W}$

$r_{8Y} = P_{8Y} + P_{87}P_{7Y} + P_{87}r_{76}P_{6Y}$

$r_{5Y} = P_{5Y} + P_{56}P_{6Y} + P_{56}r_{76}P_{7Y}$

$r_{1X} = P_{1X} + P_{12}P_{2X} + P_{12}r_{23}P_{3X}$

$r_{1Y} = P_{1Y} + P_{1X}P_{XY} + P_{12}P_{2X}P_{XY} + P_{12}r_{23}P_{3Y}$

$r_{2Y} = P_{2Y} + P_{2X}P_{XY} + P_{3Y}r_{23}$

$r_{3Y} = P_{3Y} + P_{3X}P_{XY} + P_{2Y}r_{23}$

$r_{4Y} = P_{4Y} + P_{43}P_{3Y} + P_{43}P_{3X}P_{XY} + P_{43}r_{23}P_{2Y}$

$r_{4X} = P_{4X} + P_{43}P_{3X} + P_{43}r_{23}P_{2X}$

Figure 14. Path coefficient equations.

No. of Tubers/ Plant

$$P_{rx} = \sqrt{1 - P_{2X}^2 - P_{3X}^2 - 2P_{2X}P_{3X}r_{23}}$$

Degree of Determination = $1 - P_{rX}^2$

Average Tuber Wt. / Plant (Y)

$$P_{rY} = \sqrt{1 - P_{6Y}^2 - P_{XY}^2 - P_{7Y}^2 - 2P_{6Y}P_{XY}r_{6X} - 2P_{6Y}P_{7Y}r_{76} - 2P_{XY}P_{7X}r_{7X}}$$

Degree of Determination = $1 - P_{rY}^2$

Yield (W)

$$P_{rW} = \sqrt{1 - P_{YW}^2}$$

Degree of Determination = $1 - P_{rW}^2$

Figure 15. Coefficients of determination.

proposed relationship. For simple cases where one independent and dependent variable are involved (Fig. 11A), the regression coefficient (B_{xy}) for the standardized variable and correlation coefficient (r_{xy}) are both equivalent to the path coefficient P_{xy}. Thus:

$$P_{XY} = r_{xy} = B_{xy} \text{ where } B_{xy} = b_{xy}\,(s_x)/(s_y)$$

In this simple case, the simple linear regression coefficient can be transformed into the standardized regression coefficient by the process indicated above, where b_{xy} is the simple linear regression coefficient, s_x is the standard deviation of x, and s_y is the standard deviation of y.

For uncorrelated causes involving multiple independent variables, the path correlation coefficient is no longer simply the corresponding correlation coefficient (Fig. 11B). Li (1975) has provided a more comprehensive description of the formulas and their derivations required to calculate path coefficients between uncorrelated and correlated causal variables. A summary of the equations used in the calculation of the path coefficients and coefficients of determination are listed for quick reference (Fig. 14, 15).

Solanum tuberosum Agroecosystem

A non-caged open field experiment was conducted in 1979 to examine the influence of L. decemlineata, P. penetrans and nitrogen fertilization on the growth of S. tuberosum. Seed pieces of cv Superior were planted on May 17, 1979, at the Montcalm Potato Research Farm. Each plot consisted of four rows 15.24 m in length and 0.86 m apart, with 20.5 to 30.5 spacings between plants. The plots were arranged in a completely random block-three factorial experimental design with each treatment replicated five times.

A treatment consisted of either of two levels of NPK fertilizer (0 and 560

kg/ha, NPK 20-10-10), and one of two levels of nematicide (1,3-D + MIC, broadcast at 93.5 l/ha (Table 14). Plots treated with 1,3-D + MIC were injected to a 15 to 20 cm soil depth on May 1, 1979. Those plots to receive fertilizer were also side-dressed during hilling at an application rate of 162.5 kg/ha urea (45% N) on June 22, 1979. Insect control programs were initiated at various times during the season to achieve three levels of plant defoliation (no defoliation, early-season defoliation and full-season defoliation). Within the no defoliation plots, foliar applications of methamidophos (Monitor 10G; 3.4 kg/ha active ingredient) were applied as needed for L. decemlineata control. An insect control program was not initiated until flowering within the early-season defoliation plots. Full-season defoliation plots remained untreated.

Plant growth and development was monitored at various intervals throughout the season. This was accomplished by randomly selecting two plants from the outside rows of each plot and returning them to the laboratory for analysis. In the laboratory, root weight, foliage weight and tuber weight and number were recorded for each sampling data. Soil and root population densities of P. penetrans were estimated from samples taken at these times according to techniques previously described. At harvest, the center two rows of each plot were harvested, graded and weighed. All plots were irrigated with a solid set sprinkler system according to need determined by measurements of evapotranspiration.

Table 14. 1979 Insect-nematode potato agroecosystem study treatments.

Defoliation Level	Nitrogen (kg/ha)	Fumigation (l/ha)
None[3]	0	0
	560[1]	0
	0	93.5[2]
	560	93.5
Early-season	0	0
	560	0
	0	93.5
	560	93.5
Late-season	0	0
	560	0
	0	93.5
	560	93.5

[1]Nitrogen fertilizer (NPK 20-10-10) applied at planting, plus 162.5 kg/ha Urea (45% N) at hilling on June 22, 1979.

[2]Telone II broadcast injected to a 20 cm soil depth on May 1, 1979.

[3]Foliar applications of Methamidophos 10G; 3.4 kg/ha a.i. as needed for L. decemlineata control.

RESULTS

Caged Environment

Larval feeding by L. decemlineata influenced the population dynamics of P. penetrans and the growth and development of S. tuberosum. The direct effect of L. decemlineata was a significant (P=0.05) reduction in leaf dry weight and leaf surface area, which increased with increasing plant density of L. decemlineata (Tables 15 and 16, respectively). This relationship was evident season-long, but only significant (P=0.05) during the second plant sample (DD_{10C}=668.3) for leaf dry weight and during the final two plant samples (DD_{10C}=668.3 and 954.1) for leaf surface area. As L. decemlineata reduced leaf dry weight and leaf surface area, there was a corresponding reduction in plant root dry weight (Table 17), which was significantly (P=0.05) higher in the beetle-free plots during the final plant sample (DD_{10C}=954.1). These changes are directly reflected in the significant (P=0.05) reductions in plant and tuber dry weights during the later stages of plant growth for the beetle-infested treatments (Tables 18 and 19, respectively). It was not until the final plant sample (DD_{10C}=954.1) that L. decemlineata significantly (P=0.05) reduced the number of tubers per plant (Table 20). Tuber numbers were always higher for the entire season in the beetle-free treatments. L. decemlineata had no significant (P=0.05) influence on stem or stolon dry weight season-long (Tables 21 and 22, respectively).

P. penetrans directly influenced the growth and development of S. tuberosum. P. penetrans significantly (P=0.05) increased leaf dry weight at the low initial soil population level during the first plant sampling (Table 15). Leaf dry weights were consistently higher at the lower P_i for the remainder of the

Table 15. Influence of three inoculated densities of P. penetrans and three plant densities of L. decemlineata on leaf dry weight of S. tuberosum (cv Superior).

Treatment		Leaf dry weight (Grams)[1]		
L. decemlineata[2]	P. penetrans[3]	514.2	668.3	954.1
0	Low	6.66 c[4]	19.05 b	27.17 a
0	Medium	3.73 ab	12.00 ab	19.47 a
0	High	3.36 ab	14.13 ab	27.57 a
10	Low	5.17 bc	7.31 ab	18.50 a
10	Medium	2.32 ab	10.31 ab	25.87 a
10	High	3.47 ab	5.05 a	5.73 a
20	Low	4.84 abc	9.59 ab	12.63 a
20	Medium	2.35 ab	4.45 a	7.57 a
20	High	1.81 a	3.56 a	13.17 a
0		4.45 a	13.85 b	23.25 a
10		3.70 a	8.14 a	17.55 a
20		3.00 a	5.87 a	11.12 a
	Low	5.56 b	11.98 a	19.43 a
	Medium	2.80 a	8.92 a	17.63 a
	High	12.88 a	7.58 a	15.49 a

[1]Degree day accumulation base 10 C.

[2]Maintained plant density of L. decemlineata of 0 per plant from emergence to harvest.

[3]Initial population density level of P. penetrans established at planting.

[4]Columns followed by the same letter are not significantly different (P=0.05) according to the Student-Newman-Keuls Multiple Range Test.

Table 16. Influence of three inoculated densities of P. penetrans and three plant densities of L. decemlineata on leaf area of S. tuberosum (cv Superior).

Treatment		Leaf area (cm^2)[1]		
L. decemlineata[2]	P. penetrans[3]	514.2	668.3	954.1
0	Low	2919.3 c[4]	7184.9 b	2221.1 b
0	Medium	1742.0 abc	3812.3 a	382.8 ab
0	High	1770.9 abc	3967.3 a	933.6 ab
10	Low	2590.5 c	1948.4 a	397.8 ab
10	Medium	967.4 a	3026.9 a	743.2 ab
10	High	1097.0 ab	1268.9 a	77.7 a
20	Low	1881.7 ab	2305.8 a	306.1 ab
20	Medium	1122.3 ab	1315.4 a	211.9 a
20	High	687.9 a	798.8 a	74.4 a
0		2049.3 a	4545.9 b	1084.6 b
10		1596.4 a	2270.9 a	427.9 a
20		1230.6 a	1473.3 a	197.5 a
	Low	2463.8 b	3813.0 a	975.0 a
	Medium	1277.6 a	2718.2 a	446.0 a
	High	1185.2 a	20--.7 a	361.9 a

[1]Degree day accumulation base 10 C.

[2]Maintained plant density of L. decemlineata of 0 per plant from emergence to harvest.

[3]Initial population density level of P. penetrans established at planting.

[4]Columns followed by the same letter are not significantly different (P=0.05) according to the Student-Newman-Keuls Multiple Range Test.

Table 17. Influence of three inoculated densities of P. penetrans and three plant densities of L. decemlineata on root dry weight of S. tuberosum (cv Superior).

Treatment		Root dry weight (Grams)[1]		
L. decemlineata[2]	P. penetrans[3]	514.2	668.3	954.1
0	Low	0.44 a[4]	1.12 b	1.00 a
0	Medium	0.31 a	0.60 ab	0.37 a
0	High	0.30 a	0.65 ab	0.90 a
10	Low	0.31 a	0.32 a	0.27 a
10	Medium	0.19 a	0.69 a	0.77 a
10	High	0.32 a	0.49 ab	0.23 a
20	Low	0.35 a	0.75 ab	0.27 a
20	Medium	0.24 a	0.50 ab	0.10 a
20	High	0.18 a	0.15 a	0.01 a
0		0.37 a	0.76 a	0.75 a
10		0.24 a	0.50 a	0.39 ab
20		0.26 a	0.47 a	0.28 a
	Low	0.37 a	0.73 a	0.51 a
	Medium	0.24 a	0.60 a	0.51 a
	High	0.27 a	0.43 a	0.42 a

[1]Degree day accumulation base 10 C.

[2]Maintained plant density of L. decemlineata of 0 per plant from emergence to harvest.

[3]Initial population density level of P. penetrans established at planting.

[4]Columns followed by the same letter are not significantly different (P=0.05) according to the Student-Newman-Keuls Multiple Range Test.

Table 18. Influence of three inoculated densities of P. penetrans and three plant densities of L. decemlineata on plant dry weight of S. tuberosum (cv Superior).

Treatment		Plant dry weight (Grams)[1]			
L. decemlineata[2]	P. penetrans[3]	514.2	668.3	954.1	1177.0
0	Low	16.28 b[4]	81.32 b	154.43 b	112.90 a
0	Medium	7.97 a	46.87 ab	108.83 a	69.01 a
0	High	8.13 a	50.55 ab	135.83 a	90.36 a
10	Low	14.80 b	29.30 a	117.13 a	58.82 a
10	Medium	5.64 a	31.26 a	120.83 a	36.19 a
10	High	7.69 a	18.96 a	52.33 a	9.91 a
20	Low	12.25 ab	54.11 ab	83.07 a	46.87 a
20	Medium	6.25 a	21.71 a	47.63 a	38.12 a
20	High	5.27 a	10.04 a	62.97 a	18.75 a
0		10.60 a	55.22 a	127.86 b	82.89 b
10		9.44	27.82 a	98.70 ab	37.84 a
20		7.92 a	28.62 a	64.56 a	34.58 a
	Low	14.45 b	54.91 b	118.21 a	72.86 a
	Medium	6.62 a	33.28 ab	92.43 a	47.77 a
	High	7.03 a	25.52 a	83.71 a	39.67 a

[1]Degree day accumulation base 10 C.

[2]Maintained plant density of L. decemlineata of 0 per plant from emergence to harvest.

[3]Initial population density level of P. penetrans established at planting.

[4]Columns followed by the same letter are not significantly different (P=0.05) according to the Student-Newman-Keuls Multiple Range Test.

Table 19. Influence of three inoculated densities of P. penetrans and three plant densities of L. decemlineata on tuber dry weight of S. tuberosum (cv Superior).

Treatment		Tuber dry weight (Grams)[1]			
L. decemlineata[2]	P. penetrans[3]	514.2	668.3	954.1	1177.0
0	Low	0.68 a[4]	40.10 b	110.13 a	112.90 a
0	Medium	0.01 a	22.57 ab	77.13 a	69.01 a
0	High	0.01 a	23.77 ab	91.00 a	90.36 a
10	Low	2.76 a	13.60 ab	83.93 a	58.82 a
10	Medium	0.00 a	7.77 a	76.90 a	36.19 a
10	High	0.05 a	6.17 a	40.20 a	9.91 a
20	Low	1.71 a	28.36 ab	59.07 a	46.87 a
20	Medium	0.01 a	7.97 a	30.63 a	38.12 a
20	High	0.02 a	0.62 a	40.27 a	18.75 a
0		0.22 a	26.66 b	89.72 b	82.89 b
10		1.04 a	9.42 a	67.59 ab	37.84 a
20		0.58 a	12.32 a	43.54 a	34.58 a
	Low	1.72 b	27.35 b	84.60 a	72.86 a
	Medium	0.01 a	12.77 a	61.56 a	47.77 a
	High	0.03 a	10.19 a	57.16 a	39.67 a

[1]Degree day accumulation base 10 C.

[2]Maintained plant density of L. decemlineata of 0 per plant from emergence to harvest.

[3]Initial population density level of P. penetrans established at planting.

[4]Columns followed by the same letter are not significantly different (P=0.05) according to the Student-Newman-Keuls Multiple Range Test.

Table 20. Influence of three inoculated densities of P. penetrans and three plant densities of L. decemlineata on tuber number per plant of S. tuberosum (cv Superior).

Treatment		Tuber number per plant[1]			
L. decemlineata[2]	P. penetrans[3]	514.2	668.3	954.1	1177.0
0	Low	15.7 bc[4]	47.3 ab	13.7 a	17.3 b
0	Medium	6.0 abc	25.0 ab	12.3 a	12.7 ab
0	High	7.0 abc	30.0 ab	10.0 a	10.7 ab
10	Low	18.3 c	17.7 ab	13.0 a	7.0 a
10	Medium	0.3 a	16.7 ab	12.3 a	8.0 a
10	High	5.7 abc	23.0 ab	6.7 a	4.0 a
20	Low	12.7 abc	52.7 b	9.7 a	11.0 ab
20	Medium	5.0 abc	21.7 ab	11.3 a	7.0 a
20	High	3.0 ab	10.3 ab	8.7 a	5.0 a
0		10.1 a	33.6 a	11.7 a	12.8 b
10		7.3 a	17.9 a	10.9 a	6.4 a
20		6.9 a	28.2 a	9.9 a	7.7 a
	Low	15.6 b	39.2 a	12.1 a	11.8 a
	Medium	3.8 a	21.1 a	12.0 a	9.2 a
	High	5.2 a	21.1 a	8.4 a	6.6 a

[1]Degree day accumulation base 10 C.

[2]Maintained plant density of L. decemlineata of 0 per plant from emergence to harvest.

[3]Initial population density level of P. penetrans established at planting.

[4]Columns followed by the same letter are not significantly different (P=0.05) according to the Student-Newman-Keuls Multiple Range Test.

Table 21. Influence of three inoculated densities of P. penetrans and three plant densities of L. decemlineata on stem dry weight of S. tuberosum (cv Superior).

Treatment		Stem dry weight (Grams)[1]		
L. decemlineata[2]	P. penetrans[3]	514.2	668.3	954.1
0	Low	6.76 a[4]	17.37 b	13.67 a
0	Medium	2.98 a	9.55 ab	9.13 a
0	High	3.17 a	10.06 ab	13.33 a
10	Low	5.95 a	6.58 a	12.13 a
10	Medium	2.35 a	10.20 ab	14.47 a
10	High	2.78 a	5.57 a	5.20 a
20	Low	3.88 a	12.97 ab	8.93 a
20	Medium	2.51 a	6.80 a	7.67 a
20	High	2.42 a	4.57 a	8.00 a
0		4.24 a	11.50 a	11.52 a
10		3.32 a	7.87 a	11.08 a
20		2.94 a	8.11 a	8.02 a
	Low	5.20 b	12.30 b	11.58 a
	Medium	2.62 a	8.85 ab	10.42 a
	High	2.79 a	6.73 a	8.84 a

[1]Degree day accumulation base 10 C.

