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Title: RELATIONSHIP OF *PRATYLENCHUS PENETRANS* (Cobb, 1917) POPULATION DENSITY AND YIELD ON PEPPERMINT, *MENTHA PIPERITA* L.

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Dr. Harold J. Jensen

A root-lesion nematode, *Pratylenchus penetrans*, was determined to be a major component of peppermint stand decline in Western Oregon. Regression analysis showed that *P. penetrans* root densities in August were negatively correlated ($P=0.01$) with yield, while soil densities in August and root and soil densities in April were poorly correlated with yield. Multiple regression analysis showed that soil texture, stand vigor, and nematode root densities accounted for 80% ($R^2=0.80$) of yield variability. Additional parameters; ectoparsitic nematode densities, soil pH, soil bulk density, and soluble solids did not improve regression models.

Seasonal population dynamics studies demonstrated that root population densities increased in late March and peaked in mid-May. Soil populations peaked in spring before root populations and in the fall as nematodes emigrated from senescent roots. Root and soil

populations declined to lowest densities in late winter. Seasonal distribution studies indicated that populations did not migrate vertically and the recommended depth of 15-20 cm was adequate for sampling nematodes throughout the year.

Greenhouse studies demonstrated that Murray Mitcham was most susceptible, Todd Mitcham was intermediate, and Black Mitcham was most tolerant to *P. penetrans* injury. Murray Mitcham supported lower nematode reproduction and exhibited greatest root necrosis. In a two-season study, Black and Todd Mitcham were not damaged during the first season, while Murray Mitcham plants exhibited significant top and root stunting. All cultivars were damaged during the second season.

Soil texture modified population dynamics in greenhouse pot cultures. Nematode density increased faster in Camas gravelly sandy loam than in either Newberg loam or Cloquato silt loam. Plant top biomass was not influenced by soil texture and nematode inoculation. However, root biomass was significantly reduced with nematode-inoculated plants in the loam and gravelly sandy loam, but not in the silt loam.

Carbamate nematicides were evaluated for managing *P. penetrans* damage of peppermint. Oxamyl at 0.6-16.5 kg a.i/ha produced significant yield responses. Early spring applications enhance plant growth, while fall and summer treatments were ineffective. Oxamyl applications of 1.1-2.2 kg a.i./ha 5 to 10 days before spring flaming are recommended. Management guidelines based on soil texture, stand vigor, and nematode densities were developed for oxamyl treatments.

RELATIONSHIP OF *PRATYLENCHUS PENETRANS* (Cobb, 1917) POPULATION DENSITY AND YIELD OF PEPPERMINT, *MENTHA PIPERITA* L.

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Head of Department of Botany and Plant Pathology

Redacted for Privacy

Dean of Graduate School

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INTRODUCTION

Commercial cultivation of peppermint is an economically important sector of Oregon agriculture. Peppermint is grown as a perennial crop, harvested in early August and steam distilled to extract a volatile oil. This oil is used as a flavoring by food and drug industries. Oil quality is determined by a composite balance of major components; menthone, menthol and menthofuran. High oil quality and good yield can only be produced above 40° N latitude where mid-summer photoperiod exceeds 15 hours. Major peppermint producing regions are the Pacific Northwest and states surrounding the Great Lakes; Michigan, Wisconsin, and Indiana. In 1978 Oregon had 60% of the United States' peppermint acreage and the highest yields per acre. Peppermint cash value has ranked as high as fourth among Oregon's agricultural crops with revenues in excess of $40,000,000. Five regions in Oregon have proper climatic and soil requirements for peppermint cultivation. The Willamette Valley and Central Oregon equally divide 95% of the state's mint acreage. Josephine, Umatilla, and Malheur Counties account for the remaining 5%. Importance of the mint industry in Oregon has resulted in state and industry support for pest research and management programs, including this phytonematode study.

Peppermint is usually grown as a no till perennial crop in Oregon. This cultural system is conducive to build-up of disease and pest populations. A peppermint stand without serious disease or pest problems can remain economically productive in excess of ten years. Stands with high disease, insect, weed or nematode populations may become unproductive within 2-4 years. The cost of establishing a new field is not recovered until the third harvest. Therefore, a stand must remain productive in excess of four years for peppermint cultivation to be a viable management alternative.

In 1954, Horner and Jensen (68) reported four species of phytonematodes associated with Oregon peppermint plantings; *Paratylenchus macrophallus*, *Aphelenchoides parientinus*, *Meloidogyne hapla* and *Longidorus sp.*. *Longidorus elongatus* 'the mint nematode', has been considered the major nematode pest of peppermint in Willamette River flood plain soils. Eshtiaghi (40) noted *Pratylenchus penetrans* in Oregon peppermint fields. As growers became more aware of nematode caused peppermint decline, many poor stands were sampled for nematodes. The dominent phytonematode collected from declining fields was *P. penetrans*. This species has proven to be a major pest problem in light-textured soil of the Willamette Valley, Umatilla, and Jackson Counties.

The disease syndrome is a general chronic decline in successive seasons. The first season's growth after planting may show no visible damage, although *P. penetrans* populations can be high. During the second or third season, patchy areas of stunted reddened plants develop. These plants are shallow rooted and unable to obtain water and nutrients necessary for vigorous growth when soil moisture is low. Root systems of infested plants are shallow, mat-like and darkened due to extensive necrosis which accompany lesion development. Stunted areas expand annually until large portions of the field produce no harvestable hay.

Nematode control has radically changed with the advent of systemic nematicides. Previously, soil fumigation was used to reduce populations before planting, but nematode populations can expand to damaging levels within 3-4 years after fumigation. A systemic carbamate nematicide, oxamyl, has sucessfully rejuvenated stands severely damaged by P. penetrans and L. elongatus. The cost of this nematicide necessitated establishment of damage levels which can serve as guidelines for P. penetrans management decisions. This research attempted to develop optimal sampling strategies and damage functions as a basis for treatment decisions.

Nematode management strategies must be integrated into a system that includes climatic, physiogeographic, edaphic, pest, disease and cultural components. The plant, not the disease or pest, must be the focus of this management process. A plant possesses a hypothetical maximum yield under ideal conditions. Each stress factor reduces that potential additively or synergistically, as with Pratylenchus interacting with Verticillium wilt in peppermint. Stress factors can also interact antagonistically when one stress preempts damage caused by a second stress component reducing the second's impact on plant growth. The simplest case for a P. penetrans peppermint damage function should include population levels of all phytonematodes, edaphic site characteristics, stand vigor evaluation, and cultural factors including peppermint cultivar. A complex model integrating winter stress, weed competition, insect damage, *Verticillium* wilt, and spring flaming stress may be able to incorporate such a nematode subsystem.

LITERATURE REVIEW

Pratylenchus penetrans (Cobb, 1917) Sher and Allen 1953 is a major agricultural pest in temperate latitudes. This nematode's broad host range makes it damaging to many crops and difficult to control. Oostenbrink et al. (106,107) listed 182 species of vegetables, ornamentals, forage crops, cereals, and deciduous trees as efficent hosts. Jensen (71) reported all 33 grass and legume cover crops tested in a greenhouse host range study as suitable hosts. Fifty-five weed host species were listed by Townshend and Davidson (144). They speculated that weed species are important overwintering reservoirs where surviving populations can be maintained or increased. Yorston (165) listed 72 host species in 15 families. He rated Mentha piperita as a slightly susceptible host. Ferris (51) and Wong et al. (163), however, reported peppermint to be an efficient host which supports high reproduction rates and population levels.

Pratylenchus penetrans is an endomigratory nematode which feeds and reproduces in cortical tissues of plant roots. Reproduction is amphimictic. Virgin females can lay eggs, but these eggs fail to undergo cleavage (137). Eggs are laid singly as the female moves intercellularly and intracellularly through the cortex. Newly hatched second stage larvae do not migrate (86), thus lesions contain numerous eggs and newly hatched larvae.

Maniya (86) reported that the life cycle of P. penetrans on seedling Crytomeria was temperature dependent. A complete egg to egg cycle ranged from 80 days at 18° C to 30-31 days at 30° C. No eggs developed into larvae at 33° C. The percentage of females not ovipositing was also temperature dependent, with 18 percent at 15° C, 14 percent at 20°C, and 35 percent at 33°C. Mean oviposition rates were reported as 1.25 eggs per day initially and 0.53 per day after 14 days. Reproduction rates on tea are of similar magnitude; 1.6 eggs per day for up to five weeks with a completed cycle in 45 - 48 days (54). Kimpinski (78) reported a six to seven week generation time in red clover when mean soil temperature was 3.4° C. Similarly, Dunn (37) observed egg maturation in winter soils at -1 to 3.5°C. Optimum reproductive temperature also varies with the host. Dickerson et al. (31) noted optimal reproduction on corn at 24° C, on potatoes at 16°C, but no reproduction ocurred with either host at 35°C. Even with three potato cultivars grown under uniform conditions, P. penetrans reproductive biology varied (16).

Temperature also significantly influences root-lesion nematode migration and root penetration. Kimpinski and Willis (62) observed greater numbers of P. penetrans placed on the surface of a two cm vertical soil column migrated to the bottom within four hours at 19° C than at either 30°C or 10°C. Soil movement is also greatly influenced by soil texture, moisture tension, soil aggregation, and bulk density. Townshend and Webber (148) reported maximum movement of 4.0 cm in seven days with a low bulk density sandy loam at moisture tension between 10 and 3000 cm H_2O.

Movement has been demonstrated by Lavelle and Rhode (82) to be chemokinetic. In their experiments, P. penetrans responded to root exudates from intact alfalfa, carrot, and tomato roots. Root penetration is not a random process. The zone of maximum penetration with alfalfa and red clover seedlings was behind the root cap in the region of dense root hairs (35,53,139). An individual nematode's root penetration appears to be influenced by other nematodes present in the root. Pratylenchus coffeae (118) and P. thornei (10) have been observed to penetrate en mass into citrus and wheat, respectively. P. penetrans have also been observed to aggregate near areas on red clover roots occupied by other nematodes during the first 24 hours of infection (53). Population composition, sex and development stages, influence the number of P. penetrans entering roots. Females penetrate more aggressively than do males and fourth stage larvae, while second stage larvae penetrate roots poorly (130). Temperature range for penetration also differs for females, males and third stage larvae (139). Optimal penetration temperature is reported as 20°C on corn (141) and red clover (139).

The penetration process has been studied by Oyekan et al. with pea roots on agar (104). After six hours, most individuals were probing the epidermis, within twelve hours a majority had penetrated roots and at 18 to 24 hours most individuals were in the mid-cortex. The first evidence of penetration was a small yellow-orange discoloration of the epidermis at point of penetration (4,108,113), with damage limited to point of entry (5). Cortical tissue damage resulted from cell disruption as the nematode moved intercelluarly and intracellularly parallel to the endodermis (4,113). Endodermal probing occurred, but the endodermis acted as a barrier to nematode movement into vascular tissues (108). Discoloration of celery roots was observed to move in advance of nematode infection indicating a biochemical reaction was involved. Thus, tissue damage was not confined to mechanical disruption.

The biochemical reaction is associated with phenolic compounds released by the host in response to nematode invasion. Root-lesion nematodes are known to stimulate phenolic compound accumulation in pea (108), cabbage (4), apple seedling (4), celery (142) and strawberry (143) endodermal tissues. Epidermal and cortical parenchyma phenolic accumulations have been detected in grasses (149) and strawberry (143) in response to _P. penetrans_. Mountain's (97) in vivo studies of infected peach roots revealed that _P. penetrans_ release a B-glucosidase enzyme which hydrolyzed amygdalin, a cyanophoric glucoside. Amygdalin stimulated release of benzaldehyde and hydrogen cyanide in concentrations toxic to root tissues. Patrick (110) reported that amygdalin inhibited root respiration 40 to 90% causing darkening and necrosis of meristematic tissue. Necrotic reaction severity of different cultivars in response to lesion nematode infection is thought to be related to differential amygdalin production (97).

Pratylenchus induced root necrosis alone does not necessarily cause plant growth reduction. _P. penetrans_ infected pea roots continued to function with extensive cortical damage and plant growth was only suppressed at high population levels (109). Necrotic tissues may harbor few nematodes, even though egg populations are usually present (5). Lesions also serve as infection courts for non-aggressive soil microbes. These secondary invaders are a major component in root-lesion nematode related root degeneration and plant decline (97).

Synergistic interactions between P. penetrans and Verticillum wilt fungi have been demonstrated on numerous crops including peppermint. P. penetrans increased incidence and severity of Verticillum wilt of pepper (105), tomato (28,96), eggplant (87,96) and susceptible strawberry cultivars (3). Verticillum has also been shown to increase population development of P. penetrans on eggplant and tomato (96). Faulkner and Skotland (43) reported similar population stimulation with Pratylenchus minyus and Verticillium dahlia on peppermint. This was accompanied by increased wilt severity and a shortened disease incubation period. P. penetrans and V. albo-atrium inoculated peppermint also produced wilt symptoms two weeks before Verticillium alone (13). Split-rooting techniques demonstrated that interaction factors are translocated, thus synergism was not solely an infection court phemenona (42). Changes in plant, fungus, and nematode physiology resulted in increased optimal temperature for wilt expression and a reduction in optimal P. penetrans reproduction temperature. When both pathogens were inoculated on peppermint, V. dahlia progagule levels were increased in rhizosphere soil surrounding P. penetrans- Verticillium inoculated plants when compared with plants where Verticillium was inoculated alone (165). Therefore, when both pathogens are present, peppermint yields may be reduced synergistically and a further increase in root-lesion nematode population densities may result.

Interactions between phytonematode species within a soil community are important when evaluating plant damage as a function of nematode density. Generally one species suppresses population increase of other species present by diminishing food quanity or through competition for penetration and feeding sites. *P. penetrans* significantly reduced *Tylenchorhynchus martini* development in alfalfa and red clover, but *T. martini* exhibited no adverse effect on *P. penetrans* (23). Similarly, high *P. penetrans* populations in alfalfa and red clover roots showed antagonism to *Meloidogyne incognita* penetration (150). However, Estores and Chen's (39) split-root experiments demonstrated that *M. incognita* in one part of a tomato root system could retard *P. penetrans* reproduction in isolated roots of the same plant, indicating a translocatable factor was involved. High *P. penetrans* populations in peppermint significantly reduced *Longidorus elongatus* population development (165). Conversely, high *L. elongatus* populations, 700 per liter of soil, significantly reduced *P. penetrans* levels but 70 *L. elongatus* per liter had no significant impact on *P. penetrans*. Therefore, nematode species, sequence of inoculation, host species and initial nematode density (93) determine outcome of concomitant nematode interactions.

Edaphic factors are important in dictating nematode distributions, population levels and extent of plant damage. Soil texture, bulk density and particle aggregation are closely related to soil pore characteristics. Since nematode soil activities are restricted to soil water within pore spaces, changes in soil physical characteristics can significantly modify soil air-water relationships, which in turn affect nematode reproduction, movement and survival. Soil texture has been demonstrated to influence nematode distributions (22,58,89,90), damage functions (46,75) and population response to climatic factors (166). Population dynamics also change with soil aggregation and structure (20,74,158).

Pratylenchus reproduction, migration, root penetation, overwintering survival and damage are greatly influenced by soil texture. Generally this genus was more prolific in course or light sandy soil than in heavier soils. Reproduction rates were higher in coarse and sandy loams for *P. vulnus* (126), *P. brachyurus* , and *P. zeae* (38). Reproduction of *P. vulnus* on sour orange was higher at elevated temperatures in lighter soils (126). *P. penetrans* movement was faster in sandy loam and low bulk density soils (147,148). Similarly, *P. penetrans* penetration of corn roots was observed to be greatest in coarse textured soils (141). Townshend (140) examined effects of soil type on overwinter survival of *P. penetrans* and observed no significant difference between a sandy loam and silty loam. However, Kable and Mai's (77) overwintering studies showed lower *P. penetrans* winter mortality in sandy loam than in clay soils where slow drainage resulted in waterlogged anaerobic conditions. The moisture relations of soils were also important in plant damage etiology. Lighter soils with well-drained pore space are not only better for *Pratylenchus* biological processes, but these soils also hold less available water for plant growth. Interaction between nematode feeding which caus es stunted plant root systems and low moisture content of sandy soils do not provide ample water for plants to support vigorous growth. Increased damage in light soils has been reported for P. vulnus in roses (126), P. penetrans in fruit trees (66,105,109) and tobacco (146). Therefore, it is necessary to consider soil factors in developing P. penetrans management programs.

Soil physical characteristics are not the only edaphic factors which influence nematode population and host-nematode interrelationships. Soil fertility directly affects plant growth and indirectly influences nematode biology. Mac Donald (83), using nutrient solution with a range of calcium, potassium, and magnesium milliequivalants, observed that cation balance influenced P. penetrans penetration of winter vetch roots. Burns (22) reported Pratylenchus alleni invasion of soybean roots was lowest where root potassium was high. Similary, P. penetrans population dynamics on Mentha spicata were influenced by calcium-potassium cation ratios (83).

Plants grown under stress conditions exhibited greater nematode population increase than unstressed plants. P. penetrans had accelerated reproduction rates in nutrient stressed tomatoes (98), peppermint (111) and 'Wando' peas (35). Dolliver (35), experimenting with P. penetrans infected peas, reported that mechanical, nutritional and environmental stress stimulated reproduction. He hypothesized either stressed plants produced materials favorable to nematode reproduction, or less inhibitory materials were produced. Possibily a vigorous plant can out-compete nematodes for nutrients, but nematodes are more successful in sequestering plant resources in moderately stressed plants.

Phytonematodes spend at least part of their life cycle in the soil solution. The pH of soil water can be widely variable and may directly affect nematode biology or modify a plant's suitablity as a host. Burn's (22) survey of nematode species in soybean fields showed non-stylet nematodes were most plentiful at pH 8.0, while Xiphinema sp., Hoplolaimus galetatus and P. penetrans recovery was greatest at pH 6.0. He noted at pH 4.0 that soybean root surfaces were more suberized, which reduce host suitablity. Norton (100) observed nematode community composition correlated with pH, organic matter, and cation exchange capacity in soybean fields. P. penetrans has been reported to have optimum reproduction and development at pH 5.2 to 6.2 on vetch (93) and red clover (77,160). P. penetrans populations were depressed at pH's below 4.9 and above 6.6. These pH studies did not attempt to differentiate between direct effects on the nematode and indirect influences through plant physiological or anatomical modification.

Edaphic factors dictate distribution of nematode species, however, climatic factors regulate rates and periodicity of population dynamics. Jones' (72) based a development function for ectoparasitic and endoparasitic nematodes on accumualated rainfall and temperature. His development index positively correlated with log of the area stunted by nematodes in sugarbeet fields.

P. penetrans reproduces continuously over a wide temperature range. Kimpinski (78) reported four *P. penetrans* generations per year in spring planted red clover. The last generation was in November when soil temperatures were 0 to 6.1°C. However, annual crops with shorter growing seasons may support fewer generations. Miller (94) reported bimodel *P. penetrans* population patterns in corn roots. Peaks occurred in early July and early September before the root system decomposed. Olthof (102) observed low summer and high fall soil populations of *P. penetrans* in rye-tobacco rotated fields. *P. penetrans* winter soil populations in potato fields slowly declined from September to February and increased in April. Population decline corresponded to high mortality of immature stages (31). Perennial crop roots can support *Pratylenchus* populations throughout the year, but peaks occur at periods of maximum root growth. Blackberry roots had maximum *Pratylenchus sp.* populations in the spring during maximum root proliferation. This peak was followed by rapid population decline through summer and into winter (55). Strawberry roots infected with *Pratylenchus coffeae* followed similar patterns with low winter populations, a peak in April to May and a decline in mid-summer (121). Di Edwardo (32), also working with strawberries, noted that *P. penetrans* root populations peaked in July and September. The second peak was in new roots produced during late summer. Soil populations were lowest in January, increased through spring to an early June peak, and slowly declined through the summer. Therefore, sampling roots vs soil sampling give conflicting prospectives of population dynamics. Soil populations decline as nematodes enter roots and increase when nematodes emigrate as food quality deteriorates or roots die.

In annuals or perennials, such as peppermint, where small shallow winter root systems greatly expand in early spring, survival of exposed winter populations is a major factor determining the next season's plant damage. Dunn (37) reported that winter survival of P. penetrans in potato fields was influenced by soil depth, with higher mortality at 0-15 cm than at 15-30 cm. In 0-15 cm profiles, approximately 50 percent of the population was in roots. He observed no difference between root and soil survival, but roots contained high egg counts through the winter. In 15-30 cm profiles higher proportions were recovered from soil. Eggs at this depth appeared ready to hatch in the spring before those found at 0-15 cm. Observations with fruit trees in winter also showed that P. penetrans could survive both in soil and senscent roots. Another P. penetrans potato study (31), showed that most of the population overwintered in soil, although a small population survived in tubers. Gravid females were not observed during winter. Winter survival of P. penetrans in rye-tobacco rotation fields frozen for 9-16 weeks was reported to 40 to 55 percent in soil and 50 to 65 percent in rye roots. Olthof (102) concluded from these studies that winter kill could not be depended on to drastically reduce populations. Seasonal population dynamics were inconsistant from year to year and of modest predictive value. Seasonal trends are the result of a complex interaction between soil, moisture, temperature, and host factors.

Climatic conditions also affect host plant physiology and predispose plants to nematode damage. This type of climate-induced damage generally prevails in cool springs when temperatures are adequate for nematode reproduction, but below levels necessary for root growth. Ferris (50) observed that P. penetrans infected onion seedlings had significant root stunting at 7-13^{0}C with 100 nematodes per gram of root, but comparable damage required 400 per gram at 16-25^{0} C. P. penetrans on tobacco (143) showed similar trends with damage more severe in cool wet springs than under dry warm weather patterns. Inoculated tobacco root systems at 13^{0}C had fewer nematodes per gram root than plants at 23^{0}C, but stunting was greatest at 13^{0} C. In studies with P. penetrans on apple (85) and soybean seedlings (135), high temperature (30^{0}C) and moderate temperature (21^{0}C), respectively, produced the greatest plant damage. These temperature levels maximized the difference between nematode pathogenic activities and ability of plants to withstand damage. Oostenbrink (105) concluded from P. penetrans studies in a wide range of crops, that favorable growing conditions reduced differences in damage caused by high and low population levels.