[2]Maintained plant density of L. decemlineata of 0 per plant from emergence to harvest.

[3]Initial population density level of P. penetrans established at planting.

[4]Columns followed by the same letter are not significantly different (P=0.05) according to the Student-Newman-Keuls Multiple Range Test.

Table 22. Influence of three inoculated densities of P. penetrans and three plant densities of L. decemlineata on stolon dry weight of S. tuberosum (cv Superior).

Treatment		Stolon dry weight (Grams)[1]		
L. decemlineata[2]	P. penetrans[3]	514.2	668.3	954.1
0	Low	1.75 b[4]	3.68 b	3.13 a
0	Medium	0.94 a	2.15 a	2.73 a
0	High	1.29 ab	1.94 a	3.03 a
10	Low	1.60 ab	1.49 a	2.30 a
10	Medium	0.78 a	2.29 a	2.83 a
10	High	1.07 ab	1.84 a	0.97 a
20	Low	1.47 ab	2.44 a	1.50 a
20	Medium	1.13 ab	1.99 a	1.37 a
20	High	0.83 a	1.13 a	1.40 a
0		1.32 a	2.46 a	2.62 a
10		1.14 a	1.89 a	2.10 a
20		1.15 a	1.85 a	1.42 a
	Low	1.61 b	2.54 a	2.09 a
	Medium	0.95 a	2.14 ab	2.31 a
	High	1.06 a	1.58 b	1.80 a

[1]Degree day accumulation base 10 C.

[2]Maintained plant density of L. decemlineata of 0 per plant from emergence to harvest.

[3]Initial population density level of P. penetrans established at planting.

[4]Columns followed by the same letter are not significantly different (P=0.05) according to the Student-Newman-Keuls Multiple Range Test.

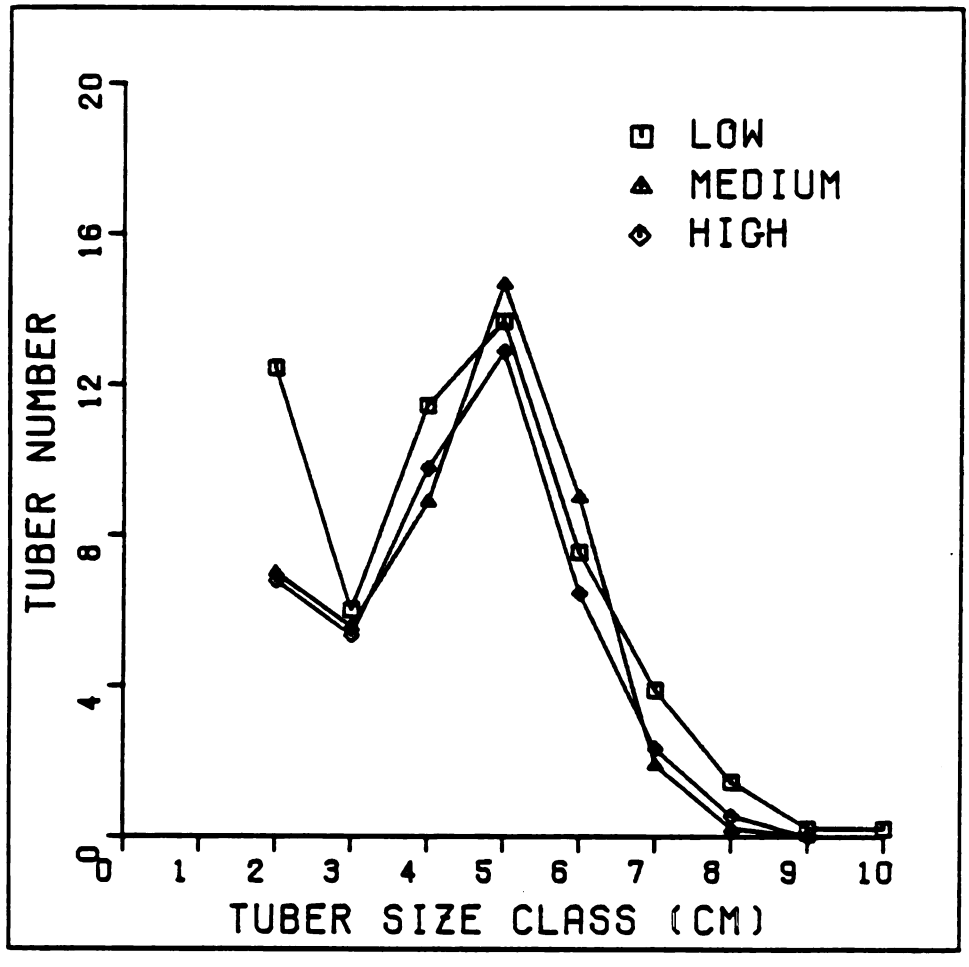

Figure 16. The influence of three initial population levels of P. penetrans on the average number of tubers in each of ten different tuber size categories of S. tuberosum at harvest.

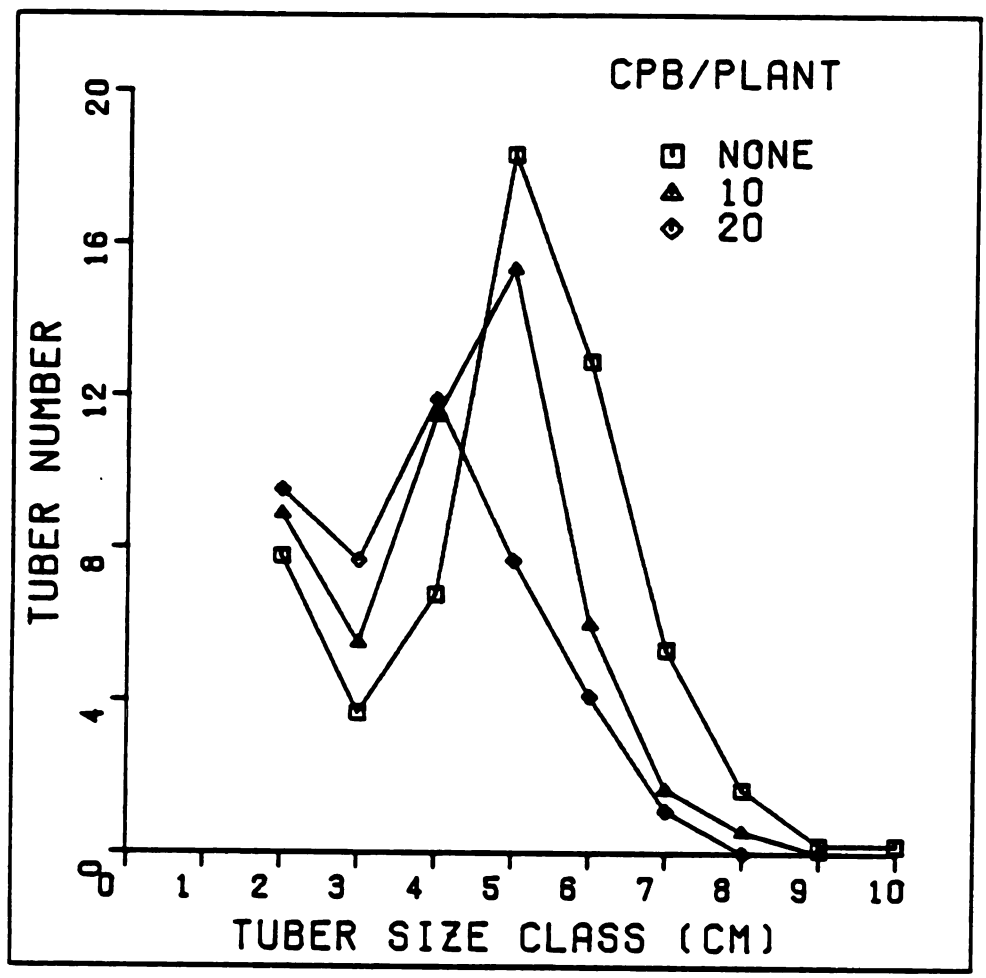

Figure 17. The influence of three plant densities of L. decemlineata on the average tuber number in each of ten different tuber size categories of S. tuberosum at harvest.

season. These same trends are evident when the influence of P. penetrans on leaf surface area is examined (Table 16). No significant (P=0.05) differences in root dry weight among P. penetrans levels were detected (Table 17). Tuber dry weight was significantly (P=0.05) higher at the low initial soil population level of P. penetrans during the first two sampling periods (Table 19). Tuber dry weight was always lower at the two highest P_i's of P. penetrans. Stolon, stem and total plant dry weight responded similarly to P. penetrans (Tables 22, 21 and 18, respectively). Dry weight significantly (P=0.05) decreased in these parameters at the higher p_i's of P. penetrans during the initial plant sample. Significant (P=0.05) reductions in the number of tubers formed per plant were evident during the initial plant sample (Table 20). Over four times as many tubers were formed at the lower population level of P. penetrans than at the higher population levels.

Both L. decemlineata and P. penetrans affect final tuber yield, with L. decemlineata having the only significant (P=0.05) impact in determining final tuber yield (Table 23). Final yield of S. tuberosum decreased with increasing L. decemlineata and P. penetrans population levels.

When final tuber yield is examined according to tuber size class, the influence of P. penetrans and L. decemlineata on the yield components, tuber weight and number per class, can be more closely scrutinized. The affect of low initial soil populations of P. penetrans on the number of tubers per size class was to significantly (P=0.05) increase the number of tubers in the smallest observed tuber size category (Fig. 16). No other significant (P=0.05) differences in tuber number were detected among the remaining tuber size classes. L. decemlineata also had a significant (P=0.05) influence on the number of tubers per tuber size class (Fig. 17). Increasing plant densities of L.

Table 23. Influence of three inoculated densities of P. penetrans and three plant densities of L. decemlineata on final tuber yield of S. tuberosum (cv Superior).

Treatment		Yield (grams/1.83 m row)
L. decemlineata[2]	P. penetrans[3]	
0	Low	4403.0 b[4]
0	Medium	3152.4 ab
0	High	3257.8 ab
10	Low	2351.9 a
10	Medium	2205.4 a
10	High	1704.6 a
20	Low	1586.1 a
20	Medium	1163.3 a
20	High	1108.7 a
0		3604.4 c
10		2087.3 b
20		1292.0 a
	Low	2780.3 a
	Medium	2173.7 a
	High	2023.7 a

[1]Degree day accumulation base 10 C.

[2]Maintained plant density of L. decemlineata of 0 per plant from emergence to harvest.

[3]Initial population density level of P. penetrans established at planting.

[4]Columns followed by the same letter are not significantly different (P=0.05) according to the Student-Newman-Keuls Multiple Range Test.

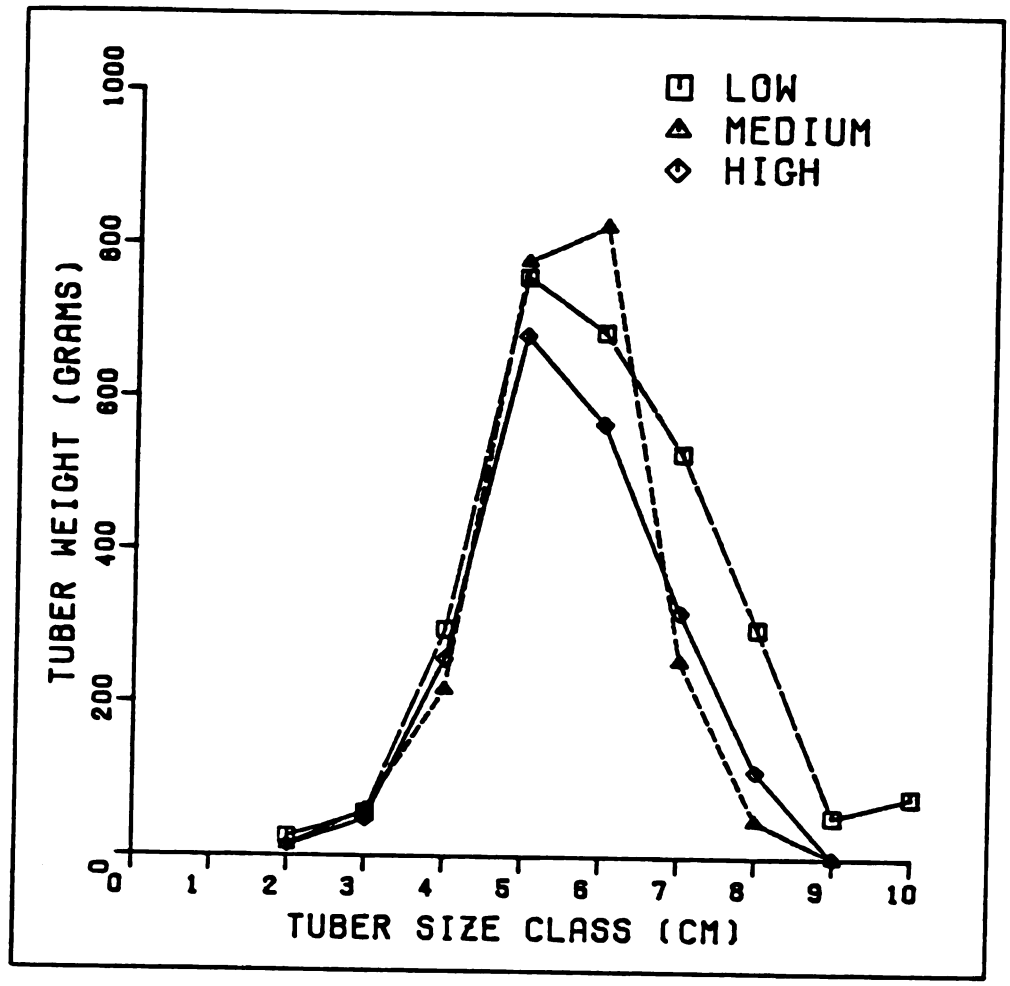

Figure 18. Influence of three initial populations of P. penetrans on mean tuber class weight in each of ten different tuber size categories of S. tuberosum at harvest.

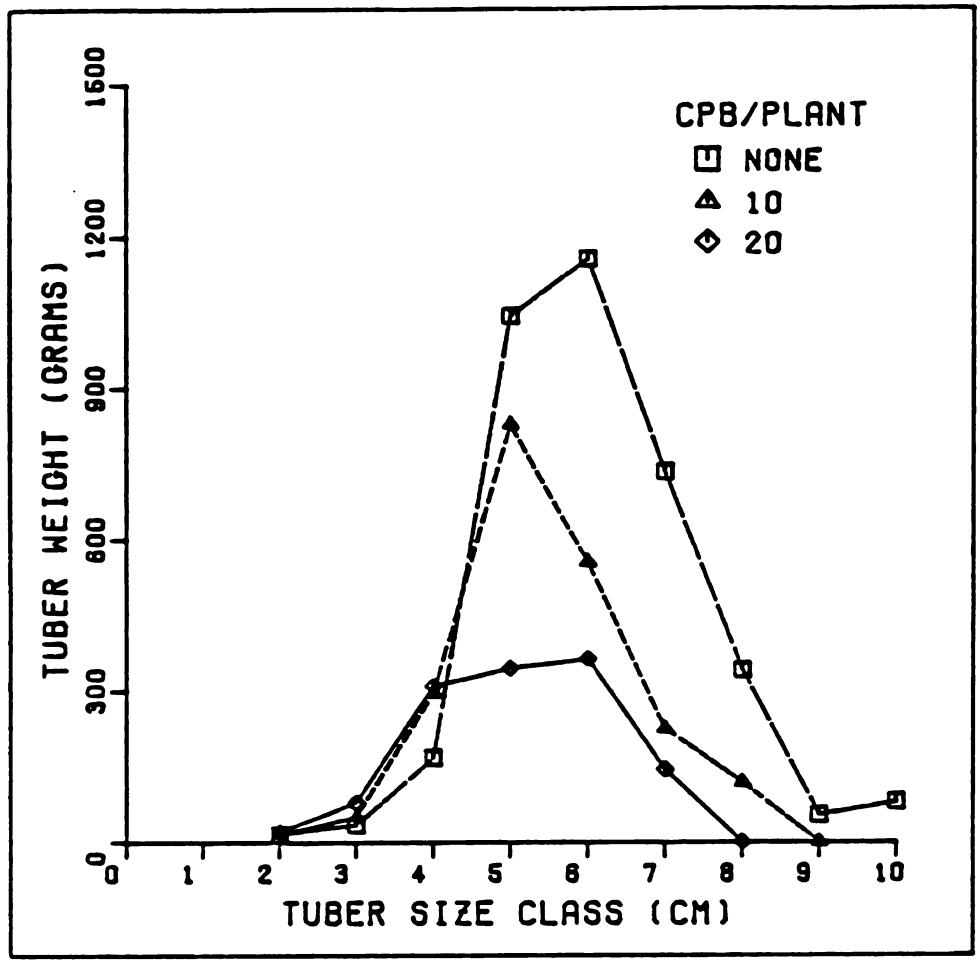

Figure 19. Influence of three plant densities of L. decemlineata on mean tuber class weight in each of ten different tuber size categories of S. tuberosum at harvest.

decemlineata, from 0 to 20 beetles per plant, shifted a greater number of tubers into the smaller tuber size categories and significantly (P=0.05) reduced the number of tubers per tuber size class. The same type of kurtotic trends can also be observed in the mean tuber weight distribution between tuber size classes for final tuber yield (1.83 m row) (Figs. 18 and 19). P. penetrans had no significant (P=0.05) influence on final tuber weight distribution among tuber size classes (Fig. 18), although differences are consistently lower in the high initial soil population levels of P. penetrans when compared to the low initial soil population levels. A mean tuber class weight shift among tuber size classes is even moe evident when the effects of L. decemlineata are examined (Fig. 19). Not only is total tuber weight significantly (P=0.05) reduced among L. decemlineata plant densities, but also a greater proportion of the total weight is shifted to the larger tuber size classes as L. decemlineata densities increase.

L. decemlineata feeding had no significant influence on soil population densities of P. penetrans season-long (Table 24). Significant (P=0.05) differences in the initial (DD_{10C}=34.9) population levels of P. penetrans were evident. Root population densities of P. penetrans were significantly (P=0.05) higher in plants maintained beetle-free during the latter part of the season (DD_{10C}=954.1)(Table 25).

PATH ANALYSIS

Correlation between yield and tuber number or average tuber weight was positive and highly significant (P=0.01, Table 26). Simple correlations between yield and root weight, leaf weight and leaf area were always positive and highly significant (P=0.01, Table 26), with the strength of the association increasing with time. Correlating final tuber yield with L. decemlineata resulted in a

Table 24. Influence of three plant densities of L. decemlineata on soil population densities of P. penetrans.

Treatment		P. penetrans per 100 cm^3 soil[1]					
L. decemlineata[2]	P. penetrans[3]	34.9	171.9	514.9	668.3	954.1	1217.5
0	Low	26.0 ab[4]	1.6 a	6.3 a	10.7 a	26.3 ab	22.3 a
0	Medium	55.0 ab	25.0 bc	30.7 a	24.3 a	104.0 b	59.7 a
0	High	92.3 c	31.7 c	16.3 a	22.7 a	54.0 ab	40.7 a
10	Low	22.3 ab	3.7 a	9.0 a	9.7 a	15.7 a	14.3 a
10	Medium	48.7 abc	14.3 ab	30.7 b	25.7 a	86.0 ab	34.0 a
10	High	68.0 bc	15.7 a	15.7 a	35.7 b	60.0 ab	41.7 a
20	Low	11.7 a	3.7 a	10.0 a	12.0 a	11.0 a	10.0 a
20	Medium	57.0 a	16.3 ab	25.3 a	31.7 a	43.3 ab	40.0 a
20	High	65.7 bc	11.3 ab	12.7 a	17.7 a	70.7 ab	36.0 a
0		56.3 a	19.4 a	17.3 a	23.0 a	62.0 a	40.9 a
10		46.8 a	12.3 a	19.1 a	19.5 a	52.0 a	30.0 a
20		44.8 a	10.4 a	16.0 a	20.4 a	41.7 a	28.8 a
	Low	20.0 a	3.1 a	8.4 a	10.8 a	17.7 a	15.6 a
	Medium	53.6 b	18.6 b	28.9 b	27.2 b	77.8 b	44.7 b
	High	75.3 c	19.6 b	14.9 a	25.3 b	61.6 b	39.4 b

[1]Degree day accumulation base 10 C.

[2]Maintained plant density of L. decemlineata of 0 per plant from emergence to harvest.

[3]Initial population density level of P. penetrans established at planting.

[4]Columns followed by the same letter are not significantly different (P=0.05) according to the Student-Newman-Keuls Multiple Range Test.

Table 25. Influence of three plant densities of L. decemlineata on the root population density of P. penetrans.

Treatment		P. penetrans per gram of root tissue[1]			
L. decemlineata[2]	P. penetrans[3]	514.2	668.3	954.1	1217.5
0	Low	10.0 a[4]	17.3 a	104.3 a	34.7 a
0	Medium	61.7 a	93.3 a	370.7 b	13.7 a
0	High	71.7 b	171.3 b	94.3 a	43.0 a
10	Low	25.7 a	24.3 a	108.3 a	16.7 a
10	Medium	39.0 a	73.3 a	126.0 a	89.7 b
10	High	26.3 a	112.3 a	50.7 a	16.3 a
20	Low	34.3 a	56.7 a	15.0 a	20.3 a
20	Medium	26.3 a	149.3 a	66.7 a	11.0 a
20	high	53.7 a	93.3 a	52.0 a	18.0 a
0		46.5 a	102.9 a	189.8 b	28.8 a
10		29.8 a	55.9 a	94.8 a	44.3 a
20		38.1 a	99.8 a	44.6 a	16.4 a
	Low	23.3 a	32.8 a	75.9 a	23.9 a
	Medium	42.3 a	105.3 b	187.8 a	38.1 a
	High	50.6 a	125.7 b	65.7 a	25.8 a

[1]Degree day accumulation base 10 C.

[2]Maintained plant density of L. decemlineata of 0 per plant from emergence to harvest.

[3]Initial population density level of P. penetrans established at planting.

[4]Columns followed by the same letter are not significantly different (P=0.05) according to the Student-Newman-Keuls Multiple Range Test.

Table 26. Simple correlation coefficients between P. penetrans and L. decemlineata and yield of S. tuberosum.

	Yield (1.83 M row)
Tuber initiation	
Leaf weight$_1$	.50841**
Root weight$_1$	.29326**
Tuber number	.17240**
Tuber bulking phase	
Leaf weight	.52749**
Root weight	.67337**
Average tuber wt.$_3$	.47217**
L. decemlineata	-.51371**
P. penetrans	
Soil$_1$	-.09496
Root$_1$	-.10077
Total$_1$	-.12366
Soil$_3$	-.05763
Root$_3$	.18678
Total$_3$	.14720

* Significantly different from r=0 at the 5% level

** Significantly different from r=0 at the 1% level

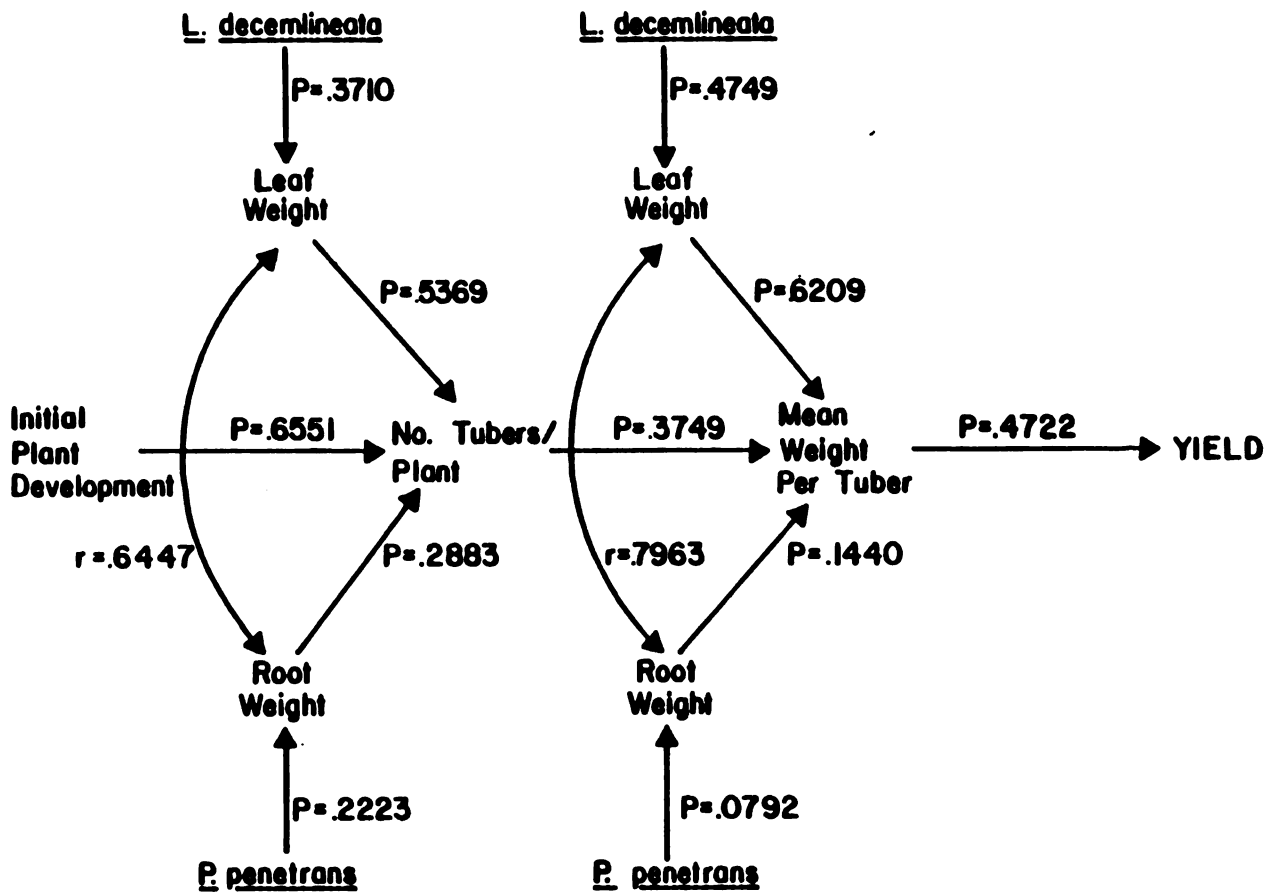

Figure 20. Path coefficient analysis of the components influencing final tuber yield of S. tuberosum (cv Superior).

highly significant (P=0.01) relationship and continued when L. decemlineata was correlated with any other yield component such as leaf weight, leaf area, tuber number, tuber weight, plant weight and stem weight (Table 26). The strength of this association increased with each successive sampling data. Highly significant (P=0.01) negative correlations of P. penetrans with these same parameters occurred mainly during the early stages of plant growth. As the season progressed, these same correlations decreased and changed sign. Only leaf weight and leaf area were significantly correlated with soil populations of P. penetrans and average tuber weight with root populations of P. penetrans. Both soil and root populations were only weakly negatively correlated with final tuber yield (Table 27). The degree of linear correlation between root population and yield not only changed sign, but the strength of the association increased.

Simple correlation coefficients between L. decemlineata and P. penetrans, including both soil and root populations, were negative and increased in value with time (Table 28).

Path coefficients were calculated according to the interrelationships between variables proposed in the path diagram. These results are represented in Figure 20. In the diagram, both leaf weight and the uncontrolled environmental effect are the most important components occurring during the early stages of plant growth with path coefficients of 0.5369 and 0.6551, respectively. This explains 86% of the total variability in the number of tubers initially formed. Changes in root weight explain only 8% of the total variability in the number of tubers formed per plant. The remaining 6% of the variability in tuber number per plant is explained by the interrelationship between leaf and root weight.

During the tuber growth phase, both the leaf and uncontrolled

Table 27. Simple correlation coefficients between P. penetrans and L. decemlineata and yield components of S. tuberosum.

	L. decemlineata	P. penetrans		
		Soil	Root	Total
Tuber Initiation Phase				
Leaf weight	-.3709**	-.4637**	-.2772**	.4044**
Root weight	-.2684**	-.3327**	-.1285**	-.2223**
Tuber number	-.1515	-.8143**	-.1678**	-.3210**
Tuber Bulking Phase				
Leaf weight	-.4749**	.1829**	.0491	.0837*
Root weight	-.4429**	.1003**	.0226	.0422
Average tuber wt.	-.5154**	-.0509	-.1442**	-.1354*

* Significantly different from r=0 at 5% level

** Significantly diffeent from r=0 at 1% level

Table 28. Simple correlation coefficients between L. decemlineata and P. penetrans.

	P. penetrans		
	Soil Population Density	Root Population Density	Total
L. decemlineata			
at tuber initiation	-.06460	-.13891	-.12895
at tuber bulking	-.20842	-.40597*	-.39591*

* Significantly different from r=0 at the 5% level

** Significantly different from r=0 at the 1% level

environmental effects are the most important components, explaining 71% of the variability in average tuber weight per plant. Changes in root weight during the tuber growth phase explaining 2% of the total variability. From this it appears that final tuber yield is determined mainly by the influences which occur later in the season during the tuber growth phase.

Introducing L. decemlineata and P. penetrans into the path diagram shows how the effects of each organism is mediated through the leaf and root systems, respectively. The greatest affect that P. penetrans has on final tuber yield occurs during the early stage of plant growth when tubers are being formed as indicated by the relative sizes of the path coefficients between P. penetrans and root weight and between root weight and its respective yield component. Not only is the path between root weight and tuber number greatest during the tuber initiation phase, P=0.2883, but the path coefficient between P. penetrans and root weight is greatest at this time, P=0.2223.

L. decemlineata exerts its primary influence on final tuber yield during the tuber growth phase. The relative affect that L. decemlineata has on leaf weight increases 9% as the season progresses, but it is during the tuber growth phase where the largest path coefficient (P=0.4749) or greatest contribution to final tuber yield is determined.

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Soil fumigation, nitrogen fertilizer and length of defoliation period by L. decemlineata all influenced final yield of S. tuberosum (Table 29). Total yield increased with nematicide and fertilizer application when no defoliation of S. tuberosum by L. decemlineata was permitted. Total yield was significantly

Table 29. Influence of selected management inputs on the final tuber yield of S. tuberosum (cv Superior).

Treatment			Tuber yield (quintal/ha)			
Defoliation[1]	Nitrogen[2] (kg/ha)	Fumigation[3] (l/ha)	5-8 cm	< 5 cm	> 8 cm	Total
None	0	0	265.7 bc[4]	8.0 ab	7.4 ab	281.0 b
	560	0	288.7 c	6.2 a	37.0 c	331.9 c
	0	93.5	282.9 c	10.0 abc	18.8 b	311.7 c
	560	93.5	289.4 c	7.6 ab	59.5 c	356.5 c
Early-season	0	0	205.4 a	9.9 abc	3.3 a	218.5 ab
	560	0	216.5 ab	7.1 ab	5.8 ab	229.4 ab
	0	93.5	218.1 ab	11.4 bc	3.3 a	232.7 ab
	560	93.5	207.0 a	7.6 ab	8.1 ab	222.7 ab
Full-season	0	0	209.4 a	7.3 ab	5.0 ab	221.7 ab
	560	0	197.1 a	9.0 abc	2.9 a	209.1 a
	0	93.5	226.1 ab	12.2 c	5.2 ab	243.6 ab
	560	93.5	221.7 ab	8.3 abc	10.0 ab	239.9 ab

[1]Foliar applications of Methamidiphos 10G; 3.4 kg/ha a.i. as needed for L. decemlineata control.

[2]Nitrogen fertilizer (NPK 20-10-10) applied at planting, plus 162.5 kg/ha Urea (45% N) at hilling on June 22, 1979.

[3]Telone II broadcast injected to a 20 cm soil depth on May 1, 1979.

[4]Column means followed by the same letter are not significantly different (P=0.05) according to the Student-Newman-Keuls Multiple Range Test.

(P=0.05) increased at the no defoliation level when compared to the unfertilized, fumigated full-season defoliation level. Total yields were significantly (P=0.05) increased at the no defoliation level, with the exception of the no defoliation level with no fertilizer or nematicide application. Highest total yield of Grade A (5-8 cm diameter) tubers was observed in the no defoliation levels (Table 29). Yield of A grade tubers was significantly (P=0.05) increased with no defoliation with the exception of the no defoliation unfertilized level with no nematicide. Highest total yield of B grade (< 5 cm diameter) occurred in both the early and full-season defoliation levels with nitrogen applied (Table 29). Yields of oversized tubers (> 8 cm diameter) increased with application of fertilizer (Table 29).

The affect of soil fumigation, nitrogen fertilizer and L. decemlineata defoliation on plant growth was inconclusive. No significant (P=0.05) differences in root fresh weight or in tuber number were observed season-long (Tables 30 and 31, respectively). No significant interaction between defoliation, fertilization or nematicide was detected. Foliage fresh weight was significantly (P=0.05) higher in the no defoliation level with nematicides during the final plant sampling (Table 32). Foliage fresh weight increased with soil fumigation, nitrogen fertilizer and as the length of the defoliation period decreased. Tuber fresh weights were generally lower as the length of the defoliation period increased and increased with fertilizer application (Table 33).