Development of nematode-plant damage models should consider interrelationship of climatic, edaphic, physiographic, and host tolerance factors in addition to nematode population data. Previously, nematode crop loss data were not quantified. Qualitative data alone has not proven of value for formulation economic thresholds. Simple linear regression of population (usually initial) and yield is well-suited for empirical loss models (8). Raw population data plotted against yield have produced curvilinear functions, but data fit has been greatly improved with log transformed population data (11,101,109). Lownsberry and Peters' (48) experiments with *Heterodera tabaccum* illustrated the predictive capability of semi-log transformed simple linear regression. They calculated increase in plant damage for each ten-fold nematode population increase for different fertilizer treatments using regression model slopes. A prediction can be made within a desired confidence limit when yield variability is sufficently explained by independent variables in the model. Improved fit can be obtained, if there are block yield effects, by transforming yield to probit or percentage yield (138). Unfortunately, simple linear regression models can not partition variability due to climatic, edaphic, cultural, and physiographic factors which modify nematode activity and plant response. Sampling date illustrated how seasonal dynamics can influence interpretation of damage function data. Kinlock (81) reported that regession slopes became progressively steeper as sampling date approached soybean planting date in a *Meloidogyne incognita* infested field. Soil type (46,58) physiographic location, and plant age (154) also can produce distinct linear regression models with the same crop and nematode species. A family of simple regression models must be generated to account for each parameter outside the scope of the model. Even with this limitation, simple linear regression models are extremely useful.

Linear models have limitations in representing biological dynamics of nematode caused crop loss (104). Jones et al. observed a ceiling population above which sugarbeet yield decline was independent of additional *Heterodera schachtii* population. A linear model was inadequate to represent damage at these high population levels, where both density independent (climate or food quality) and density dependent (competition for food, diseases, or specific natural enemies) factors limited population growth. He concluded from experiments with peas planted in *Heterodera goettingiana* infested soil that a sigmoid curve would better fit observed population damage data (58). At low populations, plants compensated for damage, at moderate population levels yield correlated well with population, and high populations became self-limiting so that additional population caused no additional plant damage.

An empirical exponential model based on Nicholson's (99) population work has been constructed by Seinhorst (124,125). Seinhorst's model accounted for plant response at extremely high and low levels, where linear models were inadequate. The model was based on two assumptions; 1) the average nematode damage was the same at all densities so that activity was not influenced by density. 2) attack on a plant was not influenced by presence or absence of other nematodes attacking the same plant. These assumptions may not always be valid because nematode behaviour is influenced by density (10,99,104). However, the model does fit nematode damage data well (8,63). It focuses on the proportion of a plant damaged by each nematode, (Z). The undamaged fraction is the part which produces crop yields. Generally, for each nematode the fraction undamaged is very near one. This exponential model incorporates nematode population (P), a tolerance population level below which no damage occurs (T), and a minimum yield where additional nematodes do not cause additional yield loss (m).

$$Y = m(m-1)Z^{P-T}$$

Seinhorst's model, like simple linear regression, bases crop yield estimates only on nematode populations. Cooke and Thomason's (28) experiments with _H schachtii_ illustrated that soil temperatures modified the shape of a Seinhorst function developed for sugarbeet yields. Other factors that interact with nematode population dynamics or plant resistance also modify function shape. Ferris (49) utilized correlation matrices to interpret effects of nematode populations and edaphic factors on grape yields. This approach could detect significant interactions, but did not incorporate these into a single damage function. Ferris (44) proposed a multi-faceted damage model where damage done by each plant parasitic nematode species was rated in comparison to damage done by root-knot nematode species (in root-knot equivalent units). Soil type and cultivar differences modified damage equivalents caused by each nematode species. This approach integrated major damage modifying factors, but was less concise then a synoptic approach reviewed by Wallace (155). A synoptic approach uses multiple regression and multi-variant statistics to develop a single statistically testable model. Stepwise regression allows evaluation of each determinant within the model and modification of the model to produce the most useful damage function.

Once a nematode damage function is developed, it can be integrated with treatment data into a computer program to develop an economic crop management model (17,44).

Pest management decisions are possible when pest control techiques are available to reduce the impact of pest damage on crops. Preplant fumigation has been the major chemical control method for plant-parasitic nematodes. However, phytotoxicity of fumigants limit their application in established perennial crops. Non-volatile systemic nematicides reduce both nematode densities and nematode injury to plants with minimal adverse effects on treated plants.

The effective nematode control demonstrated by carbamate nematicides is a function of their absorption and systemic translocation through plants. Amphimobile transloction has been reported for oxamyl (21,134,164) and carbofuran (33). Foliar oxamyl applications have been reported to reduce both plant damage and nematode densities (57,170,114,117,134). However, soil applied oxamyl was shown to produce higher concentrations of active oxamyl fractions within plant tissues, than did foliar applications (164). Although nematicidal root exudates have been reported after foliar oxamyl treatments (135), these results conflicted with radiolabelled oxamyl studies where a non-active oxamyl breakdown product, oxime, was the component found in root exudates (21,64). Carbamate nematicides did not kill nematodes at field rates. Their mode of action is assumed to involve disruption of acetylcholinesterase activity of the nematode nervous system which results in motor and sensory dysfunction. Nervous system disruption causes the behavioral modifications observed following exposure to these compounds. Among the effects reported were reduced larval movement (163), disorientation toward roots (35), disorientation to feeding sites within roots (88), reduced root penetration (2,34,57,91,120), disrupted sexual attraction in amphimictic species (13), and reduced egg hatch (64,88,92). In some experiments, nematicidal or nematistatic activity was confined to root surfaces (7,20,34), which explained why nematodes were less sensitive to these compounds once they penetrated into the root (61,69,88,159). However, hindered reproduction and retarded development have been observed after nematodes were established within roots (15,60,114,117,132). These biological affects were reported to be dependent on application timing with treatments prior to or very early after nematode invasion being the most effective (115,132,133). Finally when using carbamate nematicides, one must be cognizant of their longevity in the plant and rhizosphere. Oxamyl degradation was reported to be rapid with a half-life of one week and with only five percent of the parent compound remaining after 30 days (21). Furthurmore, soil water can leach these highly soluble and mobile nematicides out of the rhizosphere, thus reducing the effective dosage (19). These physical and biological factors illustrate why appliction timing with oxamyl can be critical for sucessful nematode control and crop response.

The steps central in developing nematode management programs are: 1) estimation of yield loss resulting from a range of nematode densities and 2) evaluation of nematicide efficacy in reducing nematode density or plant damage. Step one involves utilization of the nematode damage functions previously cited. Step two involves the development of control-cost functions which mathematically relates the cost of the control utilized to the nematode density following the control procedure. Ferris (45) discussed derivation of nematode economic thresholds developed from these two functions. He calculated that the nematode population density at the point which maximized the difference between the control-cost function and the nematode damage function equalled the economic threshold. Nematode management programs based on economic threshold analysis will maximize profit even though such programs may not minimize actual crop loss.

Plant disease expression is dictated by interactions of host biology, pathogen biology, and environment. The preceeding literature elucidated components important in regulating *P. penetrans* population dynamics and the resulting plant damage. This research was designed to identify and quantify those factors central to developing *P. penetrans*-PEPPERMINT management strategies. Four interdependent aspects of this crop-pathogen system were selected for investigation based on research with other crops: 1) quantification of the relationship between *P. penetrans* and peppermint yield, 2) seasonal dynamics studies to develop optimal sampling strategies for crop loss prediction, 3) evaluation of environmental effects, climatic and edaphic factors, which modify population dynamics and yield loss functions and 4) evaluation of host, stand vigor and cultivar tolerance effects on peppermint damage and nematode population trends. Finally, non-volatile carbamate nematicides were evaluated for control of *P. penetrans* damage in peppermint. These relationships were expressed using simple and multiple regression models and were evaluated relative to their predictive values in making nematode-crop management decisions.

GENERAL MATERIALS AND METHODS

Estimation of field soil populations

Bulked soil cores from each plot were sifted through a five cm mesh screen and mixed. Small randomly selected subsamples were tightly packed in a 50 ml beaker until filled. This soil was processed by the Baermann funnel method (26) for five days to extract nematodes. Population estimations were made by counting 25% of a calibrated dish containing the nematode suspension. All counts were adjusted to 50 ml of soil. Mean field soil population densities were based on populations recovered from the 50 ml sample.

Estimation of field root populations

Root core samples (10 x 10 x 10 cm) were soaked for one hour to soften soil, which facilitated washing and reduced root breakage. Roots were washed free of soil and debris in a pressurized water stream from a hand held nozzle. Plant material was collected on a 1.5 mm screen. All healthy and dead roots that withstood washing were trimmed from stems and rhizomes. Random samples of rewashed roots were selected until a maximum of ten grams were collected for nematode extraction. Nematode populations were extracted in an intermitent misting chamber. After seven days, collected samples were removed and nematode suspensions were brought to 100 ml with tap water. Two 10 ml aliquots of each sample were placed in separate counting dishes. Twenty-five percent of each dish was counted. Mean counts of the two dishes was multiplied by 40 to convert actual population level. Per gram root weights were calculated after processed roots air dried for two months. Mean field root population densities were based on the number of *P. penetrans* recovered per gram root sample.

Estimation of greenhouse root populations

Potted peppermint plants from greenhouse experiments were soaked for several hours prior to processing. Contents of each pot were placed in an eight liter round bottomed bowl. The root system was washed clean of soil and debris in one liter of water. Wash water was retained for collection of soil populations (see Estimation of greenhouse root populations). All roots were trimmed from rhizomes and stems. Fresh top weights (stems, foliage, and rhizomes) were recorded. Extractions and population estimations were done as with field populations. Following extraction, roots were air dried for two months before weights were recorded.

Estimation of greenhouse soil populations

Soil in root wash water was resuspended and allowed to settle for 10 seconds before decanting supernatant into a 1 liter container. A 200 ml subsample was poured through a 2 mm screen into a 350 ml centrifuge bottle. This sample was centrifuged at 425 x g for five minutes, the supernatant discarded, and the pellet resuspended in 200 ml of 1.33 molar sucrose solution. Following a 30 sec centrifugation at 425 x g, the supernatant was decanted through a 500 mesh screen. The screen was back flushed into a counting dish and populations were estimated as with field soils.

Propagation of rooted cutting

Young five cm long Black Mitcham, Todd's Mitcham, and Murray Mitcham peppermint shoots were cut from the Oregon State University certified peppermint beds. Lower leaves were removed leaving only the top whirl. Cuttings were planted in flats of sterilized sand. Rooted cuttings were dug after three weeks. Ample cuttings were produced to allow for selection of plants with uniform top and root characteristics. Prior to planting, leaves were trimmed, so all cuttings would have similar photosynthetic areas at the beginning of each experiment.

Inoculum Aquisition

Infected peppermint roots were dug from a section of the Linn County damage study site apparently devoid of other phytonematodes. *P. penetrans* inoculum was mist extracted from washed roots. The nematode suspension was kept well areated and refrigerated until used. Immediately prior to inoculation, the nematode suspension was poured unto ten layers of tissue paper in a Baermann funnel. After eight hours , active nematodes which migrated through the paper were collected. Twenty 10 ml aliquots of stock were counted to estimate nematode concentration, development stage and sex compostion. In all inoculum, mean composition percentages were 35% female, 50% immature, and 15% males. A dilution series was used to obtain desired uniform suspension volumes at each inoculum level.

Inoculation method

Cuttings were allowed to grow for several days before inoculation. Soil was carefully removed around each plant to expose the root system. Ten mls of nematode suspension were pippeted directly on exposed roots. Ten mls of distilled water were pippeted on control treatment roots. Soil was replaced and each pot was lightly watered to settle loosened soil.

Greenhouse growth conditions

Each experiment occupied a single greenhouse bench to minmize variation. A 15 hour photoperiod, 19° C night, 22° C day mean temperature ($+2^{\circ}$) regime was maintained throughout the experimental periods.

Each plant was fertilized with 50 ml of a one percent Rapid-Grow ® solution biweekly. Soil moisture was checked daily and pots watered as necessary. Plants were treated using recommended application rate for mildew (Karathane), aphids (Resmethrin), and spider mites (Pentac) several times during the experimental period.

EFFECTS OF *PRATYLENCHUS PENETRANS* POPULATIONS, EDAPHIC FACTORS AND HOST VIGOR ON PEPPERMINT HAY YIELD

Preface

Pratylenchus penetrans is widely distributed in Oregon peppermint growing areas. High populations, in many instances, occur in stunted declining stands. Little quantified damage data have been available as a basis for treatment recommendations. These studies were designed to develop damage functions and establish economic thresholds for this nematode.

Materials and Methods

In 1977-1978 over fifty peppermint fields in four Willamette Valley counties were evaluated as possible *P. penetrans* damage study sites. Five criteria were used in selection; 1) high *P. penetrans* population, 2) areas of severe nematode damage, 3) gradient of population levels and plant damage across fields, 4) minimal extraneous pest and disease components and 5) easy accessibility. Three fields were selected prior to the 1979 harvest, one in each of three mid-Willamette Valley Counties (Benton, Polk, and Linn counties). Cropping and nematode damage histories are summarized in Table 1.

Table 1. 1979 - 1980 damage study sites cropping and peppermint stand decline histories

	Benton Co.	Linn Co.	Polk Co.
Previous Cropping	cereal bush beans rotation	weed fallow bush beans dill	cereal bush beans rotation
Date Peppermint Planted	spring 1975	spring 1978	spring 1977
First Damage Observed	1977 after spring flaming	stunting lighter soil 1979	stunting on lighter soil 1978
Severe Damage	1978	1979	1979

1979 : Sixteen plots were harvested on August 6-10 in the Polk County field and ten at each other location. Plots were selected in the center of each severely stunted area, at the margains of damaged areas, and in the most vigorous areas in each field (Figure 1). Hay in each 3.05 x 3.05 m plot was mowed with an electric hedge cutter and fresh hay weight was recorded. Root and soil samples (for nematode population estimations) were collected immediately after harvest. Five 10 x 10 x 10 cm intact root cores were systematically selected in each plot; four from each quadrant and one at the center. In each plot, 2.5 x 15 cm soil cores were systematically collected and the nine cores were combined before processing to extract nematodes. Soil not used for population analysis was retained for determination of soil textural class by the hydrometer method (18).

1980 : On April 10, after new season's growth commenced, transect lines crossing soil textural, population, and 1979 yield gradients were established in each field (Figure 1). Fifteen plots were selected along these transects and population data were recorded from five root and nine soil cores as in 1979.

Prior to harvest, five additional plots were selected at each location. These included damage levels not well represented in transect line plots. On August 7-9, plots were harvested and population samples collected. In addition to *P. penetrans* soil and root populations, *Paratylenchus sp.*, *Trichodorus sp.*, and *Longidorus elonagatus* soil populations were estimated.

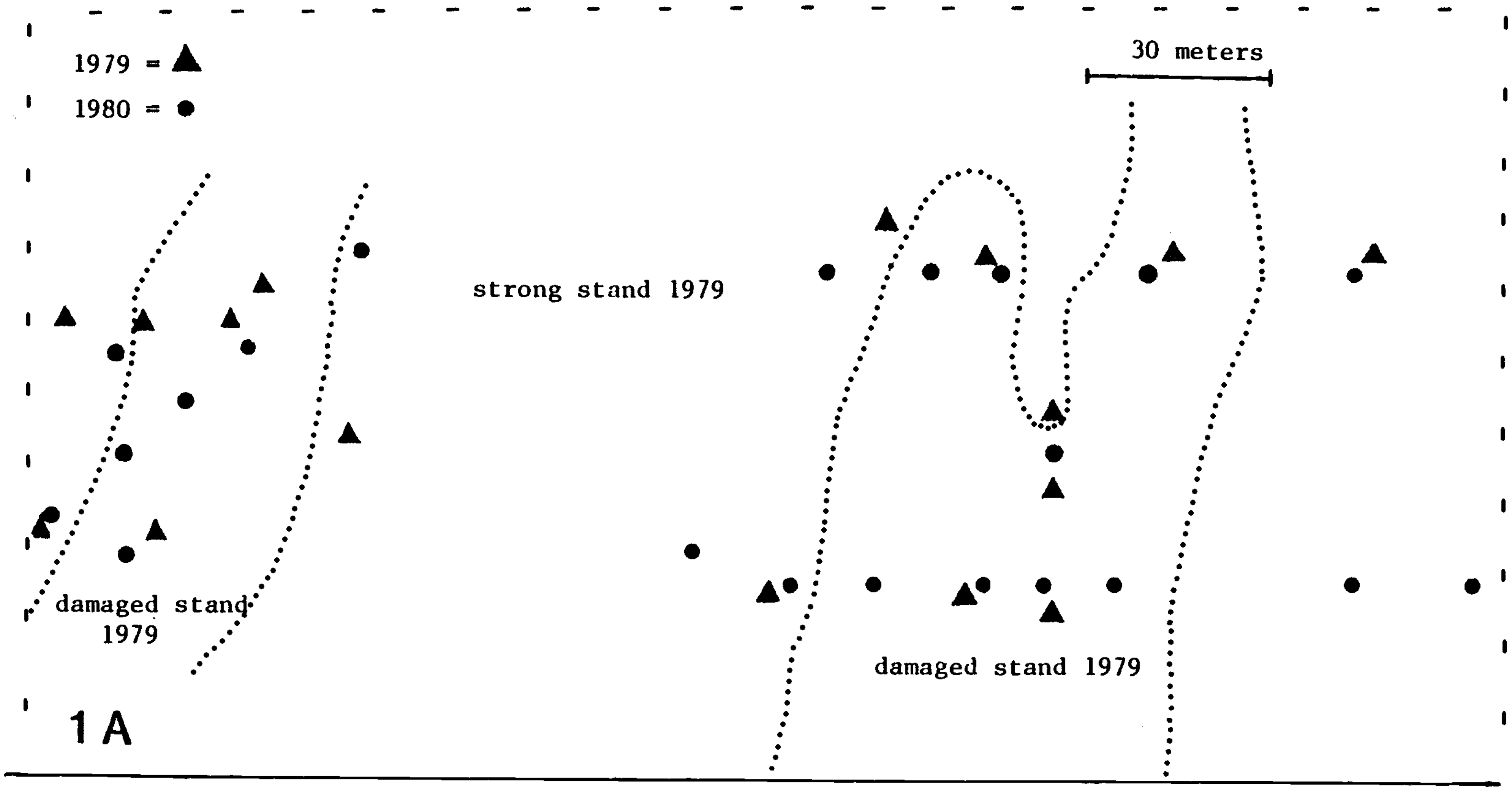
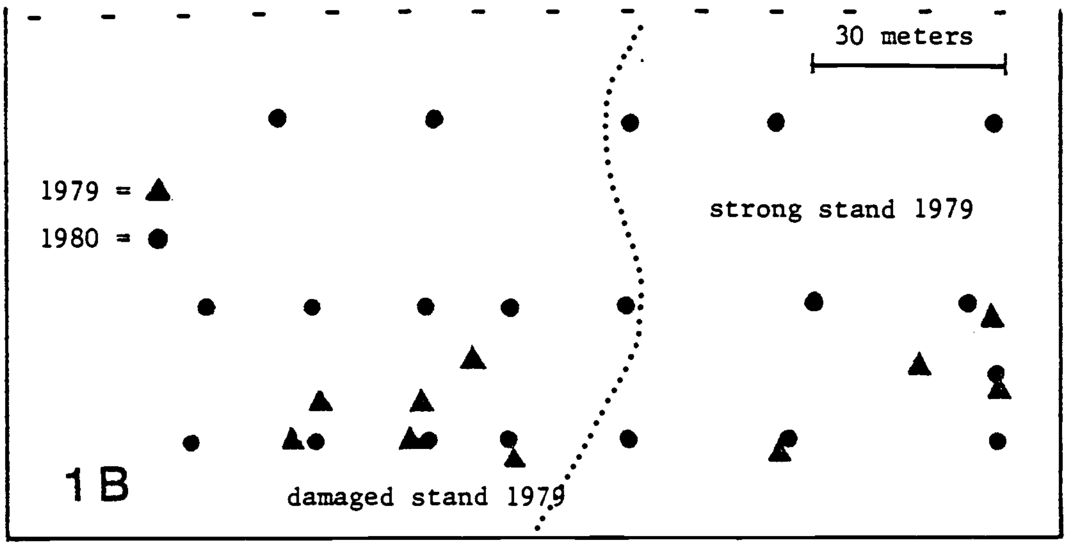


Figure 1. 1979 and 1980 plot locations within damage study sites: A) Polk County B) B) Benton County C) Linn County

areas within dotted lines ········ exhibited some degree of stunting in 1979 and corresponded to lighter textured soils

solid lines ——field boundry; dashed line -- field extends beyond this point



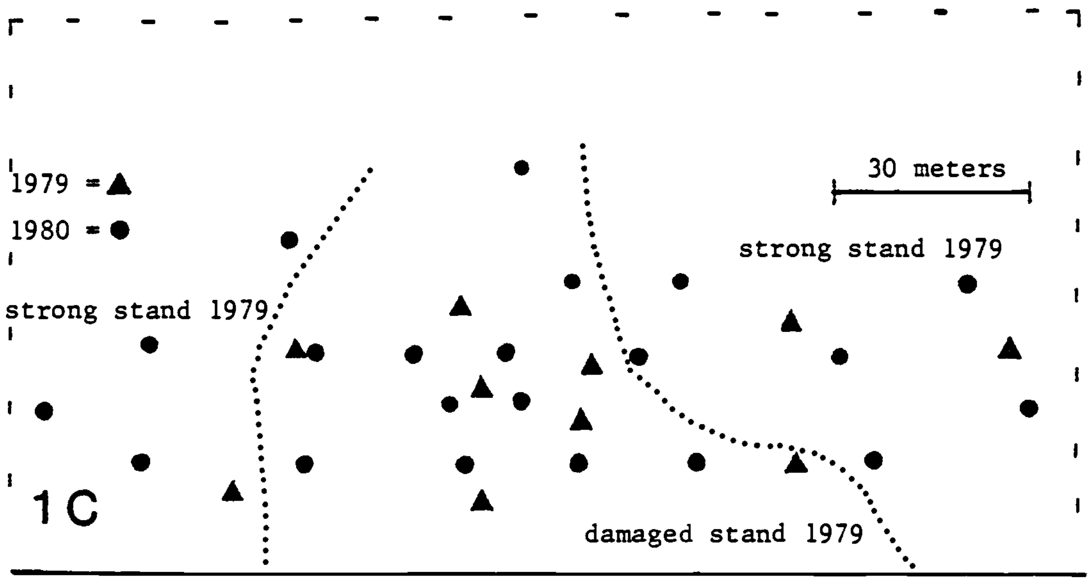


Figure 1. 1979 and 1980 plot locations within damage study sites: B) Benton County C) Linn County. Areas within dotted····lines exhibited some degree of stunting stunting in 1979 and corresponded to light textured soils.

Four additional edaphic parameters reported to be related to nematode distributions and nematode damage (pH, soil texture, bulk density, and soluble solids) were measured in all plots. Finally, previous season's vigor was rated 1, 2 or 3 (weak with estimated oil yield less than 47/kg, intermediate with 47-68 kg oil/ha, strong with greater than 68 kg oil/ha) by evaluating crop stubble in April and each plot's location in relation to areas of known 1979 yield.