No significant (P=0.05) differences in the soil population densities of P. penetrans were observed except for the sample of August 6, 1979 (DD_{10C}=561.8). Soil population densities of P. penetrans were significantly (P=0.05) lower in the early season defoliation, fumigated levels without fertilizer compared to the unfertilized early-season defoliation levels with no

Table 30. Influence of selected management inputs on root fresh weight of S. tuberosum (cv Superior).

Treatment			Root fresh weight (Grams)[5]		
Defoliation[1]	Nitrogen[2] (kg/ha)	Fumigation[3] (l/ha)	317.0	556.8	934.0
None	0	0	7.4 a[4]	10.1 a	10.4 a
	560	0	8.1 a	13.4 a	12.4 a
	0	93.5	8.3 a	10.9 a	10.8 a
	560	93.5	7.3 a	9.7 a	12.8 a
Early-season	0	0	7.9 a	12.4 a	8.5 a
	560	0	6.0 a	12.2 a	12.3 a
	0	93.5	5.5 a	12.3 a	10.1 a
	560	93.5	6.6 a	9.0 a	10.7 a
Full-season	0	0	6.7 a	10.7 a	9.4 a
	560	0	7.2 a	10.9 a	10.4 a
	0	93.5	7.2 a	10.7 a	9.2 a
	560	93.5	6.7 a	13.4 a	8.6 a

[1]Foliar applications of Methamidiphos 10G; 3.4 kg/ha a.i. as needed for L. decemlineata control.

[2]Nitrogen fertilizer (NPK 20-10-10) applied at planting, plus 162.5 kg/ha Urea (45% N) at hilling on June 22, 1979.

[3]Telone II broadcast injected to a 20 cm soil depth on May 1, 1979.

[4]Column means followed by the same letter are not significantly different (P=0.05) according to the Student-Newman-Keuls Multiple Range Test.

[5]Degree day accumulation base 10 C.

Table 31. Influence of selected management inputs on the number of tubers of S. tuberosum (cv Superior).

Treatment			Tuber number per plant[5]		
Defoliation[1]	Nitrogen[2] (kg/ha)	Fumigation[3] (l/ha)	317.0	556.8	934.0
None	0	0	0.0[4]	11.3 a	8.3 a
	560	0	0.0	13.5 a	11.3 a
	0	93.5	0.0	11.8 a	9.2 a
	560	93.5	0.0	12.5 a	13.8 a
Early-season	0	0	0.0	13.0 a	8.8 a
	560	0	0.0	13.5 a	9.2 a
	0	93.5	0.0	13.6 a	18.7 a
	560	93.5	0.0	12.6 a	9.0 a
Full-season	0	0	0.0	9.5 a	7.8 a
	560	0	0.0	10.4 a	7.7 a
	0	93.5	0.0	12.7 a	8.3 a
	560	93.5	0.0	13.8 a	9.3 a

[1]Foliar applications of Methamidiphos 10G; 3.4 kg/ha a.i. as needed for L. decemlineata control.

[2]Nitrogen fertilizer (NPK 20-10-10) applied at planting, plus 162.5 kg/ha Urea (45% N) at hilling on June 22, 1979.

[3]Telone II broadcast injected to a 20 cm soil depth on May 1, 1979.

[4]Column means followed by the same letter are not significantly different (P=0.05) according to the Student-Newman-Keuls Multiple Range Test.

[5]Degree day accumulation base 10 C.

Table 32. Influence of selected management inputs on foliage fresh weight of S. tuberosum (cv Superior).

Treatment			Foliage fresh weight (Grams)[5]	
Defoliation[1]	Nitrogen[2] (kg/ha)	Fumigation[3] (l/ha)	556.8	934.0
None	0	0	76.9 a[4]	196.9 a
	560	0	76.9 a	418.6 b
	0	93.5	86.4 a	221.3 a
	560	93.5	56.2 a	408.7 b
Early-season	0	0	75.0 a	161.4 a
	560	0	56.1 a	239.0 a
	0	93.5	54.4 a	217.6 a
	560	93.5	58.8 a	210.6 a
Full-season	0	0	57.2 a	176.5 a
	560	0	63.4 a	203.6 a
	0	93.5	69.2 a	169.6 a
	560	93.5	51.5 a	200.9 a

[1]Foliar applications of Methamidiphos 10G; 3.4 kg/ha a.i. as needed for L. decemlineata control.

[2]Nitrogen fertilizer (NPK 20-10-10) applied at planting, plus 162.5 kg/ha Urea (45% N) at hilling on June 22, 1979.

[3]Telone II broadcast injected to a 20 cm soil depth on May 1, 1979.

[4]Column means followed by the same letter are not significantly different (P=0.05) according to the Student-Newman-Keuls Multiple Range Test.

[5]Degree day accumulation base 10 C.

Table 33. Influence of selected management inputs on tuber fresh weight of S. tuberosum (cv Superior).

Treatment			Tuber fresh weight (Grams)[5]	
Defoliation[1]	Nitrogen[2] (kg/ha)	Fumigation[3] (l/ha)	556.8	934.0
None	0	0	236.9 abc[4]	668.8 ab
	560	0	228.3 abc	958.1 b
	0	93.5	251.8 bc	778.3 ab
	560	93.5	153.3 abc	867.7 ab
Early-season	0	0	273.3 c	656.5 ab
	560	0	113.8 a	648.4 ab
	0	93.5	267.4 bc	774.6 ab
	560	93.5	135.9 ab	518.4 a
Full-season	0	0	204.2 abc	676.8 ab
	560	0	165.2 abc	566.9 ab
	0	93.5	271.7 c	724.9 ab
	560	93.5	209.3 abc	589.1 ab

[1]Foliar applications of Methamidiphos 10G; 3.4 kg/ha a.i. as needed for L. decemlineata control.

[2]Nitrogen fertilizer (NPK 20-10-10) applied at planting, plus 162.5 kg/ha Urea (45% N) at hilling on June 22, 1979.

[3]Telone II broadcast injected to a 20 cm soil depth on May 1, 1979.

[4]Column means followed by the same letter are not significantly different (P=0.05) according to the Student-Newman-Keuls Multiple Range Test.

[5]Degree day accumulation base 10 C.

Table 34. Influence of selected management inputs on plant fresh weight of S. tuberosum (cv Superior).

Treatment			Plant fresh weight (Grams)[5]		
Defoliation[1]	Nitrogen[2] (kg/ha)	Fumigation[3] (l/ha)	317.0	556.8	934.0
None	0	0	84.2 a[4]	274.0 ab	895.3 ab
	560	0	85.0 a	273.4 ab	1421.7 b
	0	93.5	94.7 a	284.8 ab	1032.7 ab
	560	93.5	63.5 a	183.6 ab	1317.1 ab
Early-season	0	0	83.0 a	310.5 b	844.0 ab
	560	0	62.1 a	150.0 a	923.2 ab
	0	93.5	59.9 a	302.8 b	1027.8 ab
	560	93.5	65.4 a	166.9 ab	757.4 a
Full-season	0	0	63.9 a	237.2 ab	876.8 ab
	560	0	70.6 a	199.5 ab	799.9 a
	0	93.5	76.3 a	305.0 b	924.9 ab
	560	93.5	58.2 a	252.3 ab	816.1 a

[1]Foliar applications of Methamidiphos 10G; 3.4 kg/ha a.i. as needed for L. decemlineata control.

[2]Nitrogen fertilizer (NPK 20-10-10) applied at planting, plus 162.5 kg/ha Urea (45% N) at hilling on June 22, 1979.

[3]Telone II broadcast injected to a 20 cm soil depth on May 1, 1979.

[4]Column means followed by the same letter are not significantly different (P=0.05) according to the Student-Newman-Keuls Multiple Range Test.

[5]Degree day accumulation base 10 C.

Table 35. Influence of selected management inputs on soil population densities of Pratylenchus penetrans on S. tuberosum (cv Superior).

Treatment			P. penetrans / 100 cm^3 soil[5]					
Defoliation[1]	Nitrogen[2] (kg/ha)	Fumigation[3] (l/ha)	47.1	137.6	319.8	561.8	920.1	1204.1
None	0	0	42.8a[4]	28.0ab	20.4a	80.6b	178.4a	97.6b
	560	0	45.0a	29.4ab	17.0a	24.0ab	157.0a	78.4b
	0	93.5	59.8a	21.6ab	15.4a	26.8ab	115.2a	36.8a
	560	93.5	40.2a	18.0ab	19.6a	18.8ab	73.4a	24.4a
Early-season	0	0	34.2a	22.0ab	25.8a	80.8b	149.8a	61.2a
	560	0	46.0a	29.4ab	28.8a	9.2a	97.2a	62.2a
	0	93.5	43.0a	22.2ab	20.8a	41.0ab	128.6a	51.0a
	560	93.5	28.4a	6.6a	11.0a	15.2a	65.8a	36.8a
Full-season	0	0	31.4a	26.8a	28.6a	35.4a	160.8a	75.4b
	560	0	24.0a	43.4b	17.6a	21.4ab	94.6a	52.4a
	0	93.5	35.2a	11.0ab	18.2a	24.8ab	240.0a	26.4a
	560	93.5	31.4a	10.0ab	14.6a	18.2ab	78.0a	35.4a

[1]Foliar applications of Methamidiphos 10G; 3.4 kg/ha a.i. as needed for L. decemlineata control.

[2]Nitrogen fertilizer (NPK 20-10-10) applied at planting, plus 162.5 kg/ha Urea (45% N) at hilling on June 22, 1979.

[3]Telone II broadcast injected to a 20 cm soil depth on May 1, 1979.

[4]Column means followed by the same letter are not significantly different (P=0.05) according to the Student-Newman-Keuls Multiple Range Test.

[5]Degree day accumulation base 10 C.

Table 36. influence of selected management inputs on root population density of Pratylenchus penetrans on S. tuberosum (cv Superior).

Treatment			P. penetrans per gram root tissue[5]		
Defoliation[1]	Nitrogen[2] (kg/ha)	Fumigation[3] (l/ha)	514.2	668.3	954.1
None	0	0	104.6 a[4]	147.0 a	411.0 a
	560	0	82.8 a	150.8 a	386.0 a
	0	93.5	96.4 a	189.2 a	563.6 a
	560	93.5	50.2 a	118.4 a	288.0 a
Early-season	0	0	96.0 a	289.6 a	573.2 a
	560	0	85.4 a	143.4 a	490.6 a
	0	93.5	98.4 a	240.6 a	325.8 a
	560	93.5	54.0 a	102.2 a	207.4 a
Full-season	0	0	89.6 a	156.6 a	407.2 a
	560	0	73.2 a	171.6 a	300.6 a
	0	93.5	85.0 a	195.2 a	447.8 a
	560	93.5	49.6 a	64.8 a	284.8 a

[1]Foliar applications of Methamidiphos 10G; 3.4 kg/ha a.i. as needed for L. decemlineata control.

[2]Nitrogen fertilizer (NPK 20-10-10) applied at planting, plus 162.5 kg/ha Urea (45% N) at hilling on June 22, 1979.

[3]Telone II broadcast injected to a 20 cm soil depth on May 1, 1979.

[4]Column means followed by the same letter are not significantly different (P=0.05) according to the Student-Newman-Keuls Multiple Range Test.

[5]Degree day accumulation base 10 C.

nematicide (Table 35). There were no significant (P=0.05) differences in root population densities of P. penetrans season-long (Table 36).

DISCUSSION

Few studies have been conducted to examine the joint interaction of plant pests. Only recently has emphasis been placed on the importance of identifying crop losses associated with the joint action of organisms affecting plant growth, development and yield. Knowledge of these associations will enhance our basic understanding of the dynamics of complex agro-ecosystems and aid in the development of new pest management strategies.

Potato plants are influenced by sets of dynamic biotic and abiotic factors. Many of these factors remained uncontrolled when these studies were conducted in the field. These studies were conducted to determine the affects of L. decemlineata and P. penetrans on the growth of the potato plant in its natural environment. The uncontrolled environmental effects represent a major influence affecting plant growth in these studies. A significant portion of the variability in the number of tubers formed and the average tuber weight is not explained by the effects of L. decemlineata and P. penetrans. The sources of this variability can be attributed to such factors as genetic variability, uncontrolled environmental and pathological factors and experimental error. complementary studies need to be conducted both in field and laboratory settings where the abiotic and biotic factors can be more rigidly controlled. Adequate replication, involving more factors, may need to be examined to explain the differences in growth, development and yield of S. tuberosum.

P. penetrans and L. decemlineata are major pests of the Michigan potato cropping system. The symptoms commonly associated with P. penetrans are a

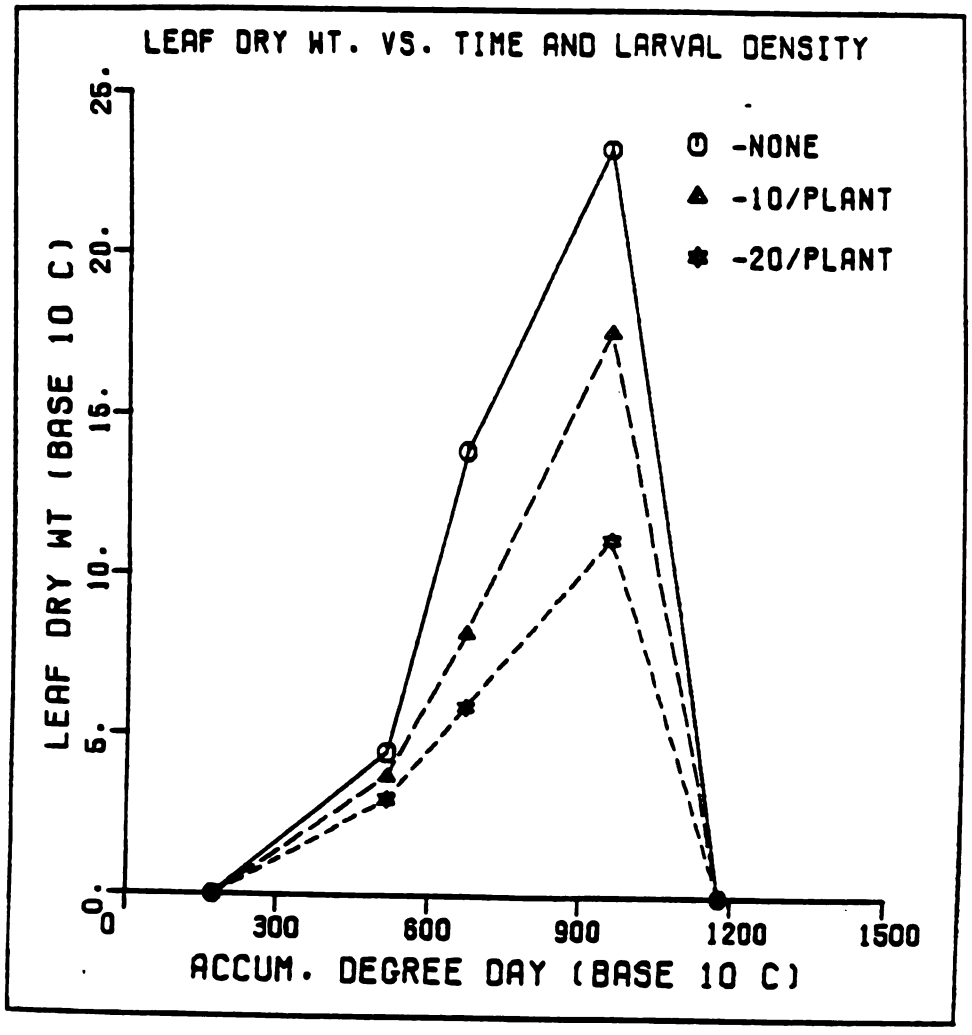

Figure 21. Influence of three plant densities of L. decemlineata on leaf dry weight of S. tuberosum (cv Superior).