Yields and populations were transformed to aid in statistical analysis. Actual yields were converted to percentage yield (each plot's yield divided by maximium yield harvested in each field x 100). This transformation facilitated comparisons among the three fields. Log transformed population data were used in all statistical analysis. Linear regression models of the general form (128)

$$Y = B_0 + B_1(X_1) + B_2(X_2) + B_3(X_3) + B_4(X_4)$$

were used to evaluate the relationships between percent yield, log nematode populations, edaphic factors and host vigor.

Results

Simple linear regression analysis of nematode population to yield at harvest (August 1979 and 1980) showed that *P. penetrans* root populations were significantly correlated with yield (Figures 2 and 3). Using analysis of variance, 1979 population-yield regression lines were statistically unseparable (P=0.05). The tolerance level (population on the regression line where yield equals 100 percent) was

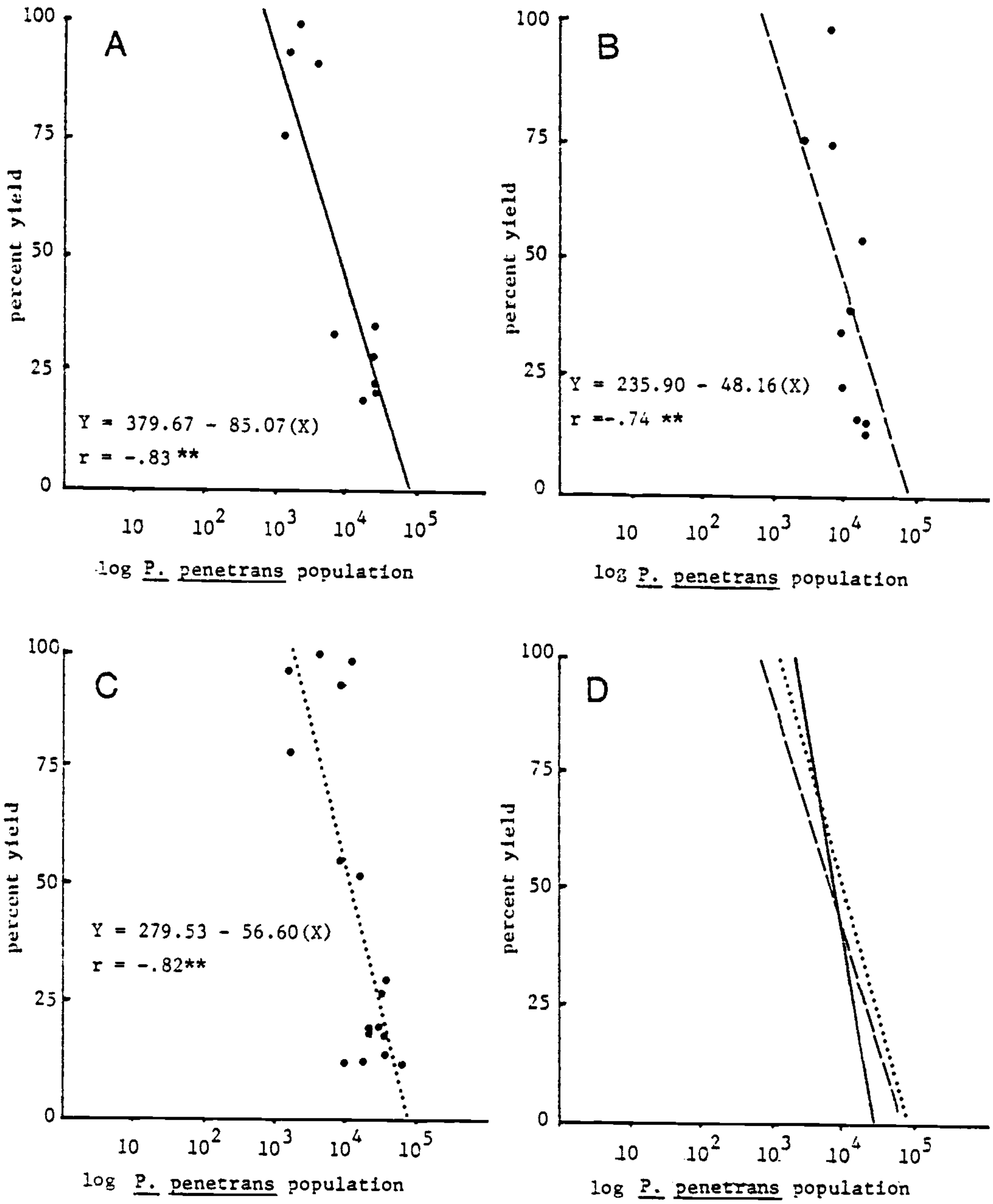


Figure 2. Regression of August 1979 Pratylenchus penetrans root populations to percent fresh peppermint hay yield at three Willamette Valley counties locations:
A) Linn County plots, B) Benton County plots, C) Polk County plots

D) Comparison of the three locations

Percentage of maximum yield harvested at each location

* and ** indicate significant regression at P=0.05 and P=0.01 respectively

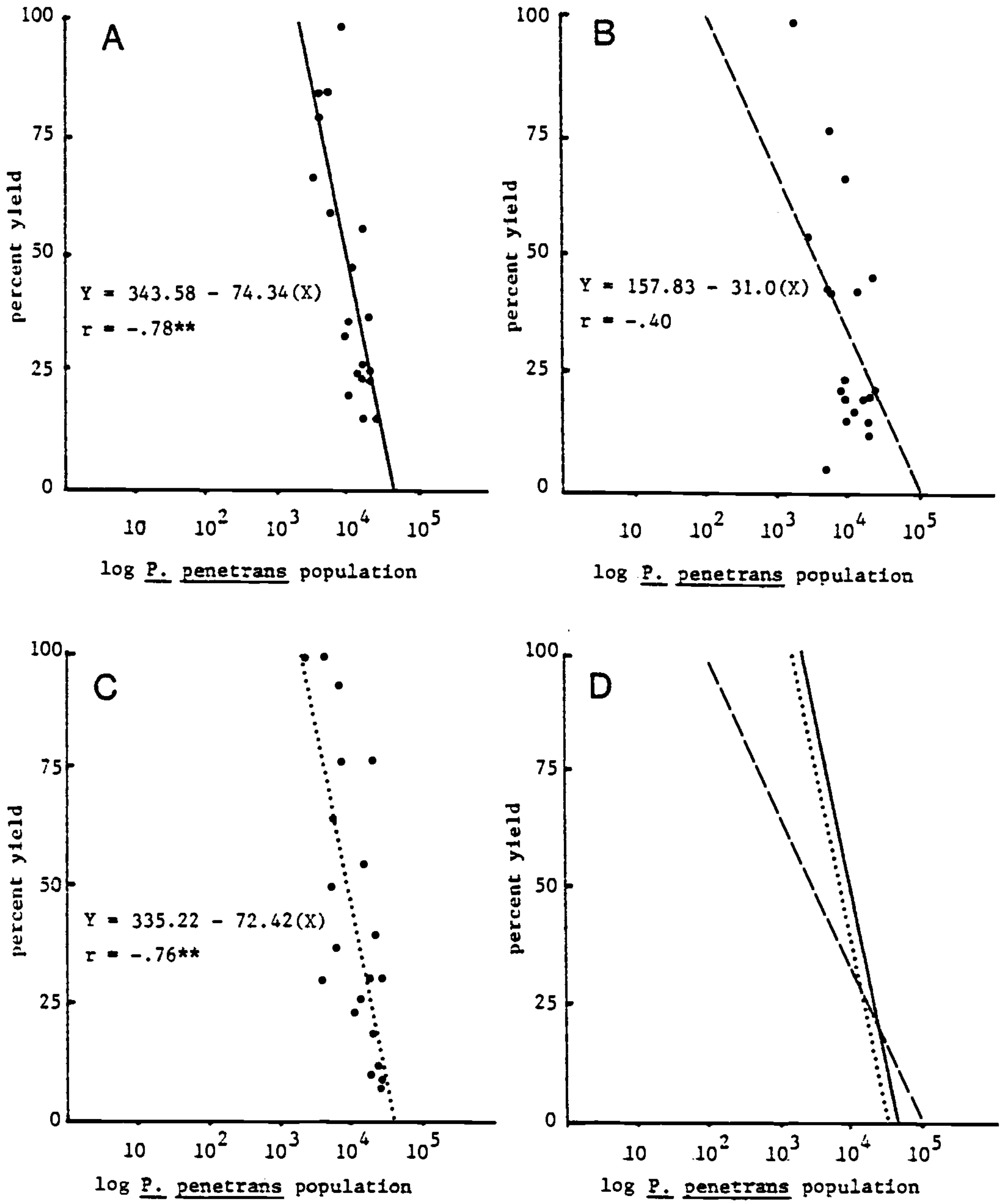


Figure 3. Regression of August 1980 Pratylenchus penetrans root populations to percent fresh peppermint hay yield at three Willamette Valley county locations:
A) Linn County plots B) Benton County plots C) Polk County plots
D) Comparison of the three locations
* and ** indicate significant regression function at P=0.05 and P=0.01
percentage maximum yield harvested in each location

approximately 1400 P. penetrans /gram dry weight root. The slope of the regression line indicates an average 63 percent yield reduction accompanied each 10 fold increase in root population above the tolerance level. The 1980 root population data exhibited similar trends. Population to yield regressions were statistically the same (P=0.05) at Linn and Polk County locations. In these two fields a ten fold population increase caused a 73 percent yield reduction when populations were above the tolerance level (approximately 1500 P. penetrans per gram of root). Only the Benton County field in 1980 exhibited August root population-yield relationship significantly different from other locations in either years.

Soil populations in August were not good predictors of yield. The 1979 harvest soil populations (Figure 4) were not highly correlated with yield, but they exhibited consistant regression models across locations. The 1980 harvest soil populations (Figure 5) were inconsistant between locations and poorly correlated with yield.

April 1980 (preseason) population data (Figure 6) were not strongly correlated with August yields. Preseason root populations at Polk and Linn County locations had similar yield-population responses, although regressions were not highly significant. At these locations approximately a 38 percent yield reduction accompanied each ten fold population increase above 630 P. penetrans per dry gram root weight. The Benton County regression model differed from those developed from Polk and Linn County data. The 1980 preseason soil populations (Figure 7), unlike root population data, showed no consistant trends among locations and were not correlated with yield.

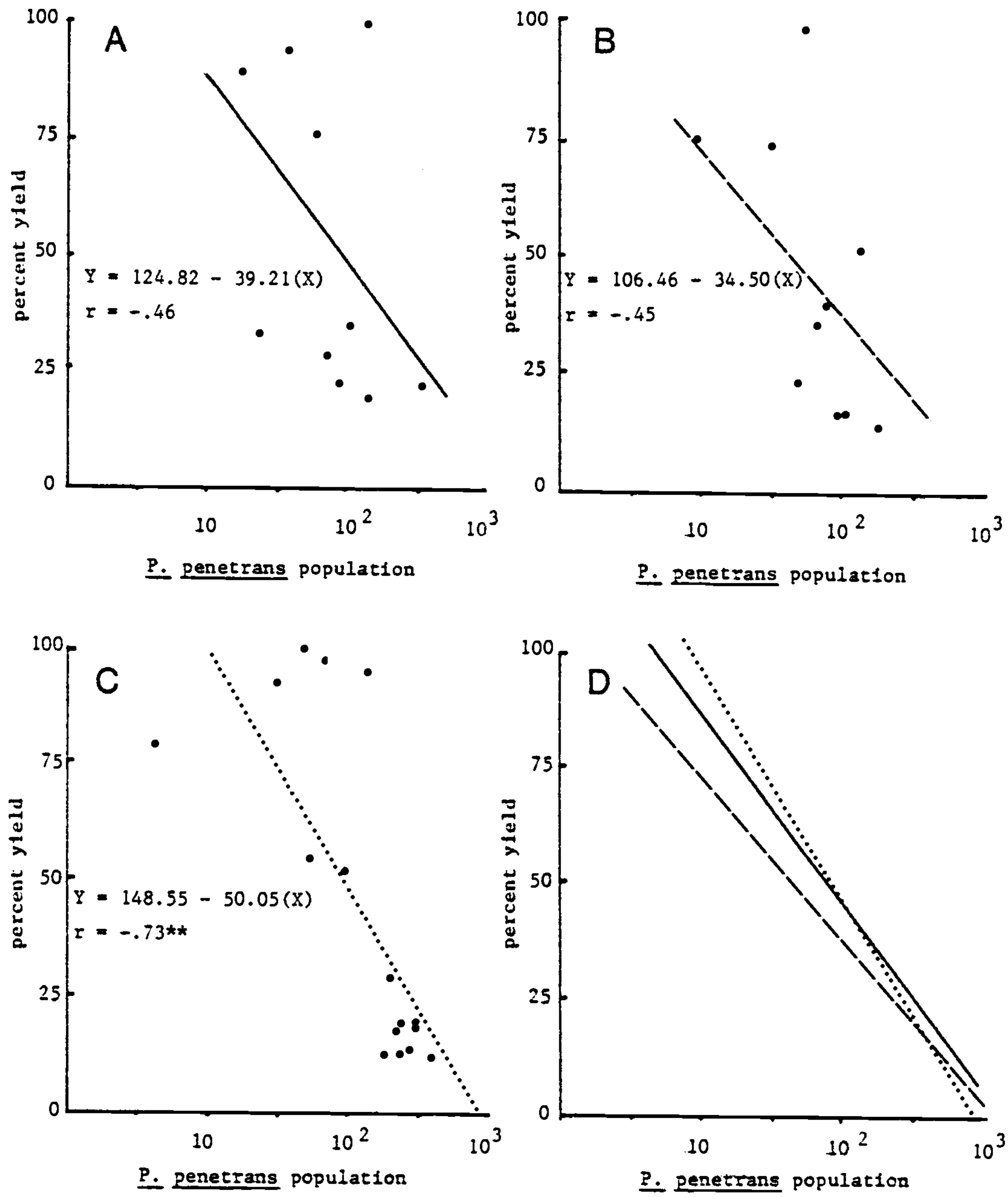


Figure 4. Regression of August 1979 Pratylenchus penetrans soil populations to precent fresh peppermint hay yield at three Willamette Valley county locations:
A) Linn County plots B) Benton County plots C) Polk County plots
D) Comparison of the three locations
* and ** indicate significant regression function at P=0.05 and P=0.01
precentage of maximum yield harvested in each location

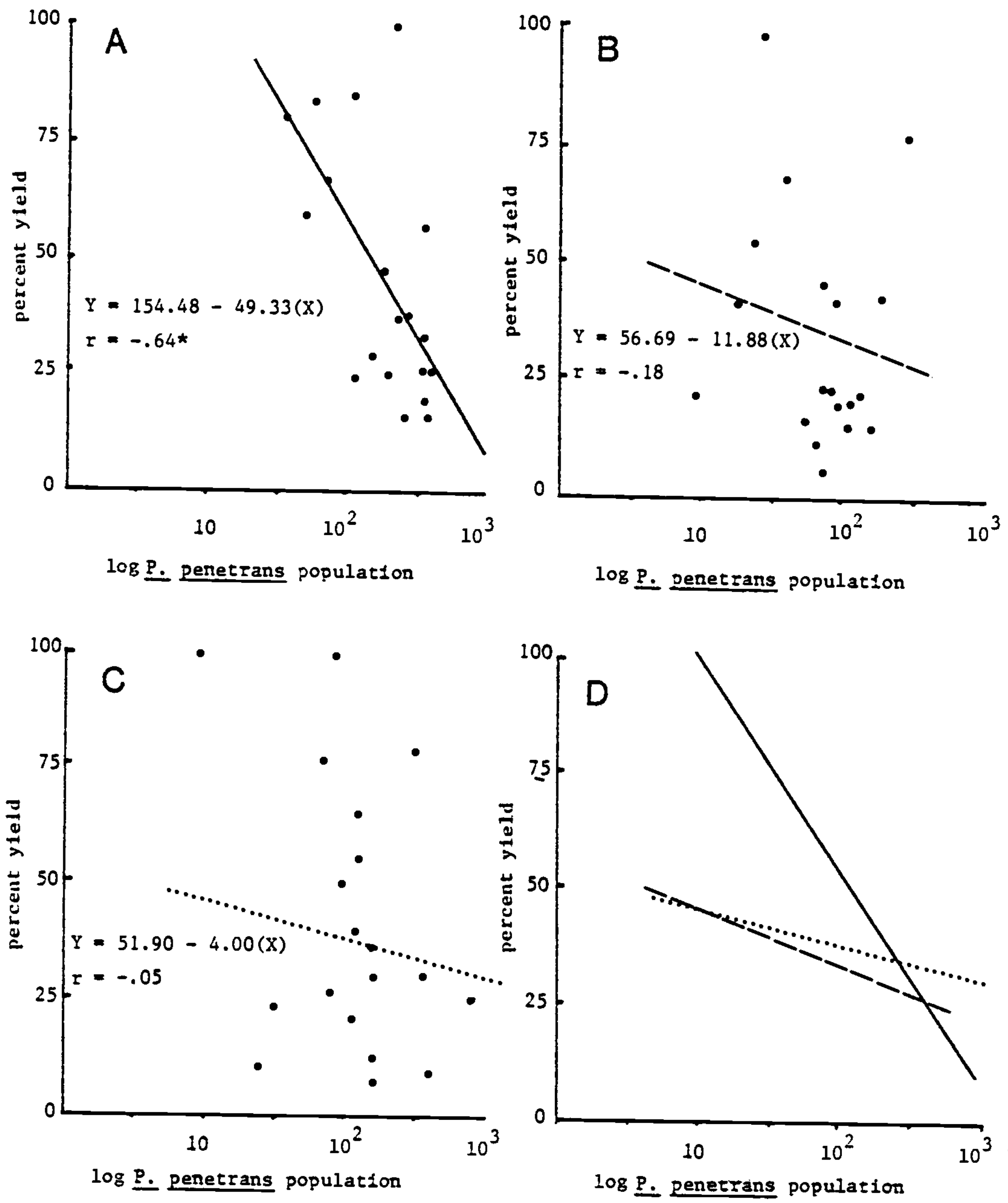


Figure 5. Regression of August 1980 Pratylenchus penetrans soil populations to percent fresh peppermint hay yield at three Willamette Valley county locations:
A) Linn County plots B) Benton County plots C) Polk County plots
D) Comparison of the three locations
* and ** indicate significant regression function at P=0.05 and P=0.01
percentage maximum yield harvested in each location

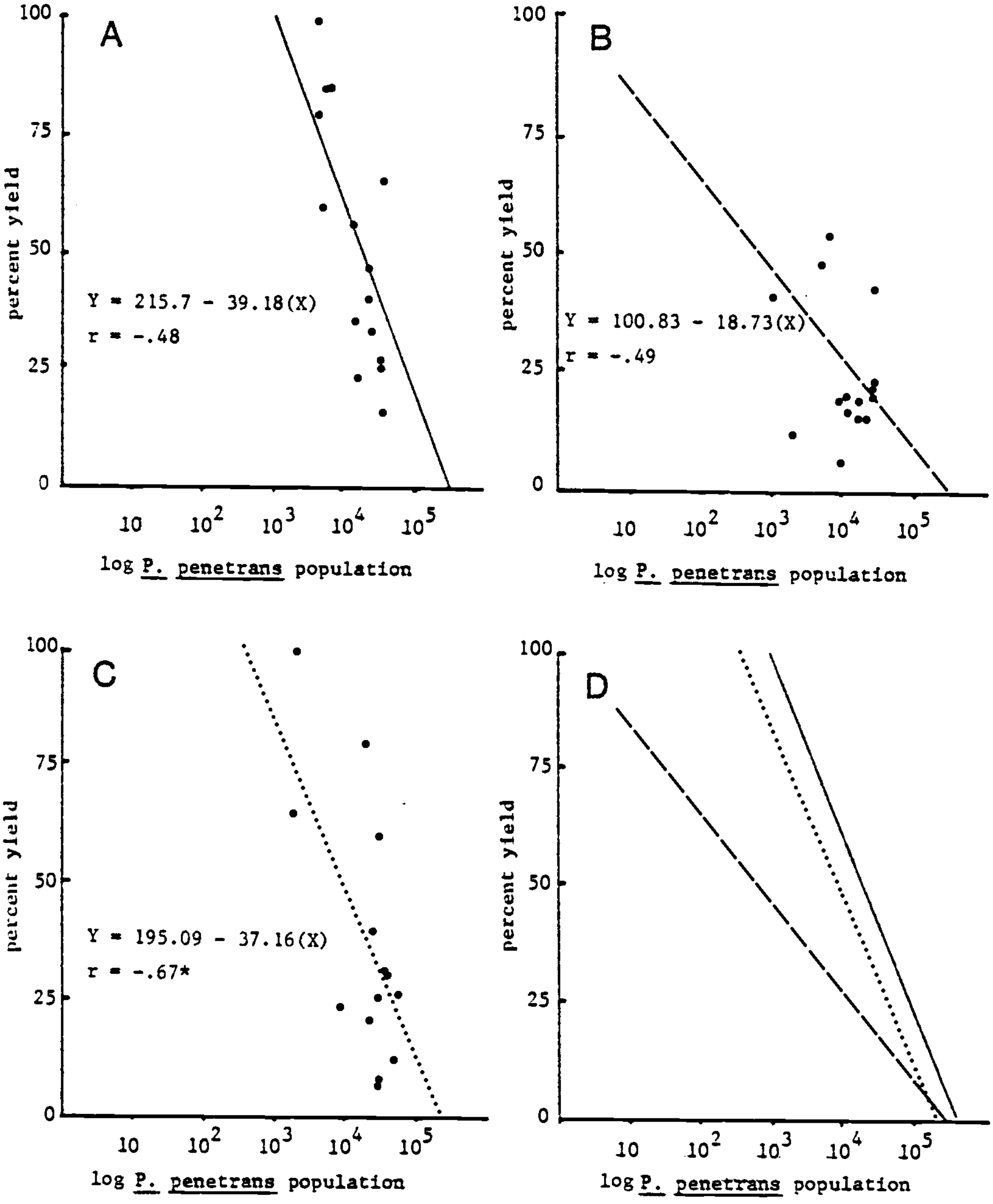


Figure 6. Regression of April 1980 Pratylenchus penetrans root populations to percent fresh peppermint hay yield at three Willamette Valley county locations:
A) Linn County plots B) Benton County plots C) Polk County plots
D) Comparison of the three locations
* and ** indicate significant regression function at P=0.05 and P=0.01
percentage maximum yield in each location