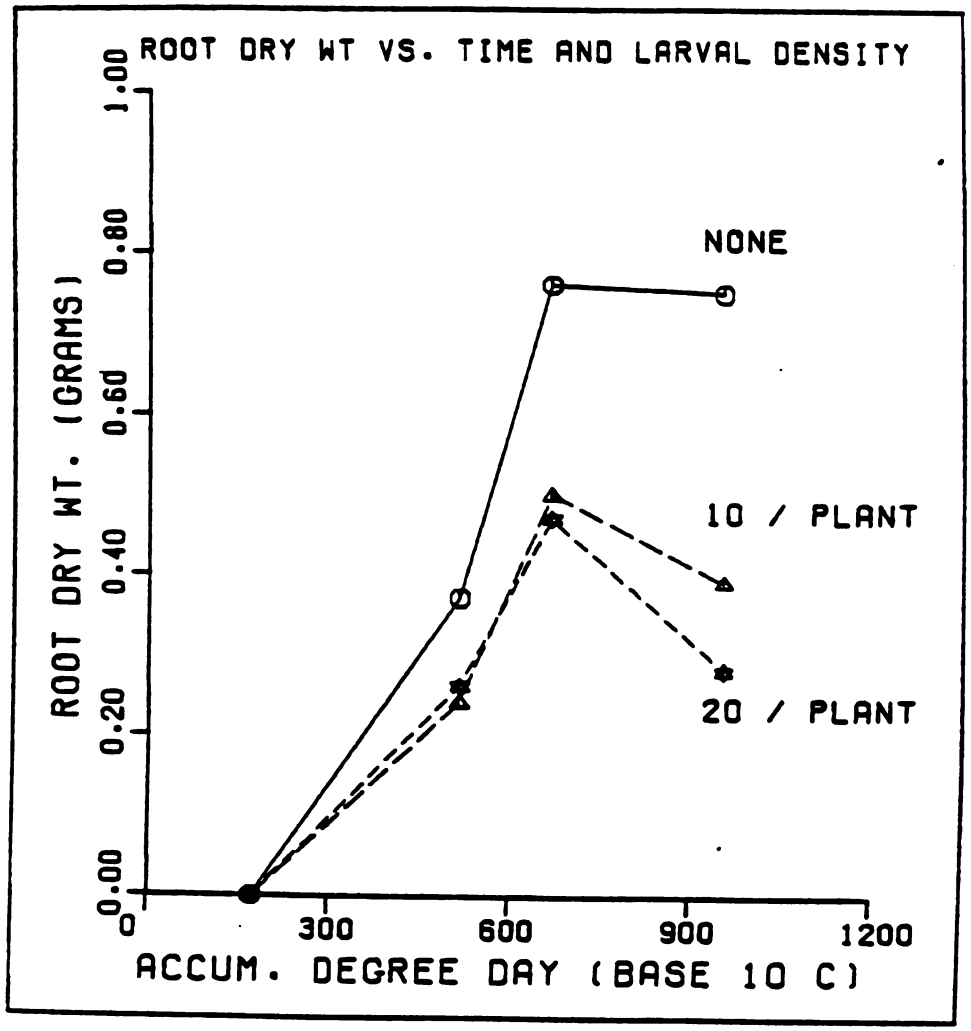

Figure 22. Influence of three plant densities of L. decemlineata on root dry weight of S. tuberosum (cv Superior).

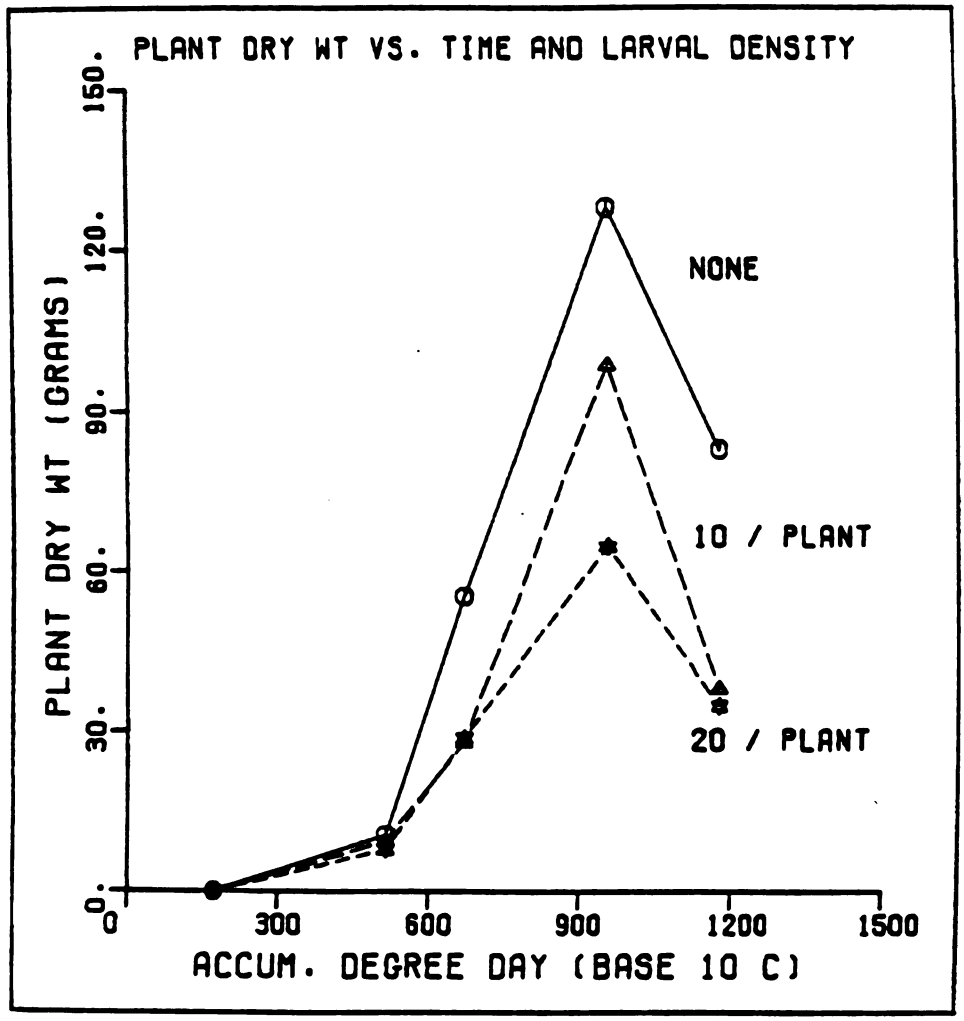

Figure 23. Influence of three plant densities of L. decemlineata on plant dry weight of S. tuberosum (cv Superior).

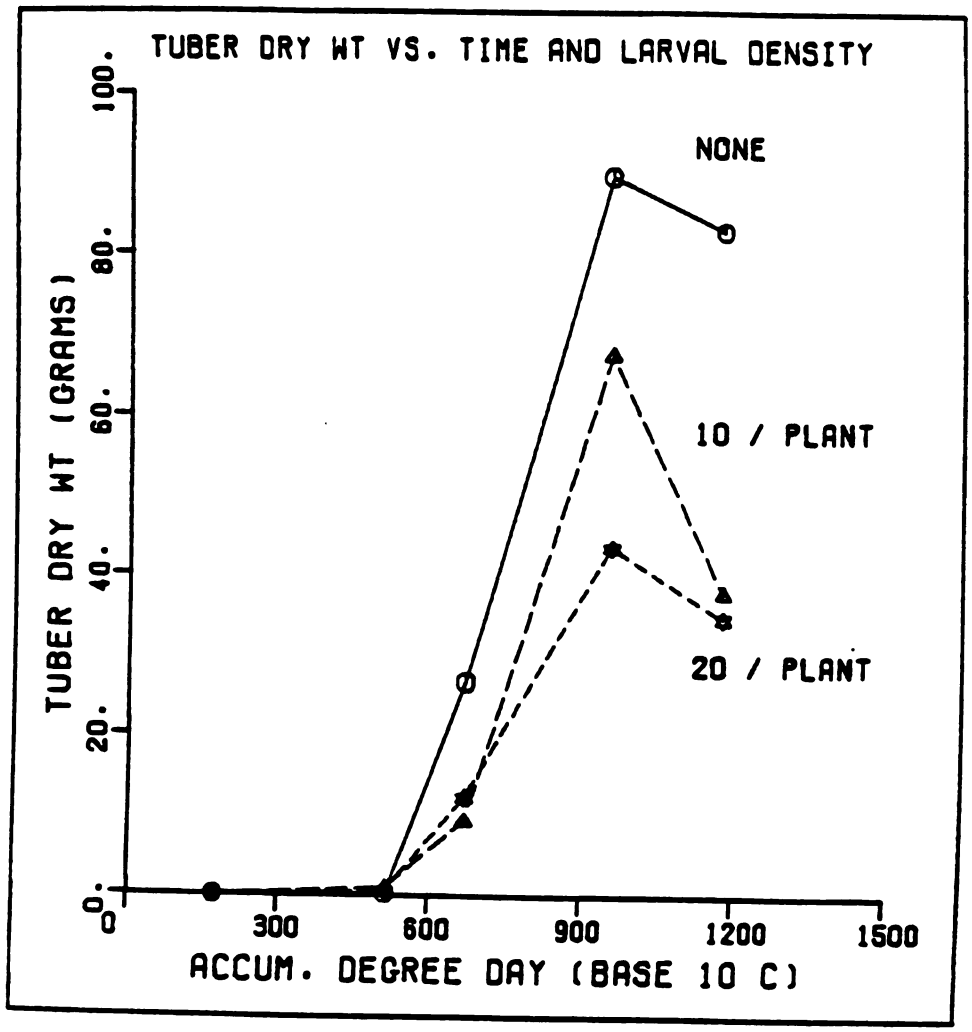

Figure 24. Influence of three plant densities of L. decemlineata on tuber dry weight of S. tuberosum (cv Superior).

gradual decline or lack of plant vigor. This is in stark contrast to the rapid, striking changes that occur as a result of defoliation of potato plants by L. decemlineata. Despite the dramatic overt differences, both pests can significantly influence growth, development and yield by the effects mediated through the root and leaf systems, respectively.

L. decemlineata and the affect it has on the leaf system is the most important biotic component influencing final tuber yield. The direct effect of L. decemlineata feeding is a reduction in leaf weight and leaf surface area. Defoliation increases with time as the larvae advance through successive instars and densities increase (Fig. 21). As beetles reduce leaf dry weight, there is a corresponding reduction in the plant root dry weight (Fig. 22). This is evidently a beetle-mediated plant response to severe levels of defoliation. These changes in the leaf and root systems are directly reflected in the reduced plant and tuber weights through time for the beetle-infested treatments (Figs. 23 and 24, respectively). L. decemlineata exerts its primary influence on final tuber yield during the tuber growth phase (Fig. 25). This is indicated in the path diagram by an increase with time in the affect of L. decemlineata on leaf weight as well as an increase in the affect of leaf weight on its respective yield component. Grafius (unpublished data) showed that defoliation occurring later in the season was far more important in determining final tuber yield than defoliation occurring earlier in the season. These results provide further evidence of the importance of late-season defoliation by L. decemlineata on final tuber yield. Future insect control recommendations based on crop phenology and field population densities of L. decemlineata are needed.

The response of plant growth to various soil population densities of P. penetrans in these studies was negligible. Few significant differences

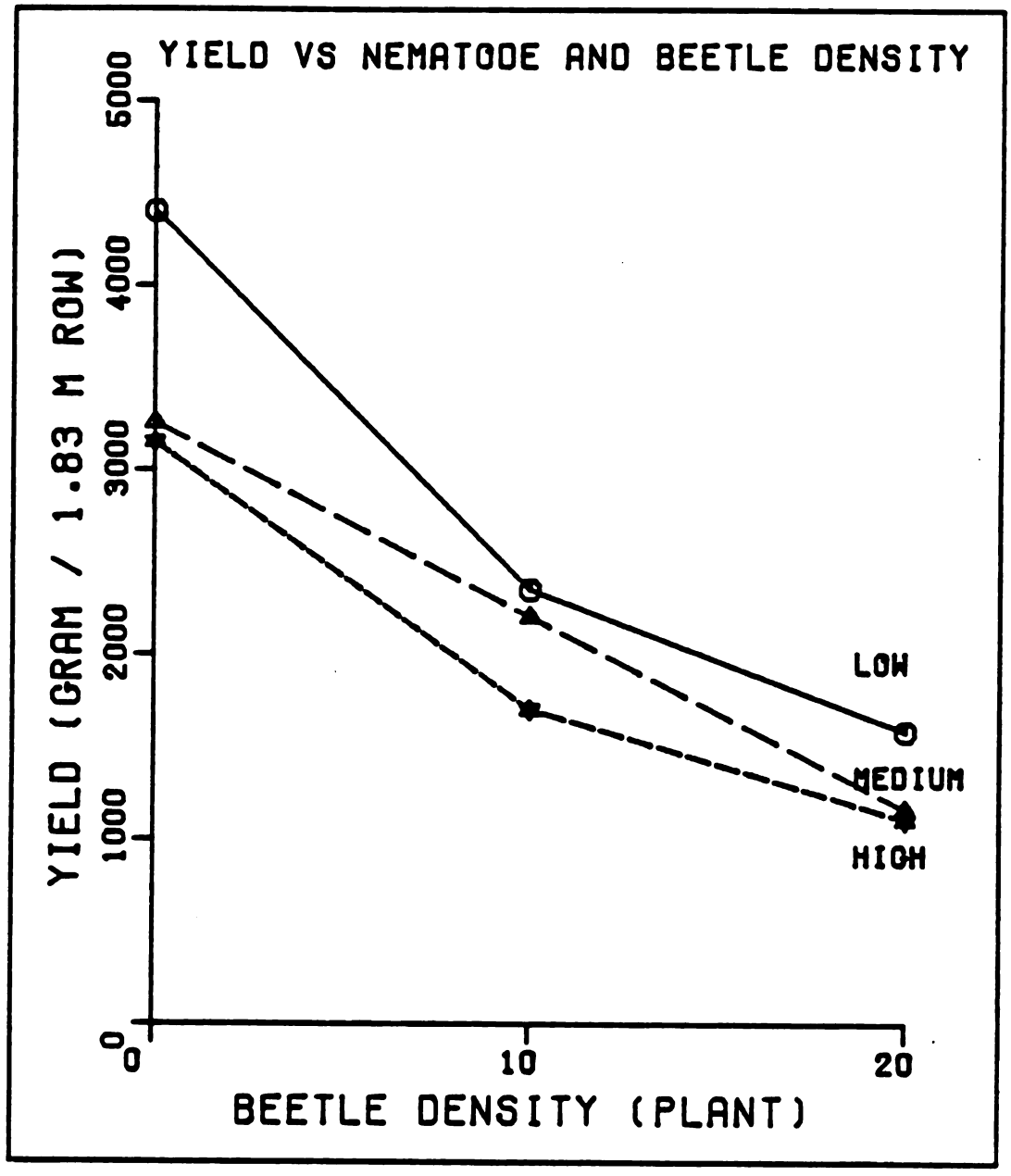

Figure 25. Influence of three population levels of P. penetrans and L. decemlineata on final tuber yield of S. tuberosum (cv Superior).

attributable to P. penetrans were evident in any of the measured plant growth parameters. Changes in root weight, which are typically used as indicators of plant response to nematode infection, were small and statistically not significant. Examining this relationship through path coefficient analysis showed that the impact of P. penetrans on root weight and influence of root weight on final tuber yield decreased as the season progressed. The major impact of P. penetrans on final tuber yield was associated with a reduction in the number of tubers formed during the early stages of plant development. A more accurate assessment of the influence of P. penetrans on plant growth may have been possible if variables which compared the inhibition or interference of root function had been used. Collecting and quantifying information of this kind is expensive, time-consuming and may have some technological constraints.

P. penetrans may have been biologically more important in its affect on the nutrient relationships of the potato plant. This is exhibited in the response of S. tuberosum to fertilizer and soil fumigants. Even though the results are inconclusive, they do indicate an increased level of plant growth and yield response to nitrogen fertilizers when nematodes are reduced to low population levels in the field. Research needs to be continued into the affect of P. penetrans on the water and nutrient relationships associated with potato plant growth.

Both P. penetrans and L. decemlineata affect final tuber yield, with L. decemlineata having the most significant impact in terms of decreasing yields (Fig. 25). Total yield of potatoes decreased 66% with increasing beetle densities per plant and 27% with increasing population density of P. penetrans. The joint impact of P. penetrans and L. decemlineata was additive in their

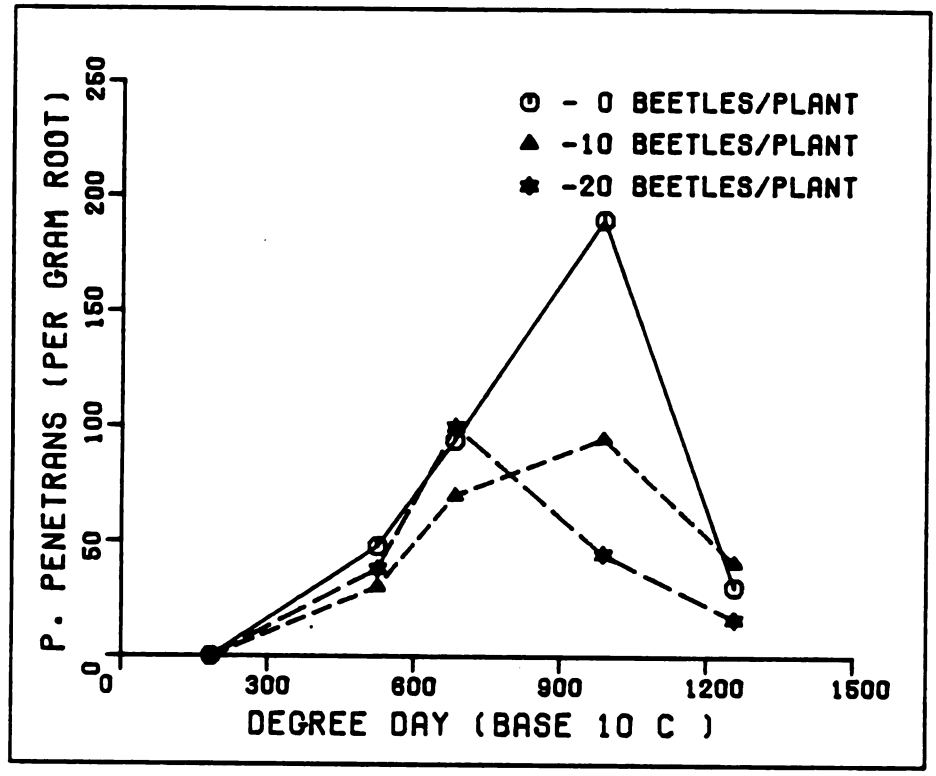

Figure 26. Influence of three plant densities of L. decemlineata on the root population density of P. penetrans.

effects on final tuber yield. Knowledge of the effects of various pests and the critical stage of plant susceptibility to these pests will aid in the development of economic thresholds that take into account the joint action concept.