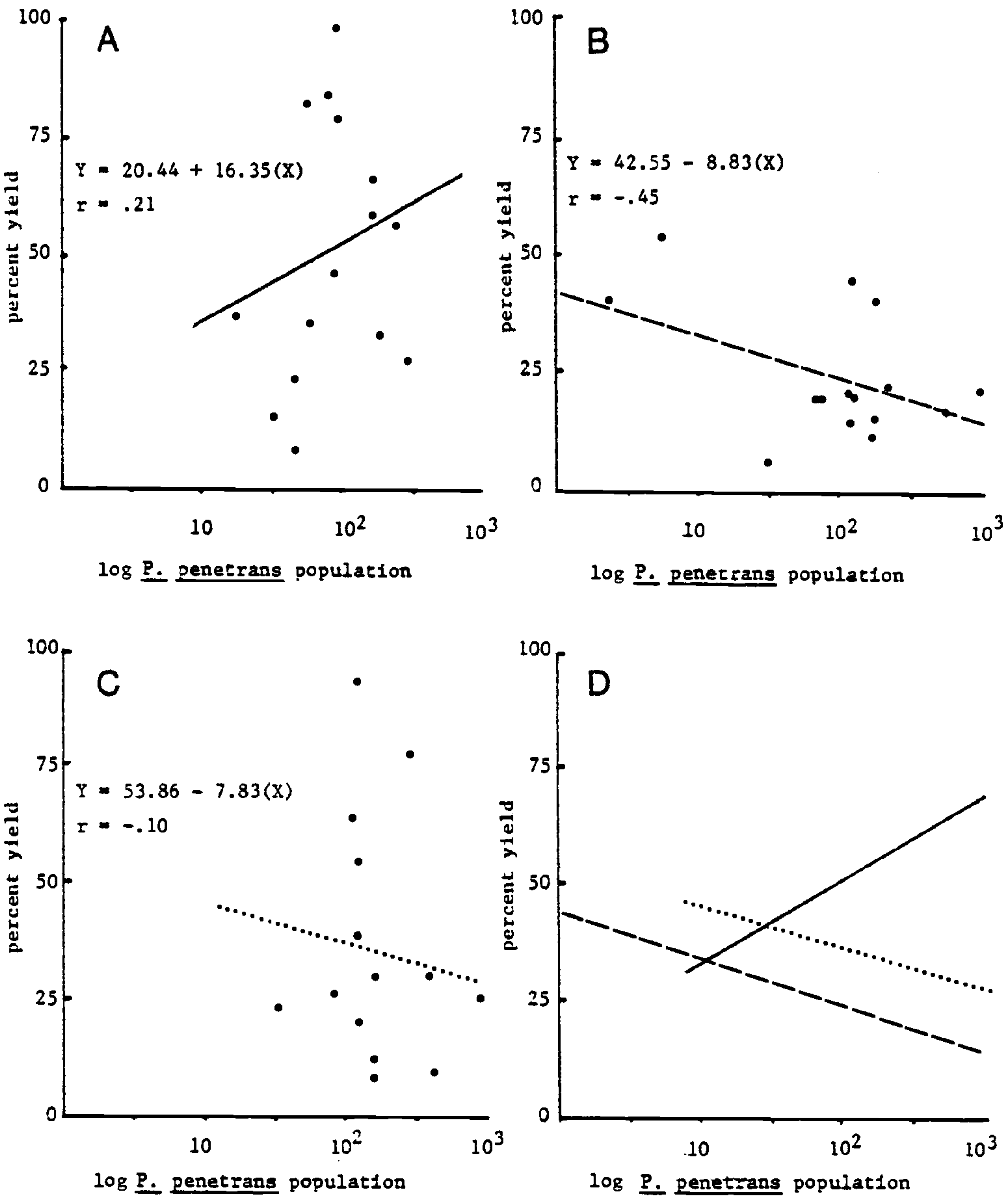


Figure 7. Regression of April 1980 Pratylenchus penetrans soil populations to percent fresh peppermint hay yield at three Willamette Valley county locations:
A) Linn County plots B) Benton County plots C) Polk County plots
D) Comparison of the three locations
* and ** indicate significant regression function at P=0.05 and P=0.01
percentage maximum yield harvested in each location

The ranges and means for all parameters measured in 1979 and 1980 are summarized in Appendix A.

In 1979, soil texture, P. penetrans root population and yield were significantly correlated (Figure 8). Yield was negatively correlated with percent sand and positively correlated with percent silt. Similarly, P. penetrans populations (soil and root) were positively correlated with sand and negatively correlated with silt. In 1980, percent sand and silt exhibited similar relations to yield and P. penetrans populations (Figure 9). Previous season's plant vigor also was significantly correlated with yield, percent sand, percent silt, and August P. penetrans root populations. Bulk density, pH and soluble solids were not consistantly correlated with either yield or P. penetrans populations.

At the August 1980 sampling date, four plant parasitic nematode genera were recovered from soil and root samples. P. penetrans was the only phytonematode associated with peppermint yield reduction. Trichodorus sp. and Longidorus elongatus distributions were patchy within fields and generally confined to coarser soils where P. penetrans populations were highest. Paratylenchus sp. , however, was positively correlated with yield and percent silt. This species was distributed in heaviest soil of each field; areas least suitable for P. penetrans population increase and plant growth reduction during periods of mid- summer water stress.

Multiple regression model development for the Linn County location is presented in Table 2. Benton and Polk County multiple regression models were similar to Linn County and are presented in

8A	1	2	3	4	5
1		-.74 **	-.45	-.76 ***	+.88 ***
2			+.87 ***	+.80 ***	-.82 ***
3				+.70 ***	-.81 ***
4					-.90 ***
5					

8B	1	2	3	4	5
1		-.83 ***	-.46	-.85 ***	+.84 ***
2			+.58	+.84 ***	-.70 ***
3				+.72 ***	-.52
4					-.99 ***
5					

8C	1	2	3	4	5
1		-.82 ***	-.73 ***	-.78 ***	+.83 ***
2			+.73 ***	+.70 ***	-.71 ***
3				+.63 **	-.63 **
4					-.97 ***
5					

1 = % maximum hay yield

2 = log P. penetrans/ gm. dry weight root

3 = log P. penetrans/50 cm^3 soil

4 = percent sand

5 = percent silt

Figure 8. 1979: Correlation matrices of *Pratylenchus penetrans* populations, peppermint growth, and soil textural composition.
A) Linn County location, B) Benton County location, C) Polk County location

*, ** and *** indicate significant regressions at the 0.05, 0.01, and 0.001 levels respectively.

9A	1	2	3	4	5	6	7	8	9	10	11	12
1		+.87 ***	-.74 **	+.62 **				-.58 **	-.78 **	+.46 *		
2			-.67 **	+.58 **				-.60 **	-.73 ***			
3				-.96 ***				+.78 ***	+.80 ***			
4								-.74 ***	-.72 ***			-.48 *
5												
6												
7												
8									+.72 ***			
9												
10												
11												
12												

Figure 9. 1980: Correlation matrices of peppermint growth, edaphic factors, and nematode populations sampled in August.
A) Linn County site, B) Benton County site, C) Polk County site

*,**, and *** indicate significant correlation coefficents at the 0.05, 0.01 and 0.001 levels respectively
blanks indicate regression is not significant

1 = percent of maximum harvested yield
2 = previous season stand vigor; 1-3(weakest-strongest)
3 = percent sand
4 = percent silt
5 = pH
6 = bulk density (gm./cm^3)
7 = soluble solids (ppm)
8 = log *P. penetrans*/50 cm^3 soil August 1980
9 = log *P.penetrans*/gm. dry wt. root August 1980
10 = log *Paratylenchus spp.*/50 cm^3 August 1980
11 = log *Longidorus elongatus*/ 50 cm^3 soil
12 = log *Trichodorus spp.*/ 50 cm^3soil

9B	1	2	3	4	5	6	7	8	9	10	11	12
1		+.85 ***	-.73 ***	+.78 ***	-.57 **	+.53 *	+.59 **			+.74 ***		
2			-.75 ***	+.72 ***	-.48 *		+.53 *			+.79 ***		
3				-.95 ***			-.58 **		+.55 *	-.81 ***		+.53 *
4							+.49 *		-.48 *	+.78 ***		-.50 *
5							-.64 **					
6								+.55 *	+.55 *			
7									-.48 *			+.57 *
8									+.64 **			
9												
10												
11												+.53 **
12												

9C	1	2	3	4	5	6	7	8	9	10	11	12
1		+.76 ***	-.62 **	+.51 *					-.76 ***			
2			-.66 **	+.55 *	+.47 *				-.65 **			
3				-.87 ***								
4												
5										+.48 **		
6												
7												
8												
9												-.48 **
10												
11												
12												

Figure 9 Continued

Table 2. Linn county multiple regression yield loss models.
A) 1979 B) August 1980 population data C) April 1980 population data

A

Constant	Root Population +	Soil Population +	Percent Sand +	Percent Silt +	R^2
235.93	-47.99**				.684
235.09	-48.99**	2.52			.684
272.22	-25.52		-2.08*		.822
84.64	-27.18			2.51*	.821
-57.30		-2.74		4.02**	.709
248.96		-4.27	-3.21		.7312
270.58	-28.05	7.94	-2.14		.828
72.86	-30.26	10.62		2.65	.831

B

Constant	Root Population	Soil Population	Previous Season Vigor	Percent Sand	R^2
343.58	-74.33***				.611
304.45	-71.91**	2.97			.612
322.31	-50.09*			-1.23	.647
-2.32			25.03***		.762
128.24	-29.45		18.54***		.806
126.32	-17.78		17.66**	-0.68	.818
131.95	-21.81	15.04	18.98**	-1.08	.829

C

Constant	Root Population	Soil Population	Previous Season Vigor	Percent Sand	R^2
215.71	-39.18				.228
184.71	-38.55	14.86			.264
204.05	7.66			-3.00**	.638
-0.18			24.27**		.697
27.10	-5.97		23.20***		.701
78.16	10.65		16.10*	-1.72	.791
86.19	-12.56	-7.68	17.06*	-1.77	.799

*, ** and *** indicates the predictor variable is significant at the .05, .01 or .001 levels, respectively, for each predictor variable (+) entering the regression model.

Appendices B and C. In 1979, root populations were the best population parameter for explaining yield reduction (R^2= .684), while soil populations alone were not good predictors of yield (Table 2). When both population parameters were inclued in the same model, there was no improvement (R^2= .684). A great improvement (R^2= .822) occurs when either percent sand or silt was added to a model containing root population. When root population and soil texture (percent sand or silt) are included in the same model, population was no longer significant in the model. Thus, soil texture is statistically a better predictor of yield than population. Since percent sand and silt are highly correlated (r = -.99), only one of these soil parameters is used in models. The full model, root and soil population plus percent sand or silt (R^2= .831), is no better than the reduced model containing only root population and percent sand (R^2= .828). Thus soil population was not important in any yield-population model.

The 1980 preseason and harvest multiple regression model development are presented in Tables 2B and 2C. Although root populations estimated at harvest are highly significant as in 1979, populations were not the best single predictor of yield. Previous season's plant vigor alone explained yield reponse better than any other predictor variable in the model (R^2= .762 at harvest and R^2= .697 preseason). When vigor is included in the model, all other predictor variables are non-significant, although in a simple linear regression with yield they are significant. As in 1979, soil texture (percent sand or silt) is singly as good a predictor of yield as root population (Figure 3). When root population, previous season's vigor and percent sand are included in a single model, 81.8 percent and 79.1 percent of yield variabililty is explained for August and April population data, respectively.

Discussion

A plant disease results from interaction of pathogen, environment, and host. Each contributing element of this disease triangle affects overall expression and severity of disease. These damage studies were conducted in established peppermint fields. Thus, yield variability was influenced by numerous factors, including many outside the scope of parameters measured in these studies. Confidence levels of models derived from these data are lower than desirable for establishing economic thresholds, but they are representative of actual field conditions and are useful in peppermint management programs.

Root populations at harvest were significantly and consistantly correlated with yield in both years. Populations at harvest are useful for diagnosing the cause of stand decline and to determine the extent that nematodes contribute to yield losses. A two year seasonal population dynamics study revealed poor correlation between fall and spring populations in damaged peppermint fields (see Seasonal population dynamics section). Therefore, fall population data alone are not strongly predictive of yield the following season.

Root populations were consistantly better predictors of yield loss than soil populations. Since *P. penetrans* feeding in root cortical tissues damage the root system, populations extracted from roots should be proportional to damage. The two year population dynamics study also demonstrated that root populations are more stable through the year than soil populations and are thus a better predictor of future population trends. Two major problems with using root population data a s the sole population parameter for crop loss predictions are 1) the difficulty in collecting and processing large numbers of root cores and 2) ectoparasitic nematodes are overlooked.

P. penetrans population distributions are not homogenous nor are root and soil populations likely to have the same distributions. Proctor and Marks (116) reported *P. penetrans* population data fit a negative binomial distribution indicating clumped distributions. Their soil sampling data from a 0.01 hectare rye-tobacco rotation field showed that to estimate populations within twenty percent of the true mean with 95 percent confidence, five subsamples from each of five 40 core (one core/0.5 m) samples per plot were required. Twenty combined core samples (one core/ 5 m) provided only a qualitative population estimation. In my study, sampling density was one core/ 1 m and one core/ 2 m for soil and roots, respectively. This sampling intensity is not cost efficent for commerical application. A rapid high intensity root sampling procedure must be developed if a quantified *P. penetrans* loss model is to become practical.

Samples should be taken after harvest or shortly before spring nematicide treatments are applied, but spring populations are not highly correlated with August hay yields (see Seasonal population dynamics section). In spring, roots are only beginning to expand into nematode infested soil, so root populations may not be representative of population levels later in the growing season. Population trends will also vary as host fitness is modified. When plants are extensively damaged, nematodes migrate into the soil, (11,17,109) and root populations may not be correlated with damage. Conversely, vigorous peppermint plants can support large P. penetrans populations without growth suppression. Even within homogenous stands nematode population trends can vary asynchronously (45). Therefore, late March P. penetrans population levels in each plot were influenced by a unique set of host, edaphic and micro-climatic factors which modify population increase and resulting plant damage.

The 1980 Benton County site, which did not conform to trends in other fields, illustrates how factors within a growing season can modify damage functions. Transect lines established in April extended into areas of vigorous 1979 peppermint growth, but these were in light soil and high population areas. Following spring flaming (for peppermint rust), these weakened stands did not recover, so only after addition of five plots in August did data include plots representing maximum yield in the field. Weed control was also inadequate, particularly in nematode damaged areas where peppermint is subject to summer water stress. Thus, non-nematode stress factors can greatly modify the slope of a damage regression function. Plotted data

(Figure 3 and 6) suggest that with additional vigorous plots (above 50 percent yield level) the regression model would conform to models developed from Linn and Polk Counties.

Soil texture parameters, percent sand and percent silt, were highly correlated with plant growth and P. penetrans populations in both years. Damage patterns in lighter soils (> 60 % sand) resulted from plant and nematode biology being influenced by soil texture characteristics. P. penetrans reproduction, migration (147,148), root penetration (141) and overwinter survival (76) are greatest in lighter soils. Elevated nematode populations extensively damage roots and plants when pruned root systems suffer water stress during the growing season in coarse well-drained soils with low moisture holding capacity. Simple linear and multiple regression models (which improved when both soil and population variables were included illustrate interdependence of nematode population, yield, and soil texture. Other edaphic factors (pH, bulk density, and soluble solids), however, were not significantly related to yield or P. penetrans populations.

Three other phytonematode genera recovered in these three fields, Trichodorus sp., Longidorus elongatus and Paratylenchus sp., were distributed in specific soil textural classes. Paratylenchus sp. populations were highest in finer soils (less than 60 percent sand) which did not support high P. penetrans populations or exhibit yield loss. Although Paratylenchus hamatus has been reported to damage peppermint (41), Paratylenchus sp. populations did not reach damaging levels in this study. Similarly, Longidorus elongatus, a major peppermint pest in western Oregon, and Trichodorus sp. populations were not correlated with plant damage. Low or moderate populations of these two species were recovered in lighter textured soils where a high P. penetrans population occurred. Possibly P. penetrans suppressed population increase of other phytonematode species (23,39,165) so that they did not reach damaging levels.

This study is based on the assumption that all other pests and diseases were uniformly distributed across fields, so that all plots were equally affected. This may not be a valid assumption because each of these organisms will be distributed according to a specfic set of environmental requirements. The models developed explained 80 percent of yield variability and included three independent variables; P. penetrans populations, soil texture, and host vigor. Plant yield, according to Seinhorst's model (124), is produced by the proportion of a plant not damaged by nematodes, where damaged proportion can not exceed one. High P. penetrans populations, in these studies, were the major pathogen and removed most of the plant yield potential. Other pathogens and pests will be economically unimportant at high P. penetrans population levels, although they may be biologically important. Their main effect will be to contribute to cumulative vigor reduction expressed in successive seasons, unless added stress causes plant death. At low P. penetrans population levels, other pests and pathogens may contribute significantly to yield reduction. However, if nematodes interact synergistically with a pathogen, such as Verticillium albo-atrium and P. penetrans (123,165), yield decrease would be greater than predicted from either component alone. Visual symptoms of *Verticillium* wilt were not observed in 1979 or 1980 plots, so *Verticillium* was not considered in damage models.

The dominant predictor variable in 1980 multiple regression models was the previous season's stand vigor. Singly it accounted for approximately 70 percent of yield variability for all locations and sampling dates. *P. penetrans* susceptibilty was observed by Oostenbrink (106) to be associated with small root system (low vigor) rather than high populations. Root damage results in plant stunting as water and nutrients become limited. These stunted plants have less photosynthate available for rhizome production. Rhizome number and vigor determine succeeding season's growth potential. Harsh winter conditions, however, can damage rhizomes between seasons and predispose peppermint stands to nematode damage. Similarly cool wet spring weather patterns can suppress plant growth without reducing nematode pathogenic activities. Nematode damage will be greater than predicted from population data under these climatic conditions (50,105). Spring flaming in moderately nematode damaged peppermint fields will also reduce plant vigor and be expressed as damage in excess of predictions derived from these regression models. Therefore, previous season's vigor must be interpreted in relation to cultural, climatic and pest stresses which can reduce vigor between seasons.

Although these models do account for 80 percent of yield variablility, multiple regression models are empirical and only describe statistical relationships between dependent and independent variables. They are not causal models which explain biological relationships. In these models the _P. penetrans_ population is biologically the major independent variable. Low vigor and soil texture are important in nematode damage models because _P. penetrans_ reduces plant vigor and causes greater yield reduction on lighter soil. Nematicide trials indirectly demonstrated that _P. penetrans_ was the principle component responsible for plant decline during these studies. In 1979 and 1981, oxamyl applictions in stunted stands on light soil sites produced yields equal to the maximum yields harvested during this two year yield loss study. Since these nematicides act by reducing nematode feeding and population densities, factors such as soil fertility, soil type and disease do not appear to be major constraints on yield under the experimental conditions. These factors would not be modified by nematicide applications, so the increased plant vigor was due to reduced nematode injury. Similarly, 1981 nematicide trials demonstrated that no significant yield responses were obtained in a vigorous stand, even though high initial _P. penetrans_ densities were greatly reduced. Thus, _P. penetrans_ feeding injury depresses yields greatly in weak and moderate vigor stands, but high nematode densities cause less plant damage in vigorous stands. These data suggest that nematicide treatment decisions can be based quantitatively on population, but only qualitatively on soil texture and plant vigor because without high _P. penetrans_ populations the other two parameters are unimportant in nematode management decisions.

The intent of this study was to precisely quantify the relationship of P. penetrans density to damage of peppermint for use in the development of economic thresholds. The study was not totally sucessful in this respect for two reasons; 1) peppermint stand variability was great both within and between sites and 2) difficulties were encountered by utilizing only naturally occurring P. penetrans populations which have highly contagious distributions. This second difficulty resulted in one major shortcoming in the study, the absence of zero P. penetrans densities within each field. Therefore, the tolerance level, the nematode density below which no nematode damage occurs, had to be derived by calculating the P. penetrans density where the regression line intercepts the 100 percent yield level in the regression models. The maximum yields across the three locations were estimated at 88 and 91 kg oil/ha in 1979 and 1980, respectively. These yields corresponded to maximum yield that the three growers harvested in their best fields which did not have nematode problems. Maximum yields recorded in the study were 23 kg oil/ha greate r than Oregon averages for 1979 (61 kg/ha) and 1980 (68 kg/ha). Thus, for the purpose of developing recommendations, it was assumed that nematode densities at 100 percent yield levels were good approximations of damage thresholds.

In reaching a treatment decision, numerous factors, unquantified in this study, will modify the extent of P. penetrans damage. If pest damage, such as mint root borer, or harsh winter conditions damage rhizomes, plant vigor may be greatly reduced and nematode damage increased. In these situations damage may be more severe than predicted by these models and the damaged areas may expand to include areas and where previous season's plant vigor was only moderately depressed. Similarly in cool springs, predicted yield loss may be underestimated because plant growth is retarded while nematode feeding continues which results in more root damage than expected and under conditions more favorable for plant growth (50,43,105). The impact of *P. penetrans* on yield would also be greater when both *P. penetrans* populations and *Verticillium* wilt are present in a stand. Future research is needed to quantify the influence of these factors so that recommendation can be based on the interaction of *P. penetrans* injury with the other major components of crop loss.

SEASONAL POPULATION DYNAMICS AND DISTRIBUTION OF *PRATYLENCHUS PENETRANS* IN FIELD PEPPERMINT

Preface

Crop economic loss models depend on consistant sampling procedures. If seasonal population trends and distributions are ignored, population estimations used in a model may produce inaccurate yield loss predictions. In these studies, annual population dynamics were monitored during 1979 and 1980. Data were utilized in developing a temporal sampling strategy for *P. penetrans* in peppermint.

Materials and Methods

1979: Linn and Benton County 1979 damage study sites, plus a third newly established Black Mitcham peppermint field were sampled biweekly from March 1 to December 11. Two 4 x 15 m plots containing 10 one meter diameter sub-plots were established at each location. Two 2.5 x 30 cm soil cores were randomly collected within each sub-plot on each date. The twenty cores collected from each plot were sectioned into 0-10, 10-20, and 20-30 cm vertical profile seqments. Profile sections from each plot were bulked together according to depth (total of twenty cores at each depth in each plot). Root cores, 10 x 10 x 10 cm, were randomly sampled within the plot perimeter. Root and soil populations were recorded on each sampling date.

1980: Sampling procedures were modified to facilitate partitioning population variance due to site characteristics; soil type, host vigor, and initial population. The thirty-six plots harvested for 1979 damage studies were sampled monthly from October 1979 until August 1980. Nine 15 cm soil cores were randomly collected from each 1 x 1 m sector in each plot. Four 10 x 10 x 10 cm root cores were dug in each plot. Subsamples from plots were bulked before nematode extraction. Root and soil populations were estimated and recorded.

Soil temperature and rainfall data were obtained from Oregon State University's Hyslop Field Laboratory records. The Laboratory is located within 20 km of fields used in 1979 and 1980 population dynamics studies. Soil temperatures, maximum and minimums, were recorded daily at 10 cm depth. Mean semi-monthly soil temperature and rainfall accumulation interpolated from daily data are presented in figure 10.

Results

Data from the three sites studied in 1979 are summarized in figure 11. Mean root population, *P. penetrans* per gram fresh weight, reached a maximum of 3100 per gram on the late May sampling date. This was followed by a decline to 1700 per gram on August 1. Root population increased slightly in the fall until October 9, then declined to 1100 per gram during November and December. The two soil

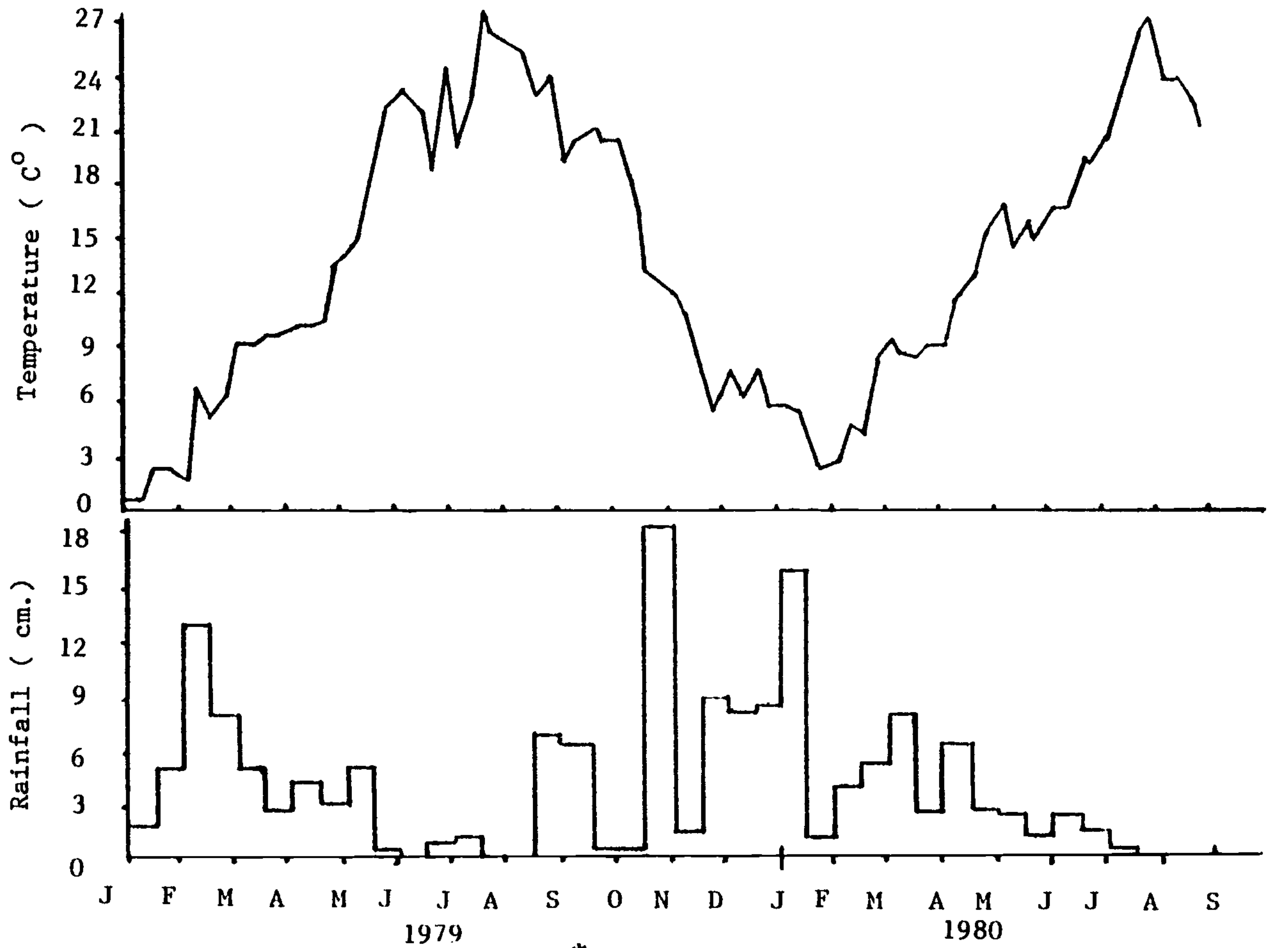


Figure 10. Annual soil temperature* and rainfall at Hyslop Field Laboratory, Oregon State University, Corvallis, Oregon

* soil temperature was recorded at 10 cm soil depth

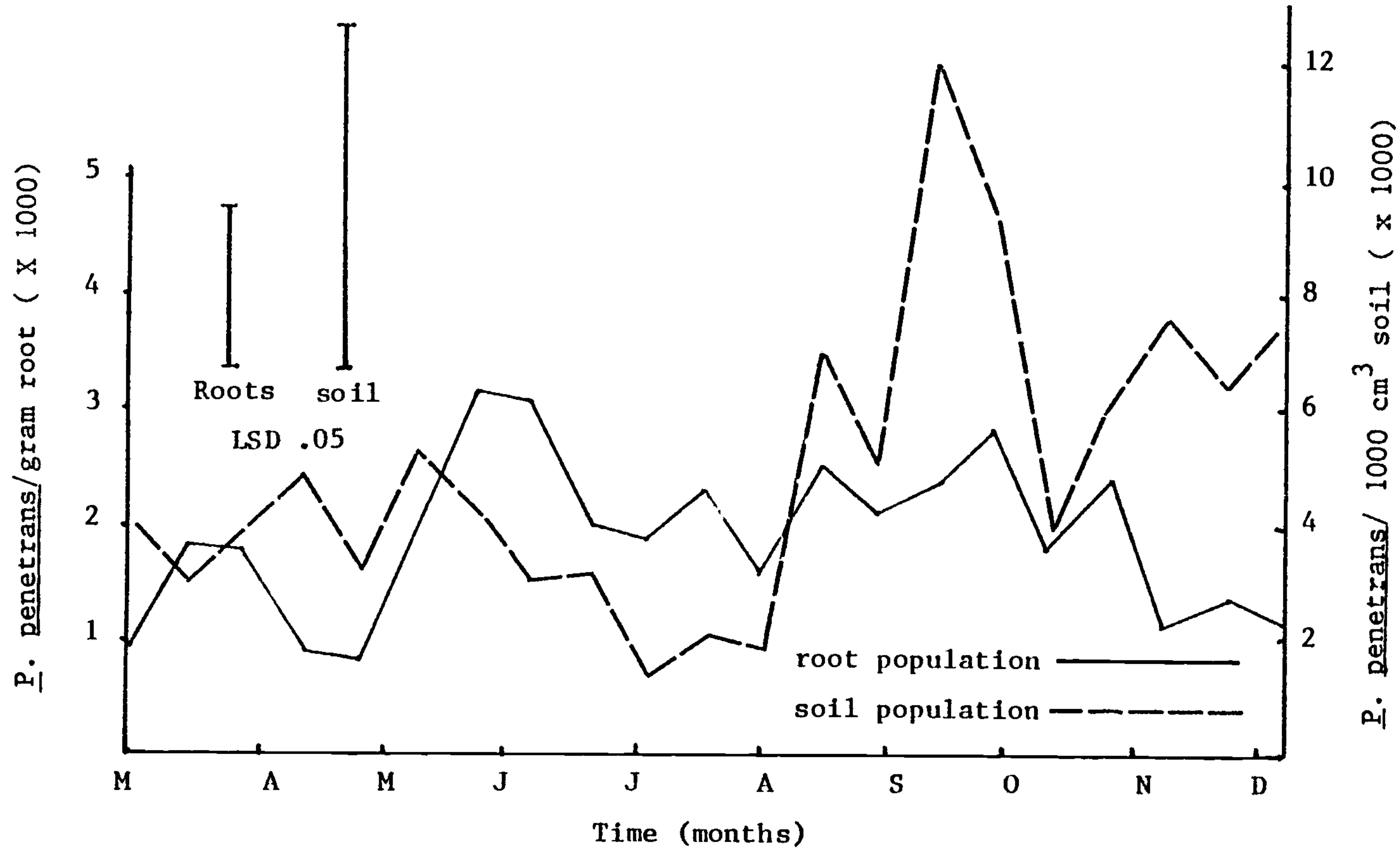


Figure 11. 1979 seasonal root and soil P. penetrans populations trends in three Willamette Valley peppermint fields.

population peaks were separated by low early summer levels. The first peak occurred in May two weeks before root populations peaked. The second peak began in early August and increased until mid-September.

Thirty-six sites studied from August 1979 to August 1980 were clustered with CLUSB , a computer program that utilizes largest scaled distances from existing clusters to establish each new cluster. Cluster parameters were; soil texture, 1979 vigor and initial population level. The three clusters defined were: Cluster 1 (17 sites; high August 1979 populations, lightest soils, poorest stands), Cluster 2 (11 sites; intermediate values), and Cluster 3 (8 sites; heaviest soils, low August 1979 populations, and vigorous stands).

Cluster 3 (figure 12) mean soil populations were stable through the year with final August 1980 populations equal to August 1979 levels. Root population peaked in mid-May after low overwintering levels. A small peak also was evident in the fall.

Cluster 2 root population trends were similar to Cluster 3; (mid-fall and mid-May peaks separated by low winter levels). Soil populations were stable through fall and winter until March when levels increased to an April peak. As with 1979 soil data, this was immediately prior to the spring root peak. Both soil and root populations declined during summer.

Cluster 1, with optimal conditions for damage, was the only group exhibiting an overall decline in both mean soil and root populations during this 12 month study. Root population declined from 4000 per gram at 1979 harvest to 1700 in March 1980. A sharp peak in root population peak (7000 per gram root) in mid-May was followed by a drop

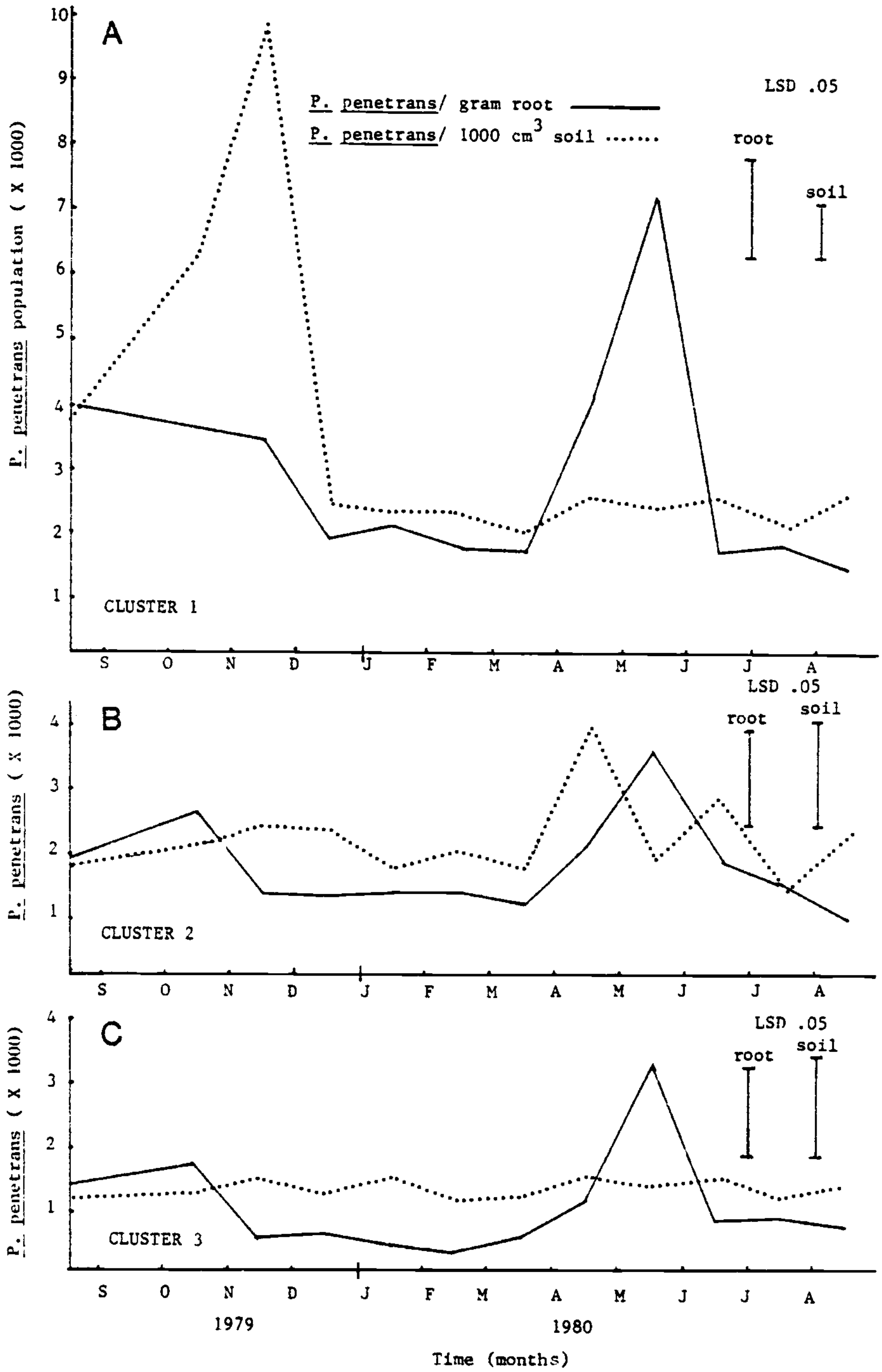


Figure 12. Annual root and soil *Pratylenchus penetrans* popultion trends in Willamette Valley peppermint fields.

A) Cluster 1: lightest soils,poorest stand, highest August 1979 population

B) Cluster 2: intermediate values

C) Cluster 3: heaviest soils, strongest stand, lowest August 1979 population levels

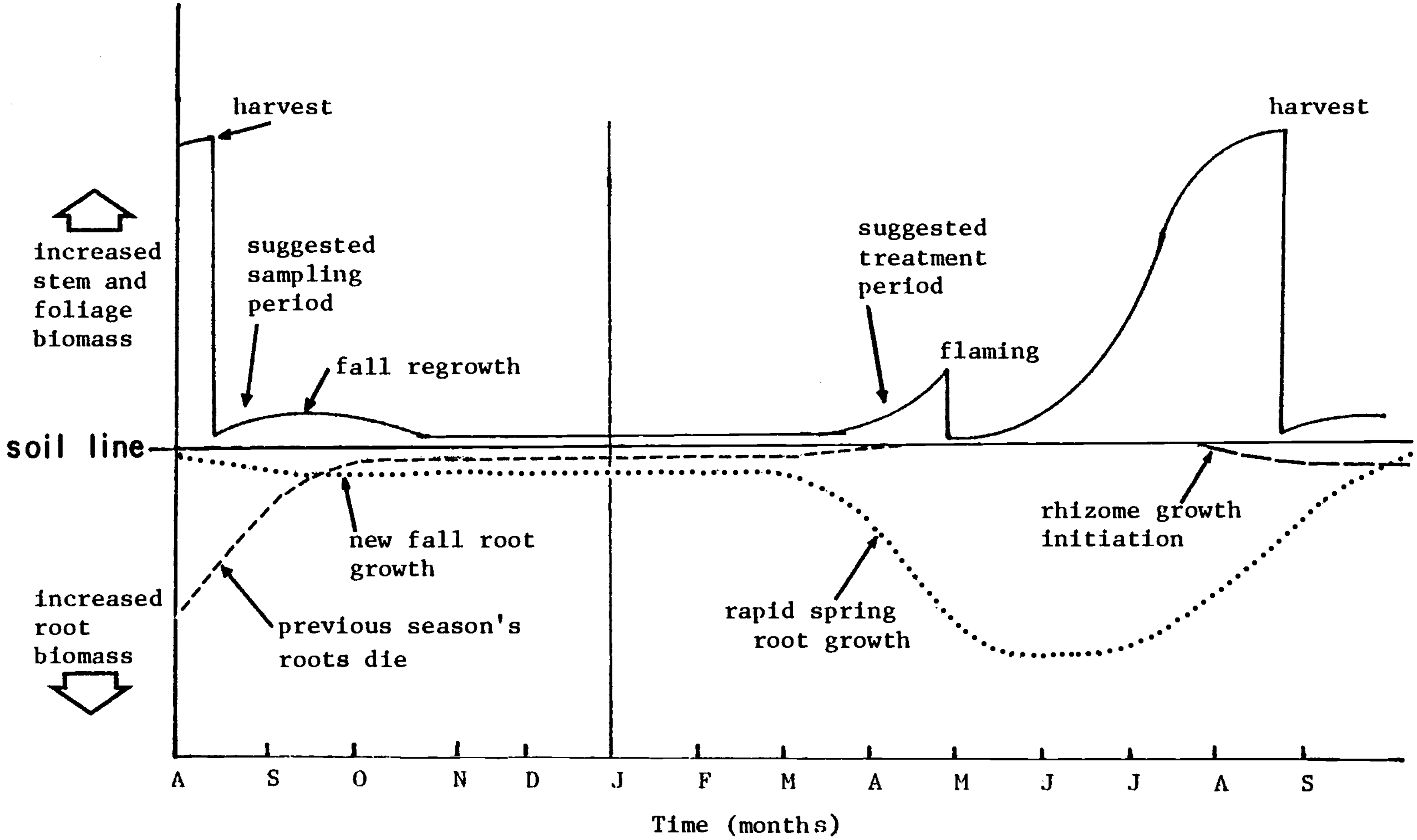


Figure 13. Annual peppermint root and top growth patterns

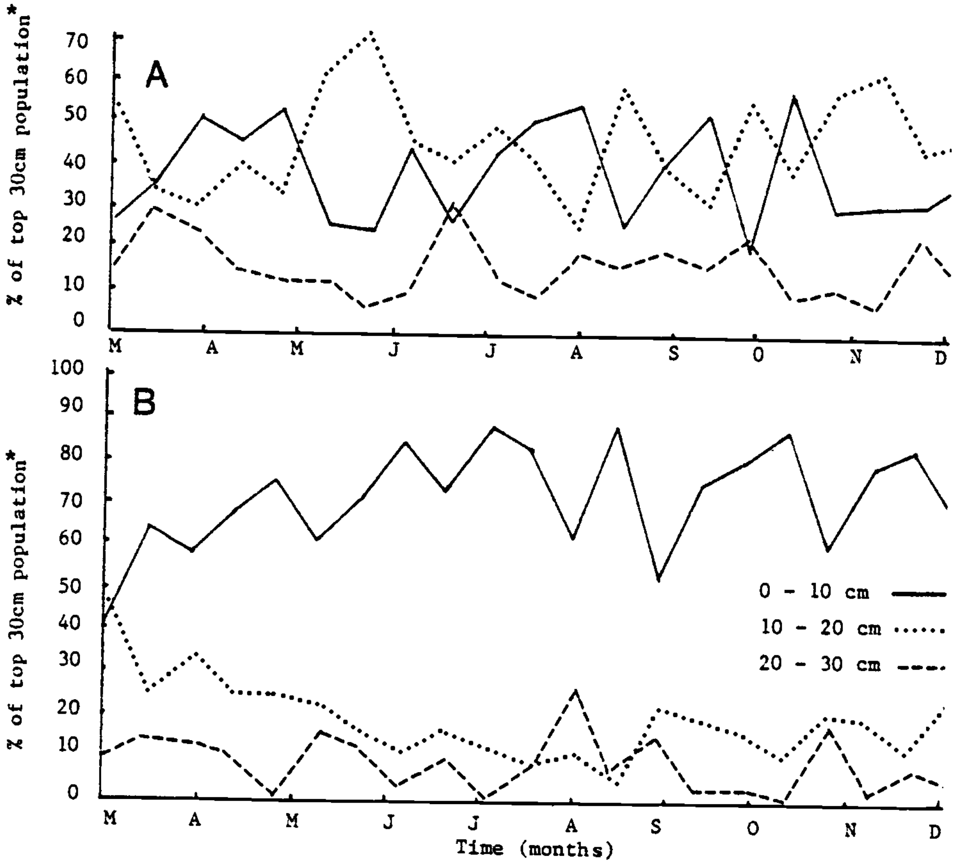


Figure 14. 1979 seasonal vertical distribution of <u>Pratylenchus penetrans</u> populations in three Willamette Valley peppermint fields

A) Mean of two vigorous plots

B) Mean of three stunted plots

* Percentage of total 30 cm population found in each 10 cm profile secton

to 1400 per gram in August. Soil populations peaked in late fall 1979 as root populations declined. Mean soil population levels fluctuated little from December until August 1980.

Roots in strong stands can penetrate below 60 cm, while *P. penetrans* stunted plant roots rarely penetrate below 15 cm. *P. penetrans* population are greatest in and around plant roots, so vertical distributions in vigorous and stunted plots were examined separately. In vigorous and stunted plots, percentage of total population distribution in each ten cm increment were significantly different, but vertical distributions did not change significantly over the 9 month study (figure 14). In stunted stands mean population percentages were: 71 percent, 20 percent and 9 percent at 0-10, 10-20 and 20-30 cm profiles respectively. In vigorous stands, populations were greater in the lower profiles; 39 percent at 0-10 cm, 44 percent at 10-20 cm, and 17 percent at 20-30 cm.

Correlation analysis (Appendix D) of all sampling dates revealed soil population to be poorly correlated between dates. *P. penetrans* per gram root were more stable. Cluster 1 plots had the most variability both within and between sampling dates. These cluster data are the most interesting for nematode management, but have least predictive population trends. Clusters 2 and 3 (root and soil population) were more constant between dates.

Discussion

Host growth patterns influence temporal and spatical distributions of plant parasitic nematodes. Peppermint is a perennial, with phenology similar to an annual. Root proliferation commences at the end of winter (figure 13) and biomass continues to increase through the early spring. As photoperiod decreases in mid-summer, rhizome production is initiated. During the fall, old root systems undergo senescence and a small flush of new root growth is initiated. Plants overwinter as dormant rhizomes and top growth is minimal until March or April. Since endomigratory *P. penetrans* mainly reproduce in host tissues, peppermint seasonal root quality and quantity modify population trends.

Pratylenchus penetrans reproduces continously over a wide temperature range (86). Depressed winter soil temperature increases life cycle duration (78). Olthof (164) reported that soils frozen for several months did not drastically reduce populations. He observed that seasonal soil temperatures are reflected in *P. penetrans* population trends and plant growth. In these studies, 1979 and 1980 soil temperature patterns (Figure 10) were similar, as were root populations which peaked in mid-May both years. Seasonal vertical distributions, unlike nematode abundance, exhibit no consistant shifts in response to climatic change and nematodes did not appear to migrate vertically. These data indicate that recommended sampling depth of 15-20 cm is adequate for estimating both soil and root *P. penetrans* densities throughout the year.

Endoparasitic nematodes, which inhabit root tissues for a majority of their life cycle, are unaffected by rainfall patterns after entering roots (72). Rainfall, supplimented with summer irrigation, provided adequate mositure and did not limit plant nor nematode development during these two years. These two seasons of population data for years of similar climatic patterns are not adequate to predict population trends in years with extremely divergent weather patterns.