It was hypothesized that the response of S. tuberosum to various combinations of stress would, in turn, influence the growth and reproductive rate of L. decemlineata and P. penetrans. No plant-mediated effects were observed that influenced larval populations of L. decemlineata. The nematode populations wee not at levels which significantly affected the quantity or apparent quality of leaf material available to L. decemlineata. This may possibly occur when nematode populations are at levels which would stunt the growth of the plant and limit the food resources available to L. decemlineata.

Larval feeding by L. decemlineata appears to directly influence the population dynamics of P. penetrans. By reducing the leaf weight through time, beetle feeding influences the size of the total root system available for nematode colonization. Smaller, less extensive root systems would limit the number of soil nematodes directly exposed to roots in close proximity, thereby reducing the probability of infection and survival. Even the nematodes which do find and penetrate potato roots are influenced by L. decemlineata defoliation. As L. decemlineata feeding continued into the season, a shift in plant maturity occurred. Early defoliation appeared to delay plant maturity. As defoliation increased, the plant was incapable of providing the necessary photosynthates to sustain normal growth. This resulted in an early senescence in roots and a decrease in the number of P. penetrans per gram of root (Fig. 26). A number of possible mechanisms to explain this are possible (e.g., limited reinfection from soil and root nematodes, a decrease in the survival or reproductive potential of females within the roots). A change in the nutritional

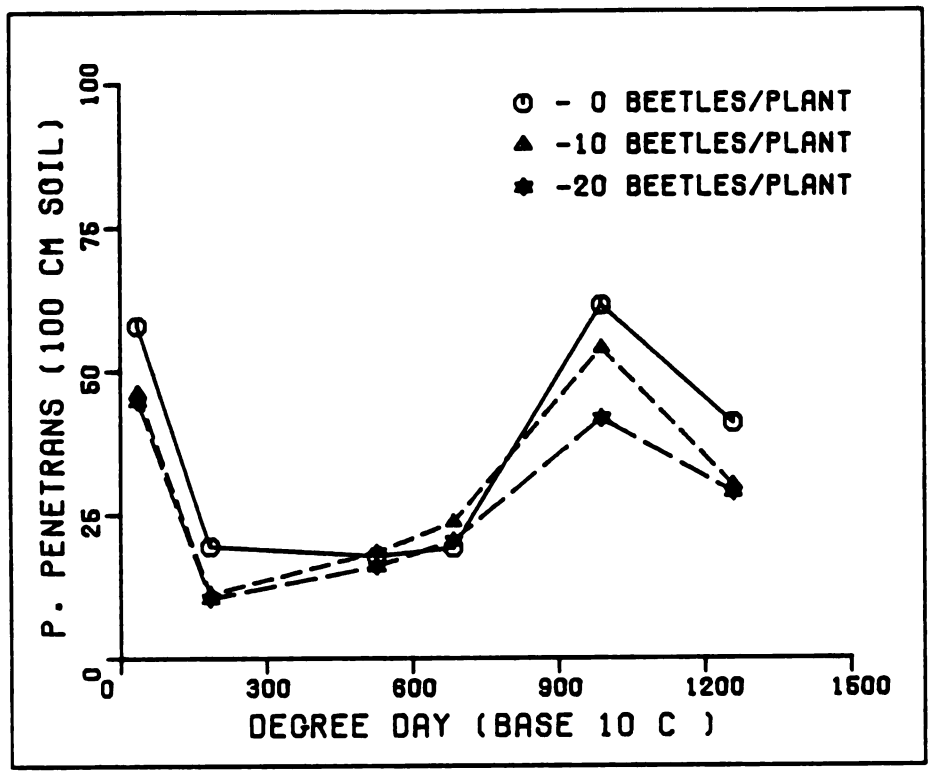

Figure 27. Influence of three plant densities of L. decemlineata on the soil population density of P. penetrans.

quality of the roots perhaps occurred which resulted in the decrease in the number of P. penetrans per gram of root in the beetle-infested treatments. This would explain why P. penetrans were not recovered in the root extraction procedures. No differences were observed in soil population densities of P. penetrans at the defoliation levels (Fig. 27).

Path coefficient analysis (PCA) was used in this study as a conceptual framework for data collection as well as a method for analyzing the results. It was used in addition to other analytical techniques. PCA was not used as a procedure for demonstrating cause and effect. It was used as a descriptive and intepretive tool to evaluate the interrelationships between variables. The technique was based on the construction of a qualitative diagram in which the path coefficients were calculated according to a specified format provided in the path diagram (Fig. 20). The diagram assumes that unit changes in leaf or root weight caused by L. decemlineata and P. penetrans, respectively, will produce changes in the various yield components of S. tuberosum. It should be noted that any ambiguities in the underlying assumptions of the path diagram will lead to ambiguities in the results obtained through path coefficient analysis. The proposed structure of the path diagram and its underlying biological and physiological assumptions must therefore be closely scrutinized and evaluated.

The path diagram is based on the sequential development of S. tuberosum and the influence P. penetrans, L. decemlineata and the environment have on the plant during their respective developmental stages. Each step in the sequence is influenced by a set of environmental factors, as well as what has occurred during earlier stages. The plant has distinct, time-ordered developmental stages in which the relationships between leaves, roots and

tubers is dynamic. The results obtained represent an assessment of the impact of stress at different times during S. tuberosum phenology. This analysis assumes that the effects of various biotic and abiotic influences can be measured at distinct points in time and space. The effects measured at these times must be representative of the impacts that the plant stress factors have on plant growth.

The interpretation of the path diagram is applicable only to the current state of the plant at the time plant samples were taken. Evaluating the effects of stress at any other time will not change the structure of the path diagram but could have a significant impact on the magnitude of the path coefficients. This can be vividly illustrated during the tuber initiation process. The phenology of the potato plant follows a distinct developmental sequence in which tubers are initiated at various times during the growth of the plant. They are continually being formed and reabsorbed during plant development. Temporary delays in plantmaturity due to pest population pressures may result in significant differences in the number of tubers observed between treatments at any one point in time. These differences in plant response ma not be evident during later plant sampling dates. Genetic variability in the population of plants being sampled may also obscure these biological and physiological relationships, especially if the number of samples or replications with the experimental design is small. Sampling errors associated with such dynamic processes as tuber formation and the obtaining of representative plant samples during these developmental processes can be great, and can lead to misinterpretation of the data. When studying correlations, it is of utmost importance to recognize the nature of the population under consideration, inasmuch as the magnitude of the correlation coefficients and the

corresponding path coefficients from which they are derived can be influenced by the choice of individuals upon which the observations are made.

Regardless of the apparent limitations involved in the interpretation of the results, path coefficient analysis does provide some useful insights into the dynamics of S. tuberosum growth, development and yield. The technique, when used in the initial conceptualization of an experiment, allows the investigator to hypothesize on how the interacting biological forces drive the system. Other statistical techniques such as regression or simple correlation analysis do not provide these powers of interpretation. They are concerned with quantitatively estimating the relationships between dependent and independent variables. It has no point of view other than describing a linear relationship among variables. Other analytical techniques have the same shortcomings.

Path coefficient analysis is flexible in that any number of variables can be examined in a more holistic and systematic manner. In this analysis, the simplest design with the fewest number of variables which will adequately describe the system within a predetermined level of precision can be determined. Not only can plant growth response to outside perturbations be speculated upon, but levels of importance can be assigned to the variables describing the interrelationships of the system.

Path coefficient analysis' most useful role in research is not in the final stages of a research program, but rather it is during the early stages when a sensitivity analysis is needed to identify the most important components influencing the trajectory of the system. Research priorities and allocation of resources can thus be optimized.

SUMMARY

Field experiments were used to evaluate the roles of nitrogen, phosphorus and edaphic pesticides on the growth, development and yield of S. tuberosum and the population dynamics of P. penetrans. Further studies examining the joint role of P. penetrans and L. decemlineata on the growth, development and yield of S. tuberosum and the biology of the concomitant species were conducted. To recapitulate some of the important findings:

1. Tuber yields decreased with increasing plant densities of L. decemlineata and P. penetrans.
2. Tuber yields increased with increasing fertilizer rate of N and P.
3. Both N and P influence the phenological development of S. tuberosum and the attainment of final tuber yield.
4. Neither N nor P had any detectable influence on P. penetrans population dynamics.
5. There was no significant interaction between fertilizer and edaphic pesticide on the growth, development and yield of S. tuberosum or the population dynamics of P. penetrans.
6. Control of P. penetrans and L. decemlineata can greatly increase tuber yield.
7. Based on P. penetrans recovered from soil and root tissue, aldicarb provided the best season-long control.
8. It appears that P. penetrans most important influence on tuber yield is through its affect on tuber set. Control of P. penetrans increased tuber set and then N or P limited yield. With an increase in N or P rate, the small tubers increased in size.

9. P. penetrans affects final tuber yield in its alteration of the nutrient requirements of S. tuberosum for optimizing yield.
10. The fungicidal properties of edaphic pesticides needs to be examined more closely in relation to tuber yields to explain why yields increase in some cases even though control of P. penetrans could not be detected.
11. Significant error factors may be involved with measuring plant biomass in units of plant fresh weight.
12. Path coefficient analysis was used as an interpretive tool to identify the importance of L. decemlineata and P. penetrans and the environmental influences on the yield of S. tuberosum. P. penetrans most important affect on S. tuberosum occurred during the tuber initiation phase, reducing tuber set. L. decemlineata's most important effect occurred during the tuber bulking phase, reducing tuber size.
13. L. decemlineata significantly increased the number of tubers in the smaller tuber size categories and decreased the number in the larger tuber size categories.
14. L. decemlineata significantly reduced the total weight of tubers in the larger tuber size categories.
15. L. decemlineata, by reducing leaf weight or surface area, reduced population densities of P. penetrans by influencing the size and possible nutritional quality of the root system.

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APPENDIX A

APPENDIX A

N data - 1978

MATERIALS AND METHODS

ROLE OF SOIL NUTRIENTS AND NEMATICIDES ON S. TUBEROSUM AND P. PENETRANS

A field experiment was conducted in 1978 to evaluate the role of soil nutrients and nematicides on the growth of S. tuberosum and the population dynamics of P. penetrans. Two potato cultivars (Superior and Russet Burbank) were grown on a McBride sandy loam soil (alfic fragiothods) at the Montcalm Potato Research Farm in Entrican, Michigan. The farm is separated into two large north-south rectangular blocks (Fig. 3). During any year, one block is utilized for current experimental research while the other block is spring planted to rye or alfalfa. The following spring it is disked and planted. Blocks are rotated every other year to enhance soil organic content and to reduce populations of soil-borne organisms and insects detrimental to S. tuberosum.

Planting Procedure

Seed pieces (whole certified seed > 5 cm diameter) were planted on May 22 and 23, 1978. Each plot consisted of four rows 0.86 m wide and 15.24 m long with seed spacing of 20 cm. All plots were irrigated with a solid set sprinkler system according to need determined by measurements of evapotranspiration.

Sampling Procedure

Plant growth and development was measured at various intervals during 1978 and 1979. The experimental area was first divided into 5 blocks of equal size to compare sampling variation within and between treatments.

In 1978 an additional study was conducted to examine the joint role of nitrogen fertilizer and nematicides. In sampling foliage, two plants were randomly selected from the outside rows of each plot. The soil immediately below each plant was carefully removed to a depth of ca 0.35 m. In 1978, the soil directly below each plant sample was hand-sifted for roots and tubers.

Soil and root populations of P. penetrans were estimated from samples taken at these times. Soil samples for nematode analysis were taken by core sampling (15-20 cores) the two outside rows of each plot and later, after plant germination, by removing the soil adjacent to the roots of the plant. Root samples were derived from plants returned to the laboratory for plant growth analysis. Soil and root populations of P. penetrans were determined using the centrifugation-flotation technique (Jenkins, 1964) and shaker technique (Bird, 1971), respectively. Estimates of soil and root nematode population densities were based on 10 cm^3 of soil and 0.1 gram of root.

At various intervals during the 1978 season, both a 10 and a 100 cm^3 soil and 0.1 and 1.0 gram root tissue sample were processed to compare the efficiency and reliability of the estimates achieved by both methods. This was achieved first by agitating the 10 ml vial of nematode suspension and extracting 1.0 ml with a 1.0 ml syringe. Nematodes were counted in a circular petri dish under a 15X dissecting microscope. Immediately afterwards, the remaining 9.0 ml of nematode suspension was counted and recorded.

Harvesting Procedure

Tuber yields were calculated from the harvest of the two center rows of each plot with a self-propelled potato harvester specifically developed for field research (Chase et al., 1978). Tubers from each plot were graded and weighed.

A completely random block-two factorial design was used, with each treatment replicated five times. The data was subjected to an analysis of variance to statistically examine differences in plant growth, development, yield and nematode control.

Nitrogen

A field experiment was conducted in 1978 to examine nitrogen levels and their interactions with selected insect and nematode control programs and to monitor growth, development and yield of S. tuberosum (cv Superior). In this experiment (Table 2), five pesticide treatments (control, aldicarb (Temik 15G), 1,3-D+MIC (Vorlex), carbofuran (Furadan 10G), and thiofanox (Dacamox 10G)) were evaluated on cv Superior growth at two nitrogen rates (84 and 168 kg/ha). All plots received 84 kg/ha of N, P_2O_5 and K_2O (15-15-15) as a starter fertilizer banded 5 cm to the side and below the seed piece. The plots to receive an added nitrogen treatment were side-dressed with urea (45% N) at an application rate of 112 kg/ha on June 13, 1978, and 84 kg/ha on June 22, 1978.

In the second nitrogen experiment in 1978, nitrogen application rate and nematicide treatment contributed significantly (P=0.05) to the total yield (Table 10). Both aldicarb and 1,3-D + MIC, at each nitrogen rate, significantly (P=0.05) increased total yield above the controls. With each nematicide used in this test, higher total yields generally occurred at the greater nitrogen rate. The 168 kg/ha nitrogen rate increased the average yield by 4%, but this was not

significant. Yield of A size tubers was similar to total yield results. The 1,3-D + MIC at both nitrogen rates was significantly (P=0.05) greater than the controls. Only thiofanox at the higher nitrogen rate significantly (P=0.05) increased large size tuber yield. There were no significant (P=0.05) differences in B size tuber yield, although thiofanox at both nitrogen rates resulted in the lowest yield.

Nitrogen fertilization had no significant (P=0.05) affect on nematode population dynamics. Aldicarb significantly (P=0.05) reduced soil population densities of P. penetrans (Table 11). This continued season-long until harvest. Significant (P=0.05) differences in root population density of P. penetrans between plots were apparent season-long (Table 12). Aldicarb at the 84 kg/ha nitrogen rate generally reduced root population densities season-long over all plots. Results of root samples taken from July 12, 1978, to harvest showed that aldicarb at both nitrogen rates resulted in the best nematode control. Carbofuran appeared to decrease root and soil population densities of P. penetrans but was significantly (P=0.05) different only from a control on August 1, 1978.

Few significant (P=0.05) differences in root weight occurred throughout the season (Table 13). Carbofuran at the higher nitrogen rate significantly (P=0.05) increased root weight during the sample of June 25, 1978. This may have, by increasing root weight early, contributed to the higher soil and root population densities of P. penetrans observed in these plots. It appears that thiofanox at both nitrogen rates delays the growth and development of the foliage and tubers (Tables 14 and 15, respectively). This resulted in lower foliage and tuber weights during early season and significantly (P=0.05) higher plant and tuber weights during the final sample. This may be due in part to the nematicidal and/or plant growth characteristics of this material.

Table A1. Influence of selected management inputs on population density of P. penetrans on potatoes (cv Superior).