P. penetrans root populations are reported to be better predictors of crop response than are soil population (66). In extensively damaged roots, however, population emigration can result in poor correlation of root population with plant damage (109). Soil and root population are inversely related (52,94). Root population peaks in 1979-1980 occurred at two periods of maximum new root growth, early spring and to a lesser extent early fall. Similar phenomena were observed with blackberry (55) and strawberry (19). Late spring decline of root populations are in part a dilution effect as roots grow away from regions of high nematode concentration. In late summer through early fall, 1979 and 1980, Cluster 1 soil population data reflect emigration from extensively damaged senscent roots. Low soil temperatures in winter may have depressed populations by slowing egg maturation (37) and lengthening the life cycle (78). In this study, no differential survival was observed between soil and root populations through the winter. The warm spring soil temperature stimulated egg hatch in soil and plant root debris and produced the soil population peak several weeks before root populations expanded.

Cluster 1 in 1980 did not exhibit this spring soil peak. Plots composing this cluster experienced extensive 1979 damage, so plants did not support large fall reproductive populations. Fall emigration and mortality resulted in low overwintering egg populations and smaller than expected spring soil populations. Cluster 1 plots, however, maintained total winter population levels higher than either other cluster mean density. In spring these lighter soil plots provided optimal conditions for nematode reproduction, such that population increase exceeded those in other clusters. These severely damaged plots continued to lose vigor and populations were not maintained into August 1980. A similar decline with high P. penetrans populations in tobacco have been reported by Olthof et al. (118).

Correlation analysis of nematode densities between sampling dates confirms their high variability. Only in Clusters 2 and 3 which were not severely stunted, did root populations correlate well between sampling dates. Similar results were observed by Wallace and Smith (127) with Helicotylenchus dihysteria in adjacent homogenous turf plots. These plots exhibited non-randomly distributed populations which fluctuated asynchronously, such that individual plot dynamics were superimposed on general seasonal trends. Olthof (102) reported P. penetrans seasonal dynamics were inconsistant from year to year. Therefore, caution is necessary when attempting to use only population data to estimate yield long in advance of a cropping season.

Seasonal population sampling to predict crop loss should identify and standardize sampling periods where populations are least variable. Sampling dates can change slopes of population-yield regressions models (80) and prediction precision (47). Estimations are more easily interpreted when populations are stable. If populations are rapidly expanding, as in April through June, a 2 week change in sampling date or population development can result in gross population density over or under-estimations.

Data from 1979 and 1980 indicated that spring (mid-March) and late summer (August or September) sampling avoids periods of rapid nematode density fluctuation. Post-harvest samples are a good diagnostic tool and are recommended. Sampling at this time facilitates assessment and partitioning of fields according to plant vigor, an important predictor of yield loss in the following season. Sampling at this time also allows ample time to make decissions concerning early spring treatments. Even though post-harvest nematode densities correlated poorly with preseason densities the subsequent season, *P. penetrans* densities do not increase over the winter and recommendations based on post-harvest densities should not underestimate crop loss. Late summer sampling is facilitated by easier field access and more favorable weather conditions than is March sampling. Finally, larger root biomass in late summer expedites root processing and nematode extraction. Sampling recommendations for IPM decision making developed from this study are: 1) partition fields by plant vigor and soil texture and sample these areas separately, 2) sample after harvest for determining if nematicide treatments are necessary the following spring, 3) root samples taken through plant crowns to a depth of 15 cm should be collected to estimate *P. penetrans* densities, 4) 15 cm deep soil samples should be taken to detect ectoparasitic nematode populations and 5) sample blocks should be no larger than 2.2 hectares with a minimum of 20 samples collected per block.

INTERRELATIONSHIP OF PLANT GROWTH AND *PRATYLENCHUS PENETRANS* POPULATION DYNAMICS ON THREE PEPPERMINT CULTIVARS

Preface

The damage function developed from 1980 field studies, illustrates plant vigor is a major component in determining *P. penetrans* population impact on peppermint yields. Vigorous plants can maintain high population levels and compensate for nematode damage. The two dominant peppermint cultivars grown in Oregon differ in vigor. Black Mitcham produces a more vigorous stand than Todd Mitcham, a *Verticillium* tolerant cultivar. Todd Mitcham shows rapid decline when stressed. It is also the cultivar grown in fields where *P. penetrans* is most evident. Murray Mitcham, a recently released *Verticillium* tolerant cultivar, has not yet been widely planted in Oregon. Therefore, two experiments were designed to investigate *P. penetrans* population dynamics and damage on three peppermint cultivars, Todd Mitcham, Black Mitcham and Murray Mitcham.

Materials and Methods

Experiment I Cultivar population dynamics

Two hundred and forty 15.5 x11.5 cm plastic pots were loosely fulled with one liter of sterilized 1:2 washed sand-loam mix. Each third of the (80) pots were planted with rooted cutting of one cultivar. Fifty-six pots of each cultivar were inoculated with a 10 ml water suspension containing 750 P. penetrans. Twenty-four pots of each cultivar served as uninoculated controls.

Experimental design was a completely randomized block with each sampling date as a block. Seven inoculated and four check pots of each cultivar were randomized within each block. Complete blocks were harvested 10, 21, 42, 63, 84, 105, 126 or 147 days after inoculations.

Soil and root populations in inoculated treatments were estimated at each sampling date. No nematode populations were recovered from roots of control treatments at 42 days, so further sampling in controls was discontinued. Dry root and fresh top weights were recorded for both inoculated and controls at each sampling date.

Experiment II. Two season plant damage evaluation:

Nematode damage of field peppermint infected with a high P. penetrans population is manifested only after several seasons. This experiment imposed artificial seasons under greenhouse conditions.

One hundred and eighty 11.5 x 11.5 cm plastic pots were loosely packed with one liter sterilized soil-sand potting mix. Each of three cultivars were planted in one-third of the pots. After three days, twelve plants of each cultivar were inoculated with 800, 1600, 3200, or 6400 P. penetrans in 10 ml of water. Twelve plants of each cultivar remained as uninoculated controls. Experimental design was a completely randomized block with 'season' as blocks. One-half the pots (six pots of each inoculum rate and six controls for each cultivar) were randomized within 'season' blocks. One hundred days after inoculation, the first season block was harvested. Soil and root populations were estimated and dry root and top weights were recorded.

At this time, one half the runners in the unharvested block were coiled in their respective pots and covered with soil. These plants were allowed to grow an additional 30 days before tops were removed. An artificial season was created by forcing dormancy with 40 days storage at 5° C. Soil moisture was monitored and adjusted when necessary during storage. Pots were transferred to the greenhouse and plants were allowed to regrow for 30 days before new growth was pruned to the soil line. Evaluation of second season nematode populations and plant growth response were made after 100 days of additional regrowth.

Results

Experiment I: The first sample was collected (Table 3) after ten days determined inoculum aggressiveness and survival. Ten day root penetration levels and soil *P. penetrans* densities were similar (P=0.05) for the 3 cultivars. Total population recovery after 10 days indicated equal inoculum mortality, with Black, Todd and Murray Mitcham recovery levels 30, 32 and 34 percent, respectively. Murray

Table 3. Effect of three peppermint cultivars on population dynamics of *Pratylenchus penetrans* in greenhouse pot culture

Population Parameter	Cultivar	*P. penetrans* population (days after inoculation) 10 days	21 days	42 days	63 days	84 days	105 days	126 days	147 days
Population/ 1000 cm^3 soil	Todd's Mitcham	109 a*	80 a	0 a	26 a	28 a	11 a	97 a	420 ab
	Black Mitcham	114 a	109 a	0 a	40 a	157 a	31 a	217 a	617 a
	Murray Mitcham	126 a	91 a	0 a	49 a	31 a	14 a	46 a	140 b
Total root population	Todd's Mitcham	129 a	199 a	454 a	619 a	1988 a	1314 a	7487 ab	22086 b
	Black Mitcham	113 a	249 a	350 a	781 a	1370 a	1704 a	1026 a	30194 a
	Murray Mitcham	127 a	215 a	387 a	442 a	1191 a	897 a	3083 b	7729 c
Population/ gm. dry wt. root	Todd's Mitcham	628 a	469 a	433 a	377 a	849 a	437 a	2634 a	7042 b
	Black Mitcham	474 a	745 a	403 a	495 a	506 a	699 a	3754 a	12709 a
	Murray Mitcham	1146 a	706 a	636 a	323 a	948 a	527 a	1526 a	3044 b

* Means at each date and within each population parameter followed by a common letter are not significantly different (P=0.05) according to Duncan's multiple-range test.

Mitcham had a significantly larger (P=0.0 5) per gram root population because of a smaller root system.

Soil populations approached zero (figure 16) at 42 days and then gradually increased during the final 115 days. T-tests show no differences between population rates of increase among cultivars at sequential dates. No cultivar soil P. penetrans density differences were significant until day 147 when Black Mitcham nematode densities were larger (P=0.05) than Murray Mitcham.

Root nematode density (Table 3) increase was observed at each sampling period, except at 105 days when extraction equipment malfunctioned. No significant difference (P=0.05) in root population dynamics were evident between sequential sampling dates. Simple linear regression of log mean root population data indicated that population increase was logarithmic during the experimental period with all cultivars. The Murray Mitcham regression line had a shallower slope was significantly different (P=0.05) than the Todd or Black Mitcham regression model (Figure 15).

Plant growth response data are presented in (Table 4). Murray Mitcham root mass remained smaller than other cultivars until day 147. Washed Murray Mitcham root systems also were consistantly darker in appearance. Control root weights were larger than inoculation plant roots, but differences were only significant for Black Mitcham after 147 days. Top growth was not different (P=0.05) between cultivars after 147 days, although Murray Mitcham was significantly lighter than Black and Todd Mitcham after 84 and 126 days, respectively. Top growth was not measurably reduced (P=0.05) in inoculated plants

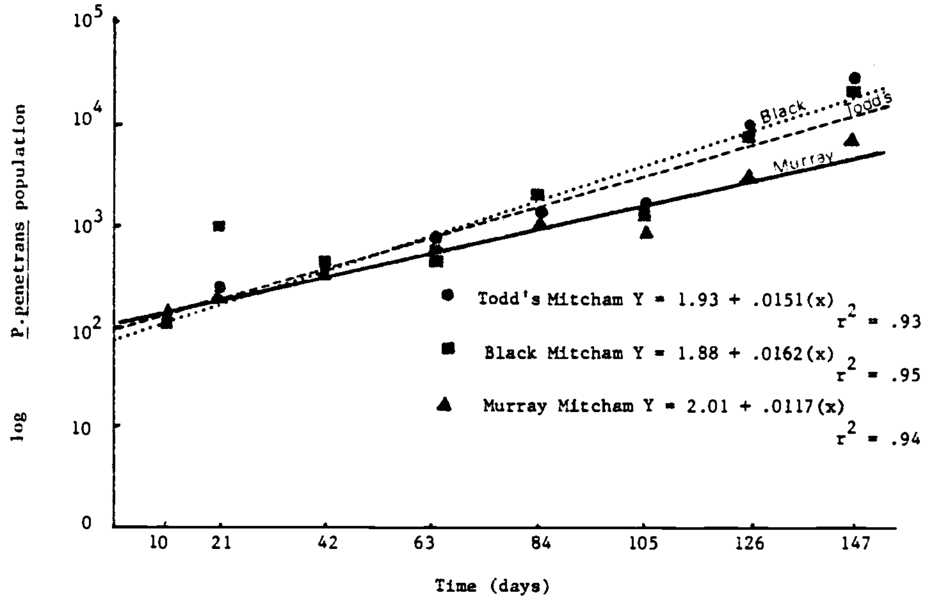


Figure 15. Regression of log Pratylenchus penetrans root population vs time (days after inoculation) on three peppermint cultivars.

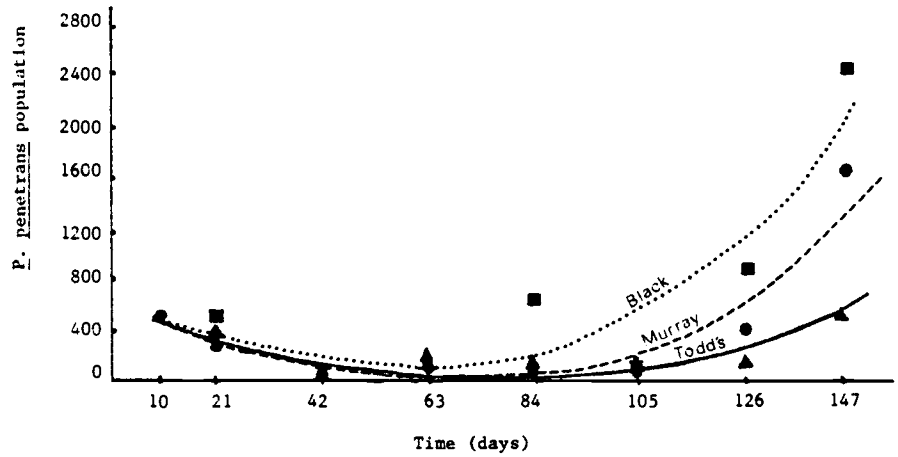


Figure 16. Pratylenchus penetrans soil population trends on three peppermint cultivars during the 150 days following inoculation

Table 4. Effect of Pratylenchus penetrans on growth of three peppermint cultivars in greenhouse pot culture

Weight in grams (days after inoculation)

Plant growth parameter	Cultivar	10 d In	21 d In	42 d In	42 d C	63 d In	63 d C	84 d In	84 d C	105 d In	105 d C	126 d In	126 d C	147 d In	147 d C
Roots$	Todd's	0.21 a*	0.49 a	1.05 a	1.19	1.83 a	1.77	2.52 a	2.79	3.30 a	3.84	3.04 a	3.57	3.30 a	4.13
	Black	0.27 a	0.37 a	0.92 a	1.03	1.61 a	1.95	2.97 a	2.60	2.84 a	3.64	3.26 a	3.12	2.58 a	3.85 +
	Murray	0.11 b	0.31 a	0.66 a	0.85	1.36 a	1.31	2.22 a	1.39	2.28 a	3.01	2.28 a	2.79	2.90 a	3.40
Top$	Todd's	-	4.0 a	20.7 a	21.7	33.5 a	30.0	45.1 ab	43.6	45.1 a	45.1	50.9 a	47.3	50.5 a	50.5
	Black	-	3.9 a	20.2 a	20.2	35.6 a	35.0	48.4 a	46.6	48.5 a	45.2	48.1 ab	48.4	51.5 a	57.8
	Murray	-	3.1 a	18.1 a	16.8	34.5 a	33.1	40.9 b	40.7	44.8 a	43.1	43.9 b	46.2	48.5 a	47.9

* Mean weights on same date followed by the same letter do not differ significantly (P=0.05) according to Duncan's multiple-range test.

\+ Underlined mean weights are significantly different (t=.95).

$ Root = dry weight root; Top = fresh weight stem, foliage and runners.

In = inoculated with 50 P. penetrans/1000 cm^3 soil, C = uninoculated control.

compared with paired cultivar control on the same data.

Experiment II: First season final population levels of all cultivars corresponded to initial inoculum and ranked the same as in Experiment I. Murray Mitcham final root and soil *P. penetrans* densities were consistantly lower at all inoculation levels. Initial population levels (Pi) of 800 on Black and Todd Mitcham produced final population levels (Pf) as great as 6400 Pi's on Murray Mitcham. *P. penetrans* per gram root densities were larger only on Murray Mitcham and reflected the smaller root growth of Murray Mitchan (Table 5).

During the first season, inoculum levels significantly ($P=0.05$) reduced plant top growth only on Murray Mitcham (Table 6). Root weights of all cultivars were generally lower than controls at each inoculum rate, but only Murray Mitcham with a density of 3200 Pi was significantly less.

All plants regrew after the forced dormancy. Differential regrowth was noted only after top pruning each plant 30 days into the second season. Although all plants produced new shoot growth, several of the weakest plants died within 50 days. At harvest, each cultivar had five to six dead entries, but these were not all from higher Pi treatments. No controls died or appeared stunted.

Second season soil and total Pf's were not significantly different ($P=0.05$) across cultivars and inoculation treatments (Table 5), but Murray Mitcham mean root Pf's and Pf per gram root were numerically lower than either Todd or Black Mitcham. Highest Pf did not occur in the highest Pi treatment. Todd and Murray Mitcham had

Table 5. Population dynamics of *Pratylenchus penetrans* on three peppermint cultivars at four initial inoculum levels over two greenhouse growing seasons.

Cultivar	P_i *P. penetrans*/ 1000 cm^3 Soil	P_f (/100 cm^3 Soil) Season 1+	Season 2+	P_f (Total Root) Season 1	Season 2	P_f (Total Soil & Root) Season 1	Season 2	P_f /gm Dry Wt. Root Season 1	Season 2
	0	0 c	0 b	0 g	0 d	0 h	0 d	0 f	0 b
Todd's	800	697 bc	4253 bc	19587 def	59787 a	20283 def	64040 a	14933 ef	32642 ab
Mitcham	1600	987 bc	7667 abc	22340 cdef	42880 abc	23333 def	50547 ab	13566 ef	42263 a
	3200	3423 a	7780 abc	46360 ab	45380 ab	49783 ab	53160 ab	39343 bc	32096 a
	6400	3897 a	3633 cd	50190 ab	39533 abc	54087 a	43167 ab	47394 ab	39260 a
	0	0 c	0 d	0 g	0 d	0 h	0 d	0 f	0 b
Murray	800	137 bc	4840 bc	6503 fg	22493 bcd	6643 fgh	27333 bcd	9438 ef	26892 ab
Mitcham	1600	240 bc	8660 ab	10467 efg	16023 bcd	10707 efgh	24683 bcd	16669 def	28611 ab
	3200	640 bc	3973 bcd	14907 ef	10213 bcd	15547 efg	14187 cd	38432 bc	21764 ab
	6400	693 bc	5340 bc	25662 cde	10707 bce	26355 cde	16047 cd	58383 a	32053 ab
	0	0 c	0 d	0 g	0 d	0 h	0 d	0 f	0
Black	800	1683 b	10200 a	31067 cd	28667 abcd	32750 bc	39093 abc	27490 cde	31286 ab
Mitcham	1600	125 bc	3980 bcd	21760 def	36533 abc	23100 de	40513 abc	19157 cdef	14624 ab
	3200	1393 bc	5407 bc	37520 bc	45040 ab	38907 bc	50488 ab	23375 cde	45980 a
	6400	3547 a	5795 abc	55680 a	35093 abc	59227 a	40888 abc	35701 bce	16220 ab

P_i = initial population, P_f = final population

Means of the 3 cultivers in a season followed by a common letter are not significantly different

(P = 0.05) according to Duncan's Multiple-Range Test

+ Season 1 = 6 months; Season 2 = 12 months after inoculation greater Pf's at 800 Pi and lowest at 6400 Pi, while Black Mitcham total Pf's are of the same magnitude in each treatment. Second season dynamics are biased by populations extracted from dead roots. These root population means (from dead plants) were 33840, 10560 and 13667 for Todd's, Murray and Black, respectively. Only with Black Mitcham was this greatly reduced from surviving plant Pf levels. Mean soil populations recovered from pots containing dead plants were 4808, 5570 and 7013 per pot for Todd, Murray and Black. Thus most nematodes remained in senescent tissues.

Nematode damage, not evident during the first season, was dramatic by the second season harvest (Table 6). Mean root weight was suppressed in all cultivars, but consistantly reduced only in Murray Mitcham. Mean root weight was not greatly influenced by plant death, since most plants died shortly before harvest. Mean root necrosis was not different (P=0.05) across inoculation and cultivar treatments. All cultivars at each Pi exhibited reduced top weight, but Black Mitcham at 1600 Pi and Todd Mitcham at 800 Pi were not significantly (P=0.05) less than controls. Evaluating only the stunting of surviving plants (Table 6) revealed data were not biased greatly by the dead plants.

Discussion

All *P. penetrans* damaged fields observed in surveys from 1977 through 1981 were planted with Todd Mitcham. One new planting of

Table 6. Effects of four Pratylenchus penetrans inoculum levels on growth of three peppermint cultivars over two greenhouse growing seasons

Cultivar	P_i P. penetrans/ 1000 cm^3 soil	Root weight Season 1+	Root weight Season 2+	Top weight Season 1	Top weight Season 2	Plants surviving 2 seasons	Root necrosis#	Mean dry top weight of surviving plants	Mean dry root weight of surviving plants
Todd's Mitcham	0	1.74 ab*	2.54 a	9.29 bc	9.53 a	6	4.00 a	9.53	2.54
	800	1.45 b	1.94 ab	10.26 ab	7.49 ab	6	2.17 a	7.49	1.94
	1600	2.47 ab	0.93 c	10.57 a	2.07 c	4	1.50 b	3.12	0.98
	3200	1.21 b	1.20 bc	9.07 bc	2.47 c	3	1.50 b	4.94	1.24
	6400	1.28 b	1.25 bc	8.10 c	5.07 bc	6	2.00 b	5.07	1.25
Murray Mitcham	0	1.32 a*	1.65 a	8.67 a	10.87 a	6	4.00 a	10.82	1.65
	800	0.75 b	0.78 b	6.59 b	4.95 b	6	2.33 b	4.95	0.78
	1600	0.57 b	0.68 b	6.19 b	1.18 c	1	1.33 b	1.22	0.67
	3200	0.42 b	0.50 b	5.04 b	1.24 c	0	1.50 b	1.24	0.50
	6400	0.62 b	0.63 b	5.54 b	1.13 c	3	1.67 b	2.26	0.73
Black Mitcham	0	1.97 a*	2.10 a	9.44 a	10.87 a	6	4.00 a	10.87	2.10
	800	1.19 b	1.22 bc	9.55 a	2.50 c	4	1.50 b	3.75	1.30
	1600	1.20 b	2.23 a	8.93 a	7.54 a	5	2.00 b	9.04	2.48
	3200	1.61 ab	1.06 c	9.52 a	3.28 bc	5	1.67 b	3.94	1.08
	6400	1.64 ab	1.90 ab	9.69 a	5.22 bc	4	1.17 b	7.81	2.25

* Means in each cultivar and season followed by a common letter are not significantly different (P=0.05) according to Duncan's multiple-range test.

\+ Season one = 6 months; Season two = 12 months after inoculation

\# Root necrosis: 5 = no necrosis, 4 = 1-25%, 3 = 26-50%, 2 = 51-75%, 1 = 76-100% necrosis.

Black Mitcham was followed during the 1979 population dynamics study. This stand exhibited no damage during the first 2 seasons. Bergeson and Green (14) reported that *P. penetrans* damaged Todd and Murray Mitcham plantings in Indiana muck soils. If there is tolerance or resistance in these cultivars, it should be integrated into nematode management strategies.