Treatment		P. penetrans per 10 cm^3 soil[4]					
Nitrogen (kg/ha)	Pesticide	139.2	241.2	373.5	543.8	768.0	983.3
84	Check	1.2 a[1]	3.8 a	4.0 a	2.8 a	5.4 b	8.4 b
84	Aldicarb[2]	0.4 a	0.2 a	0.0 a	0.0 a	0.0 a	0.2 a
84	1,3-d & MIC[3]	0.8 a	0.4 a	1.0 a	2.0 b	1.2 b	3.6 b
84	Carbofuran[2]	0.6 a	0.4 a	4.0 a	0.6 a	4.2 b	7.6 b
84	Thiofanox[2]	0.8 a	1.0 a	5.0 a	0.8 a	1.4 b	5.0 b
168	Check	1.8 a	1.4 a	6.0 a	3.0 b	5.6 b	9.2 b
168	Aldicarb	1.0 a	0.0 a	0.0 a	0.0 a	0.4 a	0.2 a
168	1,3-D & MIC	2.6 a	0.2 a	4.0 a	2.6 a	3.4 a	3.8 a
168	Carbofuran	1.0 a	0.8 a	2.0 a	2.6 a	3.8 a	5.4 a
168	Thiofanox	1.0 a	1.2 a	1.0 a	1.4 a	1.6 a	5.4 a

[1]Column means followed by the same letter are not significantly different (P=0.05) according to the Student-Newman-Keuls Multiple Range Test.

[2]Applied at planting in the fertilizer furrow at a rate of 3.4 kg a.i./ha.

[3]Injected on a broadcast basis to a soil depth of 20 cm at the rate of 93.5 l/ha on May 1, 1979.

[4]Degree day accumulation base 10 C.

Table A2. Influence of selected management inputs on population density of P. penetrans on potato (cv Superior).

Treatment		P. penetrans per 0.1 g root tissue[4]				
Nitrogen (kg/ha)	Pesticide	241.2	373.5	543.8	768.0	983.3
84	Check	44.4 b[1]	3.8 b	10.2 bc	36.8 c	6.0 ab
84	Aldicarb[2]	2.0 a	0.0 a	0.2 a	0.0 a	0.2 a
84	1,3-D & MIC[3]	20.2 ab	5.6 c	8.4 bc	10.2 b	3.2 ab
84	Carbofuran[2]	13.0 ab	2.4 bc	5.2 bc	23.2 bc	18.0 ab
84	Thiofanox[2]	20.2 ab	1.4 bc	7.4 bc	6.2 b	5.8 ab
168	Check	16.0 ab	4.0 c	18.0 c	38.6 c	14.8 b
168	Aldicarb	3.2 ab	1.8 ab	0.4 a	0.0 a	0.2 a
168	1,3-D & MIC	14.4 ab	2.6 bc	6.4 bc	18.8 b	7.8 ab
168	Carbofuran	22.6 ab	6.2 c	11.6 bc	12.2 b	5.8 ab
168	Thiofanox	8.8 ab	1.4 bc	3.4 b	6.8 b	13.8 b

[1]Column means followed by the same letter are not significantly different (P=0.05) according to the Student-Newman-Keuls Multiple Range Test.

[2]Applied at planting in the fertilizer furrow at a rate of 3.4 kg a.i./ha.

[3]Injected on a broadcast basis to a soil depth of 20 cm at the rate of 93.5 l/ha on May 1, 1978.

[4]Degree day accumulation base 10 C.

Table A3. Influence of selected management inputs on the root weight of potatoes (cv Superior).

Treatment		Root Weight (grams)[4]				
Nitrogen (kg/ha)	Pesticide	241.2	373.5	543.8	768.0	983.3
84	Check	3.1 a[1]	8.9 ab	10.1 a	11.2 a	5.3 a
84	Aldicarb[2]	3.9 a	9.7 ab	11.8 a	10.5 a	5.2 a
84	1,3-D & MIC[3]	3.5 a	9.0 ab	11.3 a	8.3 a	4.7 a
84	Carbofuran[2]	4.5 a	9.5 ab	10.3 a	10.5 a	5.3 a
84	Thiofanox[2]	3.8 a	8.7 ab	10.4 a	10.3 a	4.5 a
168	Check	3.8 a	8.8 ab	9.5 a	10.0 a	5.3 a
168	Aldicarb	3.5 a	9.7 ab	10.9 a	9.3 a	4.4 a
168	1,3-D & MIC	4.1 a	10.2 ab	12.3 a	9.2 a	4.9 a
168	Carbofuran	4.0 a	11.2 b	13.7 a	10.6 a	5.0 a
168	Thiofanox	3.0 a	6.6 a	9.9 a	9.9 a	6.8 a

[1]Column means followed by the same letter are not significantly different (P=0.05) according to the Student-Newman-Keuls Multiple Range Test.

[2]Applied at planting in the fertilizer furrow at a rate of 3.4 kg a.i./ha.

[3]Injected on a broadcast basis to a soil depth of 20 cm at the rate of 93.5 l/ha on May 1, 1978.

[4]Degree day accumulation base 10 C.

Table A4. Influence of selected management inputs on the foliage weight of potatoes (cv Superior).

Treatment		Foliage Weight (grams)[4]				
Nitrogen (kg/ha)	Pesticide	241.2	373.5	543.8	768.0	983.3
84	Check	27.2 a[1]	290.3 ab	609.7 a	475.3 a	55.7 a
84	Aldicarb[2]	29.6 a	334.1 ab	744.0 a	562.3 a	88.4 a
84	1,3-D & MIC[3]	28.8 a	388.6 b	669.6 a	495.0 a	72.2 a
84	Carbofuran[2]	31.8 a	299.2 ab	612.9 a	501.7 a	50.5 a
84	Thiofanox[2]	27.5 a	249.2 a	593.3 a	582.9 a	133.0 a
168	Check	30.2 a	286.3 ab	592.4 a	509.4 a	90.4 a
168	Aldicarb	34.8 a	406.2 b	742.9 a	535.2 a	135.0 a
168	1,3-D & MIC	30.5 a	383.0 b	788.7 a	587.6 a	111.2 a
168	Carbofuran	31.7 a	357.3 ab	671.4 a	591.2 a	116.8 a
168	Thiofanox	24.2 a	230.8 a	602.7 a	607.9 a	211.4 b

[1]Column means followed by the same letter are not significantly different (P=0.05) according to the Student-Newman-Keuls Multiple Range Test.

[2]Applied at planting in the fertilizer furrow at a rate of 3.4 kg a.i./ha.

[3]Injected on a broadcast basis to a soil depth of 20 cm at the rate of 93.5 l/ha on May 1, 1978.

[4]Degree day accumulation base 10 C.

Table A5. Influence of selected management inputs on the tuber weight of potatoes (cv Superior).

Treatment		Tuber Weight / Plant (grams)[4]			
Nitrogen (kg/ha)	Pesticide	373.5	543.8	768.0	983.3
84	Check	9.0 a[1]	310.7 a	757.7 a	871.0 a
84	Aldicarb[2]	14.9 ab	364.7 a	832.3 a	923.4 a
84	1,3-D & MIC[3]	29.1 b	370.5 a	810.6 a	1071.2 a
84	Carbofuran[2]	17.3 ab	329.7 a	733.5 a	906.0 a
84	Thiofanox[2]	8.9 a	281.8 a	726.4 a	822.8 a
168	Check	16.5 ab	266.4 a	817.2 a	871.8 a
168	Aldicarb	24.8 ab	385.7 a	775.0 a	1121.8 a
168	1,3-D & MIC	20.1 ab	419.4 a	843.4 a	1088.8 a
168	Carbofuran	20.6 ab	355.1 a	847.6 a	819.4 a
168	Thiofanox	7.3 a	266.0 a	781.0 a	1113.0 a

[1]Column means followed by the same letter are not significantly different (P=0.05) according to the Student-Newman-Keuls Multiple Range Test.

[2]Applied at planting in the fertilizer furrow at a rate of 3.4 kg a.i./ha.

[3]Injected on a broadcast basis to a soil depth of 20 cm at the rate of 93.5 l/ha on May 1, 1978.

[4]Degree day accumulation base 10 C.

Table A6. Influence of three levels of nitrogen and four pesticides on the yield and size distribution of Superior potatoes (1978).

Treatment		Yield (quintal/ha)			
Nitrogen (kg/ha)	Pesticide	Total	> 8 cm tubers	5 cm tubers	< 5 cm tubers
84	Check	337 a	14.1 a	309 a	13.4 a
84	Aldicarb	392 bc	13.4 a	370 bcd	13.2 a
84	1,3-D & MIC[3]	416 c	8.1 a	393 cd	14.3 a
84	Carbofuran	362 ab	9.4 a	337 ab	14.3 a
84	Thiofanox[2]	379 abc	17.8 a	351 abc	10.6 a
168	Check	352 ab	10.8 a	330 ab	11.0 a
168	Aldicarb	442 c	17.0 a	391 cd	13.9 a
168	1,3-D & MIC[3]	426 c	12.2 a	400 d	13.4 a
168	Carbofuran	375 abc	10.4 a	353 abc	11.9 a
168	Thiofanox	392 bc	28.8 b	252 abc	10.1 a
Treatment Means					
84	--	377 w	12.5 w	352 w	13.1 w
168	--	393 w	15.8 w	365 w	12.1 w
	Check	344 x	12.4 x	320 x	12.2 y
	Aldicarb[2]	407 z	15.2 x	380 z	13.6 y
	Carbofuran	368 xy	9.9 x	345 xy	13.1 y
	Thiofanox	384 y	23.3 y	352 y	10.4 x

[1]Column means followed by the same letter are not significantly different (P=0.05) according to the Student-Newman-Keuls Multiple Range Test.

[2]Applied at planting in the fertilizer furrow at a rate of 3.4 kg a.i./ha.

[3]Injected on a broadcast basis to a soil depth of 20 cm at the rate of 93.5 l/ha on May 1, 1978.

[4]Degree day accumulation base 10 C.

APPENDIX B

Table B1. Influence of selected management inputs on the root weight of potatoes (cv Superior).

Treatment		Root Weight (grams)[4]				
Nitrogen (kg/ha)	Pesticide	241.2	373.5	543.8	768.0	983.3
84	Check	4.9 a[1]	7.8 a	9.8 a	10.0 a	4.4 a
84	Aldicarb[2]	4.3 a	7.8 a	10.1 a	8.0 a	4.8 a
84	1,3-D & MIC[3]	4.5 a	8.5 a	9.1 a	7.0 a	5.4 a
168	Check	4.9 a	7.4 a	8.9 a	8.0 a	5.7 a
168	Aldicarb	4.1 a	8.6 a	8.1 a	7.4 a	6.5 a
168	1,3-D & MIC	3.9 a	9.4 a	8.0 a	8.4 a	4.6 a
336	Check	5.1 a	8.5 a	10.4 a	8.1 a	7.2 a
336	Aldicarb	3.5 a	10.6 a	10.6 a	7.4 a	5.3 a
336	1,3-D & MIC	5.0 a	10.6 a	7.9 a	8.0 a	6.7 a

[1]Column means followed by the same letter are not significantly different (P=0.05) according to the Student-Newman-Keuls Multiple Range Test.

[2]Applied at planting in the fertilizer furrow at a rate of 3.4 kg a.i./ha.

[3]Injected on a broadcast basis to a soil depth of 20 cm at the rate of 93.5 l/ha on May 1, 1978.

[4]Degree day accumulation base 10 C.

Table B2. Influence of selected management inputs on tuber weight of potatoes (cv Superior).

Treatment		Tuber Weight / Plant (grams)[4]			
Nitrogen (kg/ha)	Pesticide	373.5	543.8	768.0	983.3
84	Check	12.5 a[1]	237.5 a	758.4 a	984.3 a
84	Aldicarb[2]	17.7 a	307.4 a	773.5 a	880.3 a
84	1,3-D & MIC[3]	17.0 a	358.7 a	753.0 a	1147.7 a
168	Check	8.0 a	286.1 a	596.0 a	1103.4 a
168	Aldicarb	14.4 a	236.1 a	837.5 a	1071.5 a
168	1,3-D & MIC	22.3 a	331.9 a	673.4 a	963.3 a
336	Check	11.0 a	215.8 a	692.8 a	858.4 a
336	Aldicarb	14.2 a	284.4 a	808.6 a	980.0 a
336	1,3-D & MIC	26.4 a	364.9 a	762.2 a	1132.0 a

[1]Column means followed by the same letter are not significantly different (P=0.05) according to the Student-Newman-Keuls Multiple Range Test.

[2]Applied at planting in the fertilizer furrow at a rate of 3.4 kg a.i./ha.

[3]Injected on a broadcast basis to a soil depth of 20 cm at the rate of 93.5 l/ha on May 1, 1978.

[4]Degree day accumulation base 10 C.

Table B3. Influence of selected management inputs on foliage weight of potatoes (cv Superior).

Treatment		Foliage Weight (grams)[4]				
Nitrogen (kg/ha)	Pesticide	241.2	373.5	543.8	768.0	983.3
84	Check	37.1 a[1]	264.6 a	430.3 a	511.6 ab	57.1 a
84	Aldicarb[2]	32.1 a	293.4 a	624.8 a	557.9 ab	170.0 a
84	1,3-D & MIC[3]	30.1 a	397.9 ab	647.4 a	600.9 ab	149.0 a
168	Check	33.9 a	259.9 a	497.6 a	569.5 ab	112.6 a
168	Aldicarb	33.9 a	307.0 ab	588.2 a	557.9 ab	314.2 c
168	1,3-D & MIC	30.4 a	392.1 ab	583.9 a	783.0 b	156.0 a
336	Check	34.6 a	256.0 a	469.9 a	446.1 a	101.7 a
336	Aldicarb	30.2 a	367.2 ab	565.2 a	640.8 a	242.9 b
336	1,3-D & MIC	41.6.a	436.0 b	675.9 a	723.6 a	246.9 b

[1]Column means followed by the same letter are not significantly different (P=0.05) according to the Student-Newman-Keuls Multiple Range Test.

[2]Applied at planting in the fertilizer furrow at a rate of 3.4 kg a.i./ha.

[3]Injected on a broadcast basis to a soil depth of 20 cm at the rate of 93.5 l/ha on May 1, 1978.

[4]Degree day accumulation base 10 C.

Table B4. Influence of selected management inputs on tuber number of potatoes (cv Superior).

Treatment		Tuber Number / Plant (grams)[4]			
Nitrogen (kg/ha)	Pesticide	373.5	543.8	767.9	983.3
84	Check	7.1 a[1]	7.3 a	11.1 a	10.4 a
84	Aldicarb[2]	6.5 a	8.7 a	12.3 a	9.9 a
84	1,3-D & MIC[3]	10.1 ab	8.9 a	11.4 a	10.6 a
168	Check	7.3 a	7.8 a	10.5 a	11.7 a
168	Aldicarb	8.4 ab	9.0 a	10.0 a	10.1 a
168	1,3-D & MIC	12.4 b	10.6 a	10.3 a	10.3 a
336	Check	8.8 ab	6.9 a	10.0 a	8.7 a
336	Aldicarb	10.7 ab	9.0 a	11.1 a	9.4 a
336	1,3-D & MIC	10.6 ab	10.2 a	11.9 a	9.2 a

[1]Column means followed by the same letter are not significantly different (P=0.05) according to the Student-Newman-Keuls Multiple Range Test.

[2]Applied at planting in the fertilizer furrow at a rate of 3.4 kg a.i./ha.

[3]Injected on a broadcast basis to a soil depth of 20 cm at the rate of 93.5 l/ha on May 1, 1978.

[4]Degree day accumulation base 10 C.

APPENDIX C

Table C1. Influence of selected management inputs on foliage weight of potatoes (cv Superior).

Treatment		Foliage Weight (grams)[4]		
Phosphorus (kg/ha)	Pesticide	233.7	442.7	1005.4
0	Check	23.4 a[1]	216.1 a	22.4 a
0	Aldicarb[2]	26.8 a	249.9 a	65.6 a
0	1,3-D & MIC[3]	20.8 a	278.3 ab	39.8 a
56	Check	23.9 a	274.2 ab	42.2 a
56	Aldicarb	20.0 a	263.8 ab	34.2 a
56	1,3-D & MIC	20.5 a	400.1 b	40.7 a
168	Check	23.1 a	297.2 ab	49.3 a
168	Aldicarb	22.8 a	397.6 b	74.0 a
168	1,3-D & MIC	23.4 a	383.0 b	76.0 a

[1]Column means followed by the same letter are not significantly different (P=0.05) according to the Student-Newman-Keuls Multiple Range Test.

[2]Applied at planting in the fertilizer furrow at a rate of 3.4 kg a.i./ha.

[3]Injected on a broadcast basis to a soil depth of 20 cm at the rate of 93.5 l/ha on May 1, 1979.

[4]Degree day accumulation base 10 C.

Table C2. Influence of selected management inputs on stem weight of potatoes (cv Superior).