In these two greenhouse studies, Murray Mitcham supported lower reproduction rates. In Experiment I Black and Todd Mitcham final populations were of the magnitude expected given the 35 day life cycle and mean oviposition rate of .75 eggs per day reported by Maniya (86). Final population density for Murray Mitcham demonstrated lower fecundity (.375 eggs laid per day) or a longer life cycle (75 days). Similar population dynamics and life cycle modifications have been reported with *P. penetrans* on potato cultivars (12,16). My experiment did not determine whether longer life cycle, lower fecundity, or increased mortality was responsible for Murray Mitcham's poorer host status.

In experiment I, Murray Mitcham roots in inoculated treatments exhibited more necrosis than either Black or Todd Mitcham. Root system mass has been demonstrated to influence *P. penetrans* penetration rate (69) and susceptibility (106). Murray Mitcham's small root system at time of inoculation would produce higher effective inoculum rate in the rhizosphere. This cultivar's less vigorous root growth also functioned to concentrate roots near the inoculum for a longer period. The higher population per gram of root illustrates effects of root-inoculum proximity. The resulting extensive necrosis reduces food quality which retards population increase (73). Lesion nematodes emigrate from necrotic tissues, leaving only high egg populations. Since feeding and reproduction occur in the cortex, both processes cease as nematodes exit roots so that population growth is inhibited.

Tissue necrosis is a biochemical host response to nematode feeding and migration through root tissues. Damaged tissues accumulate phenolic compounds (4,141,142) which can reduce root respiration 40-90% in some hosts and results in tissue death (110). The extent of necrosis in different cultivars (99) and hosts (113) is related to differential phenolic concentrations. Murray Mitcham's severe necrotic reaction may function in this manner.

Experiment I did not demonstrate significant foliage reduction over uninoculated controls during the 150 day experimental period. Similarly, fields usually fail to show P. penetrans damage during the first two seasons of production, even when initial populations are high. Perennial crop damage is the summation of nematode stress in the current season superimposed on crop vigor from previous seasons (19,119). Multiple cuttings stressed Pratylenchus damaged plants reducing plant vigor after each successive harvest (12,15,35,161). In peppermint plantings, each season's growth is dependent on the previous season's rhizome and runner production. Thus peppermint stand decline involves reduction of plant resources available for production of rhizomes and runners when plants are damaged by nematodes. Heavily damaged fields may have little or no rhizome production, so only sparse shallow-rooted plants survive overwinter.

Experiment II evaluated two season's effects of four _P. penetrans_ population densities on growth of Black, Murray and Todd Mitcham. Consistant first season root and top growth reduction occurred only with Murray, the most susceptible cultivar. Root systems continued functioning although damaged (108). Todd and Black Mitcham top growth vigor was not reduced even when populations exceeded densities that were extremely damaging in 1979 and 1980 field studies.

Second season plant response demonstrates the cummulative effects of first season stress plus high first season population carry over. Top and root weights were reduced with all cultivars at each Pi treatment. In the second season, a high population would be more evenly distributed. Host roots could not escape damage by growing away from the inoculum and as a result had severely necrotic root systems. Possibily introduction or build-up of lesion invading microbes could account for a uniform necrosis rating between cultivars (99). The growth data are in agreement with Bergeson and Green's (14) single season evaluation of the three peppermint cultivars. They reported that Black Mitcham more tolerant at the first cutting, but all cultivars had significant foliage reduction at the second harvest.

During the first season, population increase was well above the maintainance level with all cultivars. This indicated that all cultivars were efficient hosts within these inoculum ranges when plants were vigorous. Second season population trends indicated that hosts were less efficient as plant damage increased with the population. Population responses were well below maintenance levels at the higher second season Pi's (estimated from first season Pf's).

Black and Todd's Mitcham both approached their ceiling populaton levels in second season plants as indicated by the horizontal population function (Figure 17). The nematode population density on Murray Mitcham exceeded the cultivar's ceiling in the first season as indicated by the negative slope with increased Pi (Pf season one). The ceiling level is dictated by the host suitability and vigor interacting with nematode reproduction and development. Population increase is self-limiting as food quality and quantity deterioration results from additional nematode feeding pressure (57). Jones' (73) criteria for determining host efficiency should be modified for perennials to accommodate plant vigor after consecutive seasons of damage.

Field populations of nematodes in 1979-1980 studies did not reach densities recorded in these greenhouse experiments. This could have resulted from lower biotic and abiotic mortality factors under greenhouse conditions. Since root systems were contained in concentrated nematode infested soil, the probability of a nematode finding a suitable penetration site is great. More successful root penetrations increase the reroductive population which in turn increases total population growth rates. In the field, vigorous plants grow to depths below concentrated P. penetrans populations. This would lower total root system P. penetrans populations and delay yield suppression.

These data provide a basis for recommendations for establishing peppermint plantings in P. penetrans infested soils. Murray Mitcham is the most susceptible commercial cultivar and should be avoided if

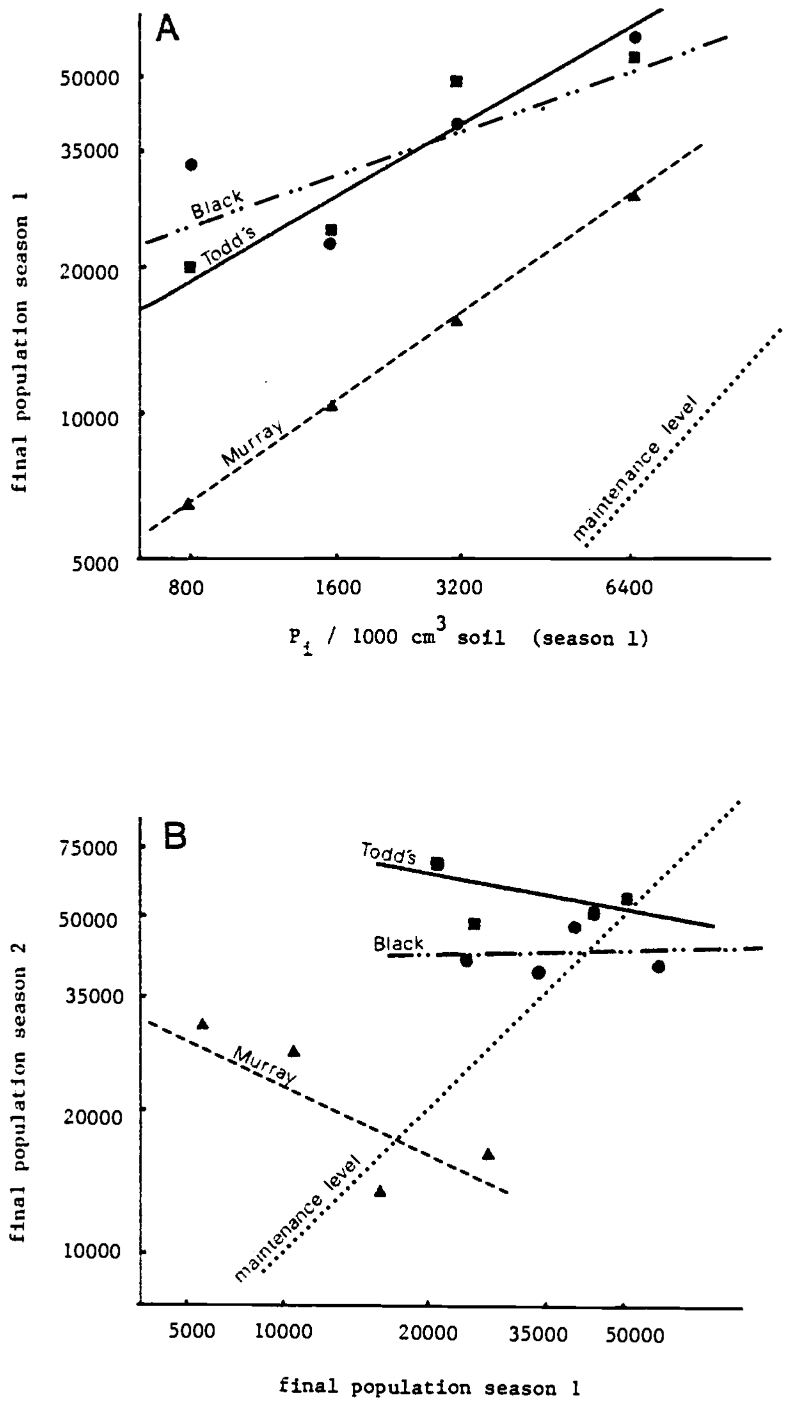


Figure 17. Relationship of intial to final Pratylenchus penetrans populations in a greenhouse study with three peppermint cultivars
A) Initial inoculum level vs. final first season population
B) Final first season vs. final second season population

P. penetrans is present. Greenhouse studies are less definative with Black and Todd Mitcham. Both cultivars had similar population and host damage responses in greenhouse experiments which were conducted under optimal plant growth conditions. Under field conditions, the less hardy Todd Mitcham could be predisposed to increased *P. penetrans* damage by environmental and cultural stress. Black Mitcham is more vigorous and should be planted in infested fields with no history of *Verticillium* wilt. The lower durability of Murray Mitcham was verified in the second year of a planting established on a sandy loam infested with high *P. penetrans* densities. Even though this Benton County field had been out of peppermint cultivation for 20 years, a large area in the field displayed sparse and stunted growth after the first winter. A Todd Mitcham field previously planted adjacent the the Murray Mitcham field did not display damage until after the third season. A Black Mitcham planting established in sandy loam infested with *P. penetrans* and observered over the past five years has not demonstrated significant ecomonic injury even though nematode densities were ten fold greater than the tolerance level established for Todd Mitcham. Differential tolerance to injury indicates that future selection and propagation of *Pratylenchus* tolerant line, as done with other crops (129), could improve the management of *P. penetrans* in peppermint.

INFLUENCE OF SOIL TEXTURE ON *PRATYLENCHUS PENETRANS* POPULATION DYNAMICS AND PEPPERMINT GROWTH.

Preface

Field yield loss studies in 1979 indicated that high population densities and low yields were highly correlated with soil texture. In this experiment the biological suitability of lighter soils and their effects on reproduction and distribution patterns of *P. penetrans* was investigated under controlled conditions.

Materials and Methods

Soils were collected from two peppermint fields in Benton County, Oregon. These soils are representative of the textural range found in Willamette River flood plain areas planted to peppermint. Two sandy loam soils were collected from the Benton County damage study field. One soil type, a Camas gravelly sandy loam, was from an area of high *P. penetrans* population and low 1979 hay yield. The second soil type, a heavier Newberg loam, was collected 100 meters away, outside the perimeter of stunted growth and high nematode population. The third soil, a Cloquato silty loam, was collected from a field with no history of nematode damage. Particle distributions of the three soils is presented in Appendix E.

Soils were throughly mixed and sifted through a five mm mesh screen to remove plant debris. One hundred liters of each soil was enclosed in doubled plastic sacks and fumigated with 0.45 kg. methyl bromide. The plastic sacks were opened after seven days and soil was allowed to aerate for one week prior to potting.

Eighty 11.5 X 11.5 cm plastic pots were loosely filled with one liter of each soil type. One Todd Mitcham rooted cutting was planted in each pot. Soil was tamped and all pots were brought to a uniform level with additional soil. After three days, 56 pots of each soil texture were inoculated with ten ml of water suspension containing 1000 P. penetrans. Twenty-four pots of each soil texture remained as uninoculated controls.

A completely randomized block design was used with sampling date as blocks. Sampling dates were 10, 25, 50, 75, 100, 125, and 150 days after inoculation. Eight inoculated and four control pots of each soil texture were randomized within each block and entire blocks were harvested at each date.

Nematode population densities were estimated for roots and soil in inoculated treatments. Population data collected from control treatments was discontinued after no nematodes were recovered from roots at day twenty-five. Plant growth data, grams dry weight root and grams fresh weight top (foliage, stems, rhizomes), were recorded for controls and inoculated plants at each date.

Results

Analysis of variance and unpaired t-tests were used to evaluate influence of soil texture on population dynamics and host growth. The highest recovery of nematodes was in Camas soil after 10 days (81 percent of inoculum recovered). The second highest nematode population was recovered from Cloquato soil (53 percent) and the fewest nematodes were recovered from the Newberg soil (48 percent) (Table 7). The high soil nematode population recovered from Camas soil was inflated by numerous immobile, granular individuals. Root penetrating nematode densities were less divergent. Highest initial penetration rates occured in Cloquato soil and the least in Newberg soil.

Soil populations declined to minimum levels after 75 day,then increased to maximum densities after 150 days (Figure 19). Final soil P. penetrans densities in Camas soil were significantly greater (P=0.05) than in the other soils. Total root and per gram root populations followed similar hierarchy, with Camas root population levels significantly larger (P=0.05) then Newberg or Cloquato soils from 50 to 150 days.

Rates of root and soil nematode population increase were not significantly different between soil teatments in t-tests of sequential date. Simple linear regression of log mean root population over time showed (Figure 18) that the rate of increase was logaritmic within the experimental period. Comparision of regression slopes and Y intercepts that indicated Newberg and Camas linear regression models are do not differ statistically (P=0.05), while both differed from the Cloqaoto model. The shallower regression slope indicated a lower mean rate of increase in Cloquato soil.

Plant growth (Table 8) was significantly supressed with inoculated plants in Camas soil during the first 50 and 75 days for

Table 7. Effect of three soil textures on population dynamics of *Pratylenchus penetrans* in greenhouse pot culture

Population Parameter	Soil Series*	P. penetrans population (days after inoculation)						
		10 days	25 days	50 days	75 days	100 days	125 days	150 days
Population/ 1000 cm^3 soil	Newberg	223 b+	95 b	80 b	20 a	168 a	210 b	598 b
	Camas	500 a	263 a	528 a	33 a	180 a	605 a	2590 a
	Cloquato	138 b	58 b	75 a	8 a	23 b	63 b	140 b
Total root population	Newberg	259 b	200 a	773 b	3480 b	11925 b	14925 b	46900 b
	Camas	317 a	287 a	1878 a	6585 a	17335 a	27080 a	105800 a
	Cloquato	392 a	326 a	1018 b	2570 b	8700 c	12091 b	36680 b
Population/ gm. dry wt. root	Newberg	630 b	218 b	551 b	1495 b	4967 b	4506 b	14667 b
	Camas	1740 a	607 a	1548 a	3757 a	7795 a	8280 a	26331 a
	Cloquato	1744 a	443 b	618 b	1118 b	4610 b	4059 b	11857 b

* Newberg loam, Camas gravelly sandy loam, Cloquato silt loam

\+ Means at each date and within each population parameter followed by a common letter are not significantly different (P=0.05) according to Duncan's multiple-range test.

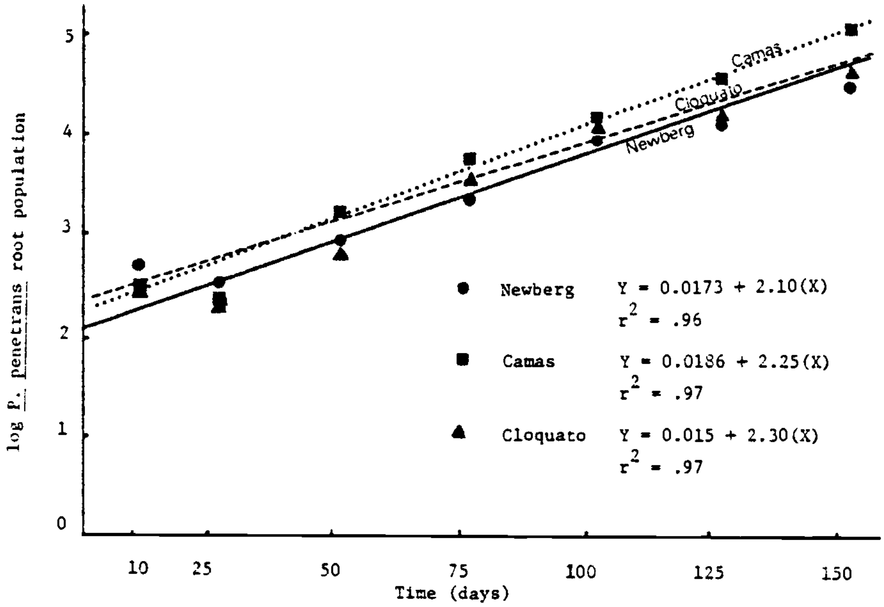


Figure 18. Regression of log Pratylenchus penetrans root populations vs time (days after inoculation) in three soil textures.

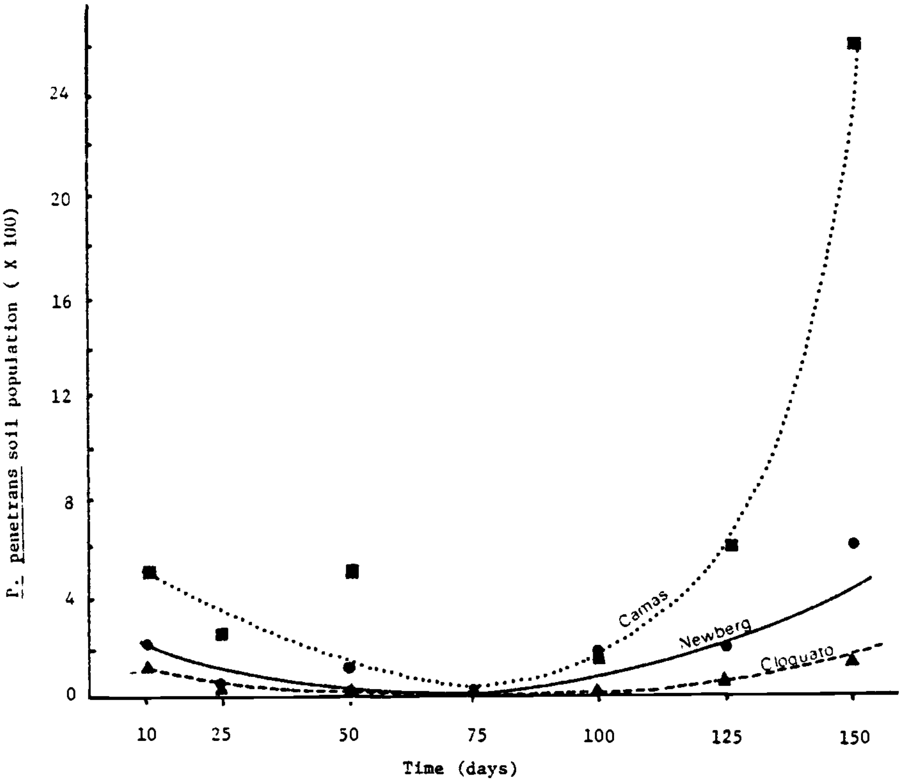


Figure 19. Pratylenchus penetrans root population trends in three soil textures during the 150 days following inoculation.

Table 8. Effect of *Pratylenchus penetrans* and soil texture interaction on peppermint growth in greenhouse pot culture

Weight in Grams
(Days After Inoculation)

Plant Growth Parameter	Soil Series	10 days In	25 days In	25 days C	50 days In	50 days C	75 days In	75 days C	100 days In	100 days C	125 days In	125 days C	150 days In	150 days C
	Newberg	0.45 a	0.88 a	1.05	1.52 a	1.74	2.40 a	3.44	2.44 a	3.53	3.31 a	3.69	3.43 a	4.63
Roots$	Camas	0.18 b	0.56 b	0.72	1.25 b	1.47	1.94 a	3.81	2.29 a	3.83	3.29 a	3.62	3.84 a	5.37
	Cloquato	0.27 c	0.81 a	1.42	1.66 a	1.63	2.35 a	2.61	1.89 a	2.76	3.15 a	4.27	3.31 a	2.74
	Newberg	5.2 a	6.8 b	7.0	20.8 a	18.5	35.1 a	35.7	53.1 a	51.0	59.6 a	58.8	62.5 a	66.5
Top$	Camas	3.1 b	3.9 c	5.8	15.6 b	14.3	24.9 b	29.7	45.7 a	50.8	64.8 a	59.4	64.3 a	64.4
	Cloquato	4.8 a	9.0 a	9.8	22.1 a	21.4	35.4 a	35.4	50.9 a	48.0	69.3 a	63.5	66.0 a	57.0

Means at each date and within each plant growth parameter followed by the same letter do not significantly differ (P=0.05) according to Duncan's multiple-range test.

Underlined mean weights are significantly different (t=.95).

$ Roots = dry weight root; Top = fresh weight stem, foliage, and runners.

In = inoculation rate of 1000 *P. penetrans*/cm^3; C = uninoculated control roots and top growth respectively. From 100 to 150 days, the soil texture-nematode interaction did not significantly influence either growth parameter. Top fresh weights of inoculated plants were not different (P=0.05) from like control plants sampled on the same date. All mean root weights were less than corresponding controls after 75 and 100 days. Final root weights after 150 days were significantly reduced in Camas and Newberg soil treatments, but not in Cloquato soil.

Discussion

Field studies indicated that distribution of *P. penetrans* was related to soil texture. Highest populations were confined to lighter soil textural classes (greater than 60 percent sand) located on elevated benches of alluvial origin. Two hypotheses can be proposed to account for this distributional pattern. 1) Initial inoculum loci were centered in each of these lighter crown areas and nematode distribution is a product of slow radial population expansion. 2) The second hypothesis assumes an initial broad distribution of the nematode population. Observed distributions are then a product of differential nematode reproduction and survival among soil textures. Direct testing of these hypotheses is impossible without complete historical site population data.

The first hypothesis has a major flaw. If radial spread independent of soil texture is assumed, the distributional patterns would be somewhat circular and extend across textural gradients. Observed patterns are elongated along major axes of lighter soil areas. Thus princple expansion from a locus would be bi-directional. The most likely initial P. penetrans introduction was either flood water carried inoculum or planting of infected rhizome stock. The first would deposit nematodes on the low areas as well as the higher sandy benches. Infected peppermint propogation stock would also uniformly distribute populations. Tillage and surface water movement would further spread populations across textural gradiants. Therefore, distributions biased to soil texture supports hypothesis two and a biological based differential rate of increase.

Seasonal dynamics from August 1979 to August 1980 (Figure 12) in cluster 2 (medium texture) and 3 (heavier texture) reveal initial and final nematode populations of the same magnitude. Only in cluster 1 plots (lightest texture) with extremely poor plant growth, did the relative soil-root population change from 1979 to 1980. Field study data during these two years, show that nematode density did not increase in heavier soil areas, while population centers expanded numerically in lighter soils. In this greenhouse study, population dynamics exhibited similar trends in response to soil texture.

Experimental results that indicated the mean rate of P. penetrans population increase did not differ between the two sandy loams, Camas and Newberg series. Only the silty loam, Cloquato series, had lower mean rate of nematode increase as determined by regression line slope. All three final P. penetrans populations approximated densities expected if the nematode population recovered after 10 days followed a

35 day life cycle with mean ovipostion rate reported by Maniya (86). Significantly larger final nematode population with Camas soil may then be the result of a higher effective inoculum level, 81 percent inoculum recovery at day ten vs. 50 percent for Newberg and Cloquato soils. This increased nematode survival is not well-documented because high numbers of dead individuals were extracted from Camas soil treatments. Many nematodes may have been carcasses from original field population remaining after fumigation. Whether differential survival or reproduction rate is responsible, soil suitability ranked as expected from field observations. Population increase was not stopped in any of these soils, but was retarded in the two heavier soil series. In fine textured soils, field populations could take additional seasons to reach potentially damaging levels. In heavy soils, a stand may succumb to other yield depressing factors and be removed before it exhibits nematode damage.