Treatment		Stem Weight (grams)[4]			
Phosphorus (kg/ha)	Pesticide	233.7	442.7	723.2	1005.4
0	Check	0[1]	45.5 a	28.9 ab	8.1 a
0	Aldicarb[2]	0	43.7 a	22.9 a	11.4 a
0	1,3-D&MIC[3]	0	47.3 a	27.9 ab	10.2 a
56	Check	0	36.9 a	39.1 b	8.6 a
56	Aldicarb	0	43.0 a	37.2 ab	6.9 a
56	1,3-D & MIC	0	35.4 a	31.5 ab	8.2 a
168	Check	0	46.0 a	26.5 ab	10.8 a
168	Aldicarb	0	48.0 a	33.9 ab	12.0 a
168	1,3-D & MIC	0	38.8 a	32.9 ab	12.5 a

[1]Column means followed by the same letter are not significantly different (P=0.05) according to the Student-Newman-Keuls Multiple Range Test.

[2]Applied at planting in the fertilizer furrow at a rate of 3.4 kg a.i./ha.

[3]Injected on a broadcast basis to a soil depth of 20 cm at the rate of 93.5 l/ha on May 1, 1979.

[4]Degree day accumulation base 10 C.

Table C3. Influence of selected management inputs on tuber number of potatoes (cv Superior).

Treatment		Tuber Number / Plant (grams)[4]			
Phosphorus (kg/ha)	Pesticide	233.7	442.7	723.2	1005.4
0	Check	0[1]	13.4 a	11.2 a	7.0 a
0	Aldicarb[2]	0	10.6 a	8.0 a	9.2 a
0	1,3-D&MIC[3]	0	14.8 a	11.2 a	7.8 a
56	Check	0	9.2 a	12.0 a	9.4 a
56	Aldicarb	0	11.2 a	13.4 a	7.4 a
56	1,3-D & MIC	0	13.4 a	14.0 a	9.0 a
156	Check	0	9.8 a	9.2 a	8.6 a
156	Aldicarb	0	14.0 a	12.4 a	7.8 a
156	1,3-D & MIC	0	7.8 a	12.8 a	8.0 a

[1]Column means followed by the same letter are not significantly different (P=0.05) according to the Student-Newman-Keuls Multiple Range Test.

[2]Applied at planting in the fertilizer furrow at a rate of 3.4 kg a.i./ha.

[3]Injected on a broadcast basis to a soil depth of 20 cm at the rate of 93.5 l/ha on May 1, 1979.

[4]Degree day accumulation base 10 C.

Table C4. Influence of selected management inputs on plant weight of potatoes (cv Superior).

Treatment		Plant Weight (grams)[4]			
Phosphorus (kg/ha)	Pesticide	233.7	442.7	723.2	1005.6
0	Check	27.0 a[1]	321.0 a	613.5 a	691.7 a
0	Aldicarb[2]	30.5 a	331.3 a	655.2 a	910.2 a
0	1,3-D & MIC[3]	24.2 a	362.8 a	796.4 a	749.7 a
56	Check	28.2 a	345.8 a	554.4 a	861.7 a
56	Aldicarb	23.0 a	340.5 a	823.8 a	782.8 a
56	1,3-D & MIC	23.8 a	472.0 a	847.0 a	878.8 a
168	Check	26.7 a	382.8 a	625.9 a	887.3 a
168	Aldicarb	27.0 a	483.1 a	790.1 a	928.8 a
168	1,3-D & MIC	26.7 a	459.8 a	859.2 a	1030.7 a

[1]Column means followed by the same letter are not significantly different (P=0.05) according to the Student-Newman-Keuls Multiple Range Test.

[2]Applied at planting in the fertilizer furrow at a rate of 3.4 kg a.i./ha.

[3]Injected on a broadcast basis to a soil depth of 20 cm at the rate of 93.5 l/ha on May 1, 1979.

[4]Degree day accumulation base 10 C.

Table C5. Influence of selected management inputs on tuber weight of potatoes (cv Superior).

Treatment		Tuber Weight / Plant (grams)[4]		
Phosphorus (kg/ha)	Pesticide	442.7	723.2	1005.4
0	Check	45.7 a[1]	524.1 a	651.9 a
0	Aldicarb[2]	24.1 a	532.2 a	822.2 a
0	1,3-D&MIC[3]	22.2 a	757.9 a	690.8 a
56	Check	21.0 a	501.9 a	796.4 a
56	Aldicarb	21.6 a	772.1 a	734.1 a
56	1,3-D & MIC	21.2 a	803.3 a	823.0 a
168	Check	25.5 a	588.5 a	818.8 a
168	Aldicarb	21.8 a	742.8 a	837.3 a
168	1,3-D & MIC	24.3 a	813.3 a	934.6 a

[1]Column means followed by the same letter are not significantly different (P=0.05) according to the Student-Newman-Keuls Multiple Range Test.

[2]Applied at planting in the fertilizer furrow at a rate of 3.4 kg a.i./ha.

[3]Injected on a broadcast basis to a soil depth of 20 cm at the rate of 93.5 l/ha on May 1, 1979.

[4]Degree day accumulation base 10 C.

Table C6. Influence of selected management inputs on root weight of potatoes (cv Superior).

Treatment		Root Weight (grams)[4]			
Phosphorus (kg/ha)	Pesticide	233.7	442.7	723.2	1005.4
0	Check	3.6 a[1]	13.7 a	12.5 a	9.3 a
0	Aldicarb[2]	3.8 a	13.6 a	11.8 a	11.0 a
0	1,3-D & MIC[3]	3.4 a	15.0 a	10.6 a	8.9 a
56	Check	4.3 a	13.6 a	13.4 a	14.7 a
56	Aldicarb	3.0 a	12.2 a	14.4 a	7.7 a
56	1,3-D & MIC	3.2 a	15.4 a	12.3 a	6.9 a
168	Check	3.6 a	14.2 a	11.0 a	8.5 a
168	Aldicarb	4.2 a	15.8 a	13.4 a	5.5 a
168	1,3-D & MIC	3.3 a	13.7 a	13.0 a	7.6 a

[1]Column means followed by the same letter are not significantly different (P=0.05) according to the Student-Newman-Keuls Multiple Range Test.

[2]Applied at planting in the fertilizer furrow at a rate of 3.4 kg a.i./ha.

[3]Injected on a broadcast basis to a soil depth of 20 cm at the rate of 93.5 l/ha on May 1, 1979.

[4]Degree day accumulation base 10 C.

Table C7. Influence of selected management inputs on population density of P. penetrans on potatoes (cv Superior).

Treatment		P. penetrans per 100 cm^3 soil and per gram root tissue combined[4]			
Phosphorus (kg/ha)	Pesticide	233.7	442.7	723.2	1005.4
0	Check	39.8 a	75.8 b	256.4 bc	133.6 a
0	Aldicarb[2]	20.0 a	13.0 a	91.4 ab	8.6 a
0	1,3-D & MIC[3]	31.6 a	35.6 ab	285.0 bc	113.0 a
56	Check	38.8 a	36.6 ab	326.0 c	237.2 a
56	Aldicarb	16.6 a	17.0 a	92.4 ab	29.4 a
56	1,3-D & MIC	34.6 a	25.2 ab	162.0 abc	203.8 a
168	Check	44.0 a	56.6 ab	255.4 bc	254.4 a
168	Aldicarb	14.8 a	13.6 a	34.8 a	14.0 a
168	1,3-D & MIC	23.6 a	29.8 ab	293.0 bc	189.2 a

[1]Column means followed by the same letter are not significantly different (P=0.05) according to the Student-Newman-Keuls Multiple Range Test.

[2]Applied at planting in the fertilizer furrow at a rate of 3.4 kg a.i./ha.

[3]Injected on a broadcast basis to a soil depth of 20 cm at the rate of 93.5 l/ha on May 1, 1979.

[4]Degree day accumulation base 10 C.

APPENDIX D

Table D1. Influence of selected management inputs on foliage weight of potatoes (cv Russet Burbank).

Treatment		Foliage Weight (grams)[4]			
Phosphorus (kg/ha)	Pesticide	233.7	442.7	723.2	1167.6
0	Check	8.8 a[1]	185.5 a	588.3 a	91.4 a
0	Aldicarb[2]	7.3 a	239.8 ab	653.7 ab	205.8 ab
0	1,3-D & MIC[3]	8.5 a	258.2 ab	779.0 ab	289.1 abc
56	Check	7.3 a	239.5 ab	668.6 ab	222.8 ab
56	Aldicarb	4.9 a	249.4 ab	803.2 ab	408.3 abcd
56	1,3-D & MIC	6.8 a	330.4 c	980.8 ab	561.1 cd
168	Check	7.8 a	250.1 ab	780.7 ab	512.6 bcd
168	Aldicarb	7.7 a	259.7 ab	889.1 ab	489.1 bcd
168	1,3-D & MIC	6.6 a	300.4 bc	1059.1 b	677.3 d

[1]Column means followed by the same letter are not significantly different (P=0.05) according to the Student-Newman-Keuls Multiple Range Test.

[2]Applied at planting in the fertilizer furrow at a rate of 3.4 kg a.i./ha.

[3]Injected on a broadcast basis to a soil depth of 20 cm at the rate of 93.5 l/ha on May 1, 1979.

[4]Degree day accumulation base 10 C.

Table D2. Influence of selected management inputs on stem weight of potatoes (cv Russet Burbank).

Treatment		Stem Weight (grams)[4]			
Phosphorus (kg/ha)	Pesticide	233.7	442.7	723.2	1167.6
0	Check	0[1]	39.3 a	28.9 a	16.5 a
0	Aldicarb[2]	0	34.6 a	33.2 a	21.4 ab
0	1,3-D & MIC[3]	0	43.2 a	32.2 a	23.7 ab
56	Check	0	32.9 a	32.2 a	23.1 ab
56	Aldicarb	0	33.4 a	33.6 a	27.0 ab
56	1,3-D & MIC	0	46.2 a	36.1 a	34.1 b
168	Check	0	34.5 a	35.4 a	25.4 ab
168	Aldicarb	0	27.3 a	37.6 a	27.0 ab
168	1,3-D & MIC	0	43.8 a	44.9 a	35.6 b

[1]Column means followed by the same letter are not significantly different (P=0.05) according to the Student-Newman-Keuls Multiple Range Test.

[2]Applied at planting in the fertilizer furrow at a rate of 3.4 kg a.i./ha.

[3]Injected on a broadcast basis to a soil depth of 20 cm at the rate of 93.5 l/ha on May 1, 1979.

[4]Degree day accumulation base 10 C.

Table D3. Influence of selected management inputs on plant weight of potatoes (cv Russet Burbank).

Treatment		Plant Weight (grams)[4]			
Phosphorus (kg/ha)	Pesticide	233.7	442.7	723.2	1167.6
0	Check	11.5 a[1]	241.0 a	1036.5 a	946.6 a
0	Aldicarb[2]	9.4 a	294.7 ab	1159.8 a	1211.1 ab
0	1,3-D & MIC[3]	10.5 a	322.7 ab	1327.7 a	1486.6 ab
56	Check	9.1 a	292.6 ab	1122.1 a	1284.8 ab
56	Aldicarb	6.5 a	301.9 ab	1274.4 a	1491.5 ab
56	1,3-D & MIC	8.9 a	399.6 c	1583.2 a	2001.0 b
168	Check	9.5 a	303.3 ab	1259.1 a	1647.3 ab
168	Aldicarb	10.1 a	304.3 ab	1412.2 a	1613.7 ab
168	1,3-D & MIC	8.8 a	364.3 bc	1710.5 a	2015.2 b

[1]Column means followed by the same letter are not significantly different (P=0.05) according to the Student-Newman-Keuls Multiple Range Test.

[2]Applied at planting in the fertilizer furrow at a rate of 3.4 kg a.i./ha.

[3]Injected on a broadcast basis to a soil depth of 20 cm at the rate of 93.5 l/ha on May 1, 1979.

[4]Degree day accumulation base 10 C.

Table D4. Influence of selected management inputs on tuber number of potatoes (cv Russet Burbank).

Treatment		Tuber Number / Plant (grams)[4]			
Phosphorus (kg/ha)	Pesticide	233.7	442.7	723.2	1167.6
0	Check	0[1]	8.8 a	14.0 a	12.0 a
0	Aldicarb[2]	0	4.8 a	17.0 a	9.2 a
0	1,3-D & MIC[3]	0	11.0 a	18.6 a	14.0 a
56	Check	0	6.4 a	20.0 a	12.6 a
56	Aldicarb	0	4.6 a	17.0 a	11.0 a
56	1,3-D & MIC	0	6.2 a	24.0 a	17.2 a
168	Check	0	2.6 a	22.0 a	11.0 a
168	Aldicarb	0	3.2 a	19.8 a	11.8 a
168	1,3-D & MIC	0	5.2 a	24.8 a	15.4 a

[1]Column means followed by the same letter are not significantly different (P=0.05) according to the Student-Newman-Keuls Multiple Range Test.

[2]Applied at planting in the fertilizer furrow at a rate of 3.4 kg a.i./ha.

[3]Injected on a broadcast basis to a soil depth of 20 cm at the rate of 93.5 l/ha on May 1, 1979.

[4]Degree day accumulation base 10 C.

Table D5. Influence of selected management inputs on tuber weight of potatoes (cv Russet Burbank).

Treatment		Tuber Weight / Plant (grams)[4]			
Phosphorus (kg/ha)	Pesticide	233.7	442.7	723.2	1167.6
0	Check	0[1]	1.5 a	400.9 a	822.1 a
0	Aldicarb[2]	0	0.7 a	453.7 a	968.3 a
0	1,3-D & MIC[3]	0	2.7 a	497.5 a	1156.4 a
56	Check	0	1.4 a	400.7 a	1025.2 a
56	Aldicarb	0	1.7 a	416.9 a	1035.2 a
56	1,3-D & MIC	0	2.5 a	548.3 a	1385.6 a
168	Check	0	0.3 a	424.7 a	1092.7 a
168	Aldicarb	0	0.9 a	464.8 a	1076.5 a
168	1,3-D & MIC	0	0.7 a	583.2 a	1282.0 a

[1]Column means followed by the same letter are not significantly different (P=0.05) according to the Student-Newman-Keuls Multiple Range Test.

[2]Applied at planting in the fertilizer furrow at a rate of 3.4 kg a.i./ha.

[3]Injected on a broadcast basis to a soil depth of 20 cm at the rate of 93.5 l/ha on May 1, 1979.

[4]Degree day accumulation base 10 C.

Table D6. Influence of selected management inputs on root weight of potatoes (cv Russet Burbank).

Treatment		Root Weight / Plant (grams)[4]			
Phosphorus (kg/ha)	Pesticide	233.7	442.7	723.2	1167.6
0	Check	2.6 a[1]	14.8 a	18.4 a	16.7 a
0	Aldicarb[2]	2.1 a	19.6 a	19.2 a	15.7 a
0	1,3-D & MIC[3]	2.0 a	18.6 a	19.0 a	17.4 a
56	Check	1.8 a	18.8 a	20.6 a	13.7 a
56	Aldicarb	1.6 a	17.3 a	20.6 a	21.0 a
56	1,3-D & MIC	2.1 a	20.5 a	18.0 a	20.2 a
168	Check	1.7 a	18.5 a	18.3 a	16.6 a
168	Aldicarb	2.4 a	16.5 a	20.7 a	21.2 a
168	1,3-D & MIC	2.2 a	19.4 a	23.3 a	20.4 a

[1]Column means followed by the same letter are not significantly different (P=0.05) according to the Student-Newman-Keuls Multiple Range Test.

[2]Applied at planting in the fertilizer furrow at a rate of 3.4 kg a.i./ha.

[3]Injected on a broadcast basis to a soil depth of 20 cm at the rate of 93.5 l/ha on May 1, 1979.

[4]Degree day accumulation base 10 C.

Table D7. Influence of selected management inputs on population density of P. penetrans on potatoes (cv Superior).

Treatment		P. penetrans per 100 cm^3 soil and per gram root tissue combined[4]			
Phosphorus (kg/ha)	Pesticide	233.7	442.7	723.2	1167.6
0	Check	31.2 ab[1]	62.6 ab	99.2 d	153.4 b
0	Aldicarb[2]	7.6 a	16.4 a	9.0 a	7.0 a
0	1,3-D & MIC[3]	50.8 a	51.8 ab	102.4 a	176.0 b
56	Check	24.6 ab	78.8 b	91.4 a	99.8 b
56	Aldicarb	8.4 a	7.8 a	24.6 a	3.2 a
56	1,3-D & MIC	32.6 ab	41.6 ab	60.8 a	127.4 b
168	Check	29.4 ab	43.4 ab	70.0 a	160.8 b
168	Aldicarb	8.6 a	13.4 a	19.2 a	13.8 a
168	1,3-D & MIC	29.0 ab	56.6 ab	73.4 a	152.2 b

[1]Column means followed by the same letter are not significantly different (P=0.05) according to the Student-Newman-Keuls Multiple Range Test.

[2]Applied at planting in the fertilizer furrow at a rate of 3.4 kg a.i./ha.

[3]Injected on a broadcast basis to a soil depth of 20 cm at the rate of 93.5 l/ha on May 1, 1979.

[4]Degree day accumulation base 10 C.