Soil texture greatly influences moisture tension characteristics of soils. Fine soils have small pores which retain water at higher moisture tensions than well-drained course soils. Biological processes of soil nematodes are dependent on an aqueous film surrounding pore surfaces. Under saturated conditions, water filled pores impede gas diffusion. The resulting low oxygen tensions have been shown to reduce nematode reproduction, egg hatch, moulting processes, root penetration, and survival (30,76,149,151,156,157). Nematode movement is also dependent on critical water film thickness and surface tension (153). These three experimental soils had different pore sizes and moisture characteristics. Each pot was equally watered, but the lighter soil drained more rapidly to optimal moisture tension for nematode biological activities. Higher moisture tensions are required for P. penetrans reproduction as the clay content increases in soil (76). Initial soil inoculum recovery and final nematode populations were lowest in the Cloquato series and greatest in the Camas series, as would be expected when low oxygen tensions associated with saturated conditions prevail in the heavier soil.

Initial root penetration was not reduced in the Cloquato series treatment when compared to the two sandy loams. Nematode inoculum placed on the exposed root system required negligible movement to find and enter roots. Nematode soil densities rapidly declined during the first 75 days indicating high mortality of those nematodes that had not successfully penetrated roots. As infected root necrosis becomes extensive, nematodes leave damaged tissues, migrate to and penetrate healthy roots. Migration is dependent on soil texture and moisture tension. Moisture tension also influences host root physiology which in turn regulates nematode biology within host tissues. Therefore, initial survival, differential reproductive rates, subsequent dispersal and host physiology interact to produce differences observed with these three soils.

The experimental period was not long enough for the nematodes to reduce plant top growth. In this experiment Camas soil treatment plants were smaller during the first 75 days, but final plant top growth was equal in all three soil treatments. As in the field, young vigorous plants can support high nematode populations and can produce strong yields. An indication of future vigor decline was reduction of root mass in the two sandy loams. Several seasons of root decline would culminate in shallow-rooted stunted plants as soil water and nutrients become limiting. In heavier slow-draining soils where moisture does not become limiting to summer growth, a peppermint stand may continue to produce economically acceptable yields as *P. penetrans* populations increase to high densities.

Population patterns under field conditions involve a complex of additional factors associated with soil texture. *P. penetrans* overwinter survival studies by Kable and Mai (77) noted lower survival in a clay soil than in sandy loam. Heavier soils remained saturated while loam drained allowing adequate gas exchange. Similar soil conditions occur in Oregon when lower oxygen tensions prevail in heavier soils during periods of high rainfall from October to May. Conversely, the heavier soils would retain more moisture during xeric summer periods when irrigation is needed. Plants in heavier soils would suffer less water stress between irrigation sets. Plant stress has been demonstrated to accelerate *P. penetrans* reproduction rates (35).

Soil fertility and divalent cation milliequivalents are generally lower in well-drained lighter soils. Soil nutrient deficency stress was observed to increase *P. penetrans* reproduction in peppermint (111). Similarly, calcium and potassium cation balance can influence *Pratylenchus* penetration and reproduction (83,86). Plants in this experiment were grown under optimal conditions, so total soil effects are masked.

Effects of soil type on *P. penetrans* were not clearly elucidated in this experiment. Under field conditions intact soil profiles would have characteristics different from pot cultures. Lighter Camas gravelly sandy loam did yield higher nematode populations, as expected from field observations. Differences between population dynamics at high and extremely low population densities are compounded with amphimictic species. At very low densities the proportion of females mated will be low because chances of male-female encounters are reduced and populations will increase slowly. Distributions in the study fields along soil textural gradients are the summation of differential winter mortality, restricted movement, reduced root penetration and modified host physiology. All these phemomena are influenced by a multi-faceted mosaic of edaphic factors.

UTILIZATION OF CARBAMATE NEMATICIDES TO MANAGE *PRATYLENCHUS PENETRANS* DAMAGE OF PEPPERMINT

Preface

Peppermint, as with many perennial crops, often has disease and pest populations increase to economically damaging densites during the years after planting. Fumigants effectively reduce nematode populations, but mechanical damage from application equipment and fumigant phytotoxicity limit their use to preplant treatments. The establishment of new peppermint stands requires substantial capital investment which may not be recovered until the third year of production. Thus a nematode management technique was needed to rejuvenate declining stands after nematode populations surpass damaging densities. A carbamate nematicide, oxamyl, has been shown to control *Longidorus elongatus* damage of peppermint in greenhouse and field experiments (70 112). Although oxamyl is nematicidal at high rates, field rates have been shown to be nematistatic and function by inhibiting nematode feeding, movement, and and root pentration (2,34,88,91,163). In July 1978, oxamyl was granted a section 18 emergency use permit for peppermint in Oregon. Experiments to evaluate the efficacy of carbamate nematicides for controlling *P. penetrans* damage of peppermint commenced in 1978 and continued through 1983. These experiments were designed to evaluated nematicide or nematistatic rates, determine most effective timing of applications, and identify soil and stand characteristics which limit crop response to nematicide treatments.

Materials and methods

Site selection: During 1978 to 1981, forty peppermint fields were evaluted as potential sites for nematicide trials and plots were established at five of these locations. First, two to four hectare blocks were sampled within fields that displayed spotty or stunted growth during the previous season. All experimental plots were restricted to sandy loams, a soil conducive to plant damage, except in 1981 when one trial was established on a silty loam. Secondly, blocks with substantial *P. penetrans* population densities were subdivided into one-quarter hectare sub-blocks and establishment of plots were only considered if population densities exceeded 2000 per gm fresh root weight. The final criteria for selection was proximity to the field border, within 50 meters. This facilitated easy equipment movement through dense peppermint stands. All plots recieved standard cultural practices used by the grower throughout the experimental period, except for nematicide applications which were restricted to more than 15 meters from plot areas.

Population sampling: Nematode population densities were sampled three times during the growing season, pretreatment (late March or early April), mid-season (mid-June), and after harvest (early August). In 1979 plots, *P. penetrans* populations were sampled for two additional years in April 1980 and 1981. Nine 2.5 cm x 15 cm deep soil cores were randomly collected and bulked for each treatment entry. Soil was processed by Bareman funnel method. Five intact root cores, 10 x 10 x 15 cm deep, were taken through randomly selected plant crowns in each plot. These five plant cores were washed free of soil and the roots were trimmed from crowns and rhizomes. Roots were bulked from each entry and a randomly selected 10 gm subsample was placed in a mist extraction chamber for seven days. All plant parasitic nematode genera extracted from both soil and root samples were counted. However, root population data are better predictors of plant damage and all populations reported in these experiments are expressed as the total number (adult and juvenile _P. penetrans_) per gm of fresh root. Soil samples contained ectoparasitic nematodes, _Trichodorus sp._, _Paratylenchus sp._, and _Longidorus elonagatus_, which were at densities determined not to significantly contriburtte to crop loss.

Plant response estimation: In 1979, three one meter square areas were randomly selected and harvested within each treatment entry. A three sided metal frame was place in the plots and all stems arising within its perimeter were cut 3 cm above the soil surface with an electric hedge trimmer. Fresh hay was immediately collected and weighed. During 1980, plots at the Linn County site were accidentally harvested by the grower prior to our data collection. Therefore, plant response was based on the number of stems per 0.092 square meter, percent ground cover of stems (where percentage was rated: 1 = less than 25 percent, 2 = 25-50 percent, 3 = 50-75 percent and

4 = greater than 75 percent) and stem diameter obtained from three 0.84 square meter areas sampled in each entry. Stem diameter was rated; 1 = mean diameter less than 2.5 mm, 2 = 2.5-3.5 mm, 3 = 3.5-4.5 mm. and 4 = mean diameter greater than 4.5. The vigor rating was calculated by multiplying the values for each parameter together. The 1980 Benton County plots were harvested as in 1979. In 1981, a forage chopper equiped with a 0.9 meter cutting bar was used to mow two 4.9 x 0.9 meter strips through each entry. Fresh cut hay was blown into burlap sacks and weighed.

1979 Experiments: Trials were established in a five year old stand situated on a sandy loam bench which had a history of poor peppermint growth. Plots, 3.1 x 3.1 meters, were arranged in a completely randomized block design with four replications. Three nematicides, oxamyl (2 L), sulfone (75 WP) and carbofuran (4E) (see Appendix F), were applied in two liters of water as broadcast sprays. The first spray was applied when plants were five to 10 cm tall. All treated plots received 5.5 kg a.i./ha of a nematicide on April 5, two thirds of these plots received a second application on May 3, and one-half of these recieved a third application on June 2. Total nematicide applied was 5.5, 11.0 and 16.5 kg a.i./ha for each material. Untreated plots were included as checks. Nematode populations were sampled on March 29, June 28, and August 7, the harvest date. Later April *P. penetrans* population and August yield data were collected for two additional seasons, 1980 and 1981.

1980 Experiments: Two experimental plots were established in 1980, one adjacent to the 1979 plot and a second in a Benton County field with similar soil type and crop history. Experimental design was a completely randomized block design with 3.1 x 3.1 meter treatment plots and four replications. Fall applications of 2.2 kg a.i./ha carbofuran and 2.2 kg a.i./ha oxamyl were made on September 12, 1979 to evaluate nematicide efficacy in reducing overwintering nematode populations. A portion of fall treated plots received a single 2.2 kg a.i./ha oxamyl application on April 7 or May 13, 1980. The remaining plots, not treated the previous fall, received either a single 2.2 or 4.4 kg a.i./ha oxamyl application on April 7, a single 2.2 or 4.4 kg a.i./ha oxamyl application on May 13, or 2.2 kg a.i./ha applications on both dates. All treatments, as in 1979, were applied as broadcast sprays using a backpack sprayer equiped with a one meter spray boom. No treatment received more than 4.4 kg a.i./ha of nematicide during this study. Untreated plots were included as checks. Populations data was collected September 12, 1979, March 25, 1980 and June 25, 1980. Plant growth reponse was evaluated on August 15.

1981 Experiments: Experimental plots were established at two locations, the Marion County trials on a Newberg fine sandy loam and the Linn County trials on a Chehalis silt loam. Plots, 4.5 x 4.5 meters, were arranged in a completely randomized block design with five replications. Single 0.6, 1.1, 2.2, and 4.4 kg a.i./ha oxamyl applications were broadcast sprayed on April 2. Check plots received no nematicide application. Population data were collected April 2, June 10 and August 26. Plots were harvested and yield data collected on July 30.

Results

1979: Populations densities prior to nematicide applications were not significant different (P=0.05) between plots, although# there was great population density variability within the experimental area. All post-treatment samples collected on June 28 had significantly (P=0.05) lower *P. penetrans* densities compared to check plots (Table 9). Oxamyl at 3 x 5.5 kg a.i./ha reduced nematode densities to a detection threshold level of one per gm root tissue. Only in 1 x 5.5 kg a.i./ha sulfone and check plots were densities greater than pretreatment levels, ie. the change in *P. penetrans* density was greater than one. All treatments had population resurgence from June densities to havest on August 7. However, except for 1 x 5.5 kg a.i./ha sulfone and carbofuran plots, mean *P. penetrans* densities in treatments were significantly (P=0.05) lower than in check plots. Two sulfone treatments, 2 x 5.5 and 3 x 5.5 kg a.i./ha, and 3 x 5.5 kg a.i./ha, carbofuran had population increase to nearly one-half pretreatment densities (*P. penetrans* density change = 0.5), while increases with 2 x 5.5 and 3 x 5.5 kg a.i./ha oxamyl were to 0.04 and 0.01 times pretreatment densities, respectively. In all other treatments, *P. penetrans* densities in August exceeded March pretreatment levels. Similar ranking of treatment population densities was evident in April 1980, one year after nematicide applications. At this time, nematode densities in all treatments were significantly (P=0.05) less than in checks. However, all nematode

Table 9. Effect of three carbamate nematicides on Pratylenchus penetrans population density; 1979 experiments

Treatment		Sampling date								
		March 29 1979	June 28 1979		August 7 1979		April 1980		April 1981	
nematicide	number of 5.5kg a.i./ha applications	root pop.	root pop.	pop. change	root pop.	pop. change	root pop.	pop. change	root pop.	pop. change
oxamyl	1	2239 a	88 b	.109 b	437 bcd	1.123 ab	628 bcd	.678 bc	1758 ab	2.927 a
oxamyl	2	883 a	9 b	.023 b	32 d	.038 b	300 cd	.707 bc	1376 ab	2.947 a
oxamyl	3	1568 a	1 b	.001 b	7 d	.012 b	37 d	.039 c	792 b	.969 a
sulfone	1	1128 a	576 b	1.658 ab	1524 ab	2.144 a	1663 b	3.183 ab	1526 ab	3.694 a
sulfone	2	1485 a	303 b	.270 b	699 bcd	.491 ab	1209 bcd	1.21 bc	1414 ab	1.473 a
sulfone	3	1546 a	234 b	.164 b	444 bcd	.416 ab	1137 bcd	.983 bc	1782 ab	1.077 a
carbofuran	1	1147 a	425 b	.489 b	1430 ab	1.224 ab	1373 bc	1.450 bc	657 b	.903 a
carbofuran	2	1310 a	98 b	.081 b	959 bcd	1.209 ab	765 bcd	.775 bc	1280 ab	1.263 a
carbofuran	3	1218 a	137 b	.416 b	236 cd	.380 ab	467 bcd	1.135 bc	2234 ab	3.655 a
check	0	1780 a	2782 a	2.355 a	2295 a	1.911 ab	4586 a	3.947 a	2885 a	2.728 a

Means followed by the same letter do not significantly differ ($P = 0.05$) according to Duncan's multiple range tests

* root pop. = P. penetran population density per gram fresh root weight

\# pop. change = P. penetrans population density at date indicated divided by pretreatment P. penetrans density densities approached or exceeded pretreatment levels, with the exception of 3 x 5.5 kg a.i./ha oxamyl where P. penetrans density equaled 0.039 times the March 1979 level. In April 1981, two years after nematicide applications, P. penetrans densities in all treatments equaled or exceeded pretreatment levels, even though 3 x 5.5 oxamyl and 1 x 5.5 kg a.i./ha carbofuran treatments had population densities significantly (P = 0.05) less than check plots.

Crop preformance was evaluated for three seasons following nematicide applications (Table 10). In 1979 fresh hay yields in all treatments were significantly greater (P=0.05) than check plots (0.74 kg/m), with 3 x 5.5 oxamyl and 1 x 5.5 kg a.i./ha sulfone best (2.66 kg/m) and poorest (1.86 kg/m) treatments, respectively. Similarly, in 1980 crop response based on stem count, stem diameter, and percent stem cover, showed all treatments more vigorous than check plots. This vigor rating agreed with a subjective estimation of hay growth observed several days before the grower inadvertantly harvested the plots. By 1980, treated plots adjacent to check plots encroached 20 to 40 cm into check plots and vigor parameters were recorded in the central portion of check plots. Third season hay yields were depressed from 1979 levels in all plots, but in all plots yields were greater than 1979 check yields. Only in check plots where runners from vigorous adjacent treated plots had extensively invaded, did yields exceed 1979 levels.

1980: Populations were sampled at both locations one month after 1979 harvest. Plant regrowth was extremely sparse at this time. March 1980 P. penetrans densities (Tables 11 and 12) were not reduced by application of oxamyl or carbofuran applied the previous September. P. penetrans densities in all plots declined from fall 1979 densities, which reflect normal overwinter P. penetrans population dynamics in Oregon peppermint fields. Conversely, June 25 P. penetrans densities following spring applications of oxamyl were significantly (P=0.05) less than the check and significantly less than both September and March densities. No significant (P=0.05) nematode density differences were observed between early spring (April 7) and mid-spring (May 13) treatments nor between 2.2, 2 x 2.2 and 4.4 kg a.i./ha oxamyl rates. June P. penetrans densities were of similar magnitude to those collected in 1979 1 x 5.5 kg a.i./ha oxamyl plots 12 weeks after treatment.

Prior to treatment, 1980 stands at both locations were less uniform and vigorous than stands selected for 1979 trials. In Benton County plots (Table 12), checks produced yields among the poorest. However, in no spring treatment was P. penetrans density reduction accompanied by an acceptable yield increase. Similarly, plant vigor ratings from Linn County plots were less than the poorest plant vigor rating from second year 1979 plot which were located in the same field (Table 11). Therefore, no 1980 treatment produced the significant plant growth response as observed in 1979 trials.

1981: The two locations differed in soil texture and pretreatment stand vigor, but possessed similar pretreatment (April 2) P. penetrans densities (Table 14). Marion County plots were established in a uniformily stunted stand on a Newberg sandy loam, while the Linn County plots were in a moderately vigorous stand on a Chehalis silt

Table 10. Effect of three carbamate nematicides on crop growth and crop value in a *Pratylenclus penetrans* infested peppermint field; 1979 experiments.

Treatment		Crop growth response or value*						
		1979			1980	1981		
nematicide	number of 5.5 kg a.i./ha applications	kg hay/m^2	kg oil/ha	dollar value	vigor rating	kg hay/m^2	kg oil/ha	dollar value
oxamyl	1	2.50 a	68.2	1500	60.8 ab	1.71 abc	46.7	1027
oxamyl	2	2.28 ab	62.2	1368	47.7 ab	1.59 abc	42.4	955
oxamyl	3	2.66 a	72.6	1597	66.5 a	1.95 ab	53.2	1170
sulfone	1	1.86 b	50.7	1115	47.8 ab	1.85 ab	50.5	1111
sulfone	2	2.48 ab	67.7	1489	35.9	1.24 c	33.8	744
sulfone	3	2.59 a	70.7	1555	56.1 ab	2.10 a	57.3	1261
carbofuran	1	2.37 ab	64.7	1423	35.5 a	1.94 abc	52.9	1164
carbofuran	2	2.14 ab	58.4	1285	71.9 a	1.62 abc	44.2	972
carbofuran	3	2.42 ab	66.0	1452	60.0 ab	1.96 ab	53.5	1177
check	0	0.74 c	20.2	444	11.4 c	1.52 bc	41.4	911

Means followed by the same letter do not significantly differ (P = 0.05) according to Duncan's multiple range tests

* Crop growth response = In 1979 and 1981, kg fresh hay weight per square meter. Oil yield was calculated by (fresh hay weight x .22) = hay dry weight; (dry weight x .0125) = oil weight. The oil cash value was calculated by (kg oil weight x $ 22.00 / kg).
In 1980, crop vigor rating was calculated by (percent ground cover x number of stems/0.092 m^2 x mean stem diameter) where stem diameter was rated 1 = less than 2.5 mm, 2 = 2.5-3.5 mm, 3 = 3.5-4.5 mm, and 4 = greater than 4.5 mm.

Table 11. Effect of oxamyl and carbofuran application timing on Pratylenchus penetrans population density and peppermint growth; 1980 Linn County site.

Treatment			Sampling date: Sept. 1979	March 25, 1980		June 25, 1980		crop[+] growth
nematicide	kg a.i. /ha	timing*	root pop. **	root pop. **	pop. change #	root pop. **	pop. change ##	response
carbofuran	2.2	Fall	2720 ab	2453 a	1.02 a	1332 a	1.19 b	17.2 ab
carbofuran oxamyl	2.2 2.2	Fall E Sp	2751 ab	1395 a	0.71 a	153 b	0.09 c	17.4 ab
oxamyl	2.2	Fall	4244 a	1467 a	0.45 a	1515 a	1.17 c	15.0 ab
oxamyl	4.4	Fall	3234 ab	1083 a	0.40 a	1860 a	2.34 a	20.7 ab
oxamyl	2.2 2.2	Fall E Sp	3329 ab	2370 a	0.79 a	94 b	0.07 c	22.1 ab
oxamyl	2.2 2.2	Fall L Sp	3433 ab	1282 a	0.40 a	325 b	0.26 c	26.5 ab
oxamyl	2.2	E Sp	2817 ab	1914 a	0.75 a	183 b	0.07 c	18.7 ab
oxamyl	4.4	E Sp	1886 a	1279 a	0.69 a	48 b	0.18 c	29.8 ab
oxamyl	2.2	L Sp	3862 ab	1802 a	0.45 a	196 b	0.18 c	34.9 a
oxamyl	4.4	L Sp	3847 ab	2517 a	0.64 a	129 b	0.08 c	11.3 b
oxamyl	2.2 2.2	E Sp L Sp	3924 ab	945 a	0.29 a	88 b	0.23 c	22.1 ab
check	-	-	4242 a	2024 a	0.59 a	1248 a	0.74 a	27.6 ab

Means followed by the same letter do not differ significantly (P = 0.05) according to Duncan's Multiple Range Tests

* Timing: Fall = applied on September 12, 1979
E Sp = applied on April 7, 1980
L Sp = applied on May 14, 1980

** root pop. = P. penetrans / gm fresh root weight

\# pop. change = March 1980 P. penetrans density divided by the September 1979 population density

\## pop. change = June 1980 P. penetrans density divided by the March 1980 population density

\+ crop growth response = (percent cover x number of stems per 0.092 m^2 x mean stem diameter)

Table 12. Effect of oxamyl and carbofuran application timing on Pratylenchus penetrans population density and peppermint growth; 1980 Benton County site.

Treatment			Sampling date					Yield
			Sept. 1979	March 25, 1980		June 25, 1980		
nematicide	kg a.i. /ha	timing*	root pop.**	root pop.**	pop. change #	root pop.**	pop. change ##	kg fresh hay / m^2
carbofuran	2.2	Fall	1562 ab	2267 ab	1.57 bc	1245 bc	0.62 bcd	1.00 bcd
carbofuran oxamyl	2.2 2.2	Fall E Sp	1851 b	1242 bc	0.69 a	203 d	0.19 d	2.09 a
oxamyl	2.2	Fall	2414 ab	1784 abc	0.79 a	2084 ab	1.26 d	0.66 cd
oxamyl	4.4	Fall	2513 ab	1414 bc	0.61 a	2197 a	1.51 a	1.05 bcd
oxamyl	2.2 2.2	Fall E Sp	1693 b	1151 bc	0.97 a	167 d	0.14 d	1.43 abcd
oxamyl	2.2 2.2	Fall L Sp	1778 b	1394 bc	0.84 a	446 cd	0.37 cd	1.25 abcd
oxamyl	2.2	E Sp	1700 b	1066 bc	0.67 a	279 c	0.29 d	1.21 abcd
oxamyl	4.4	E Sp	2384 ab	1265 bc	0.51 a	48 d	0.06 d	1.11 abcd
oxamyl	2.2	L Sp	2356 b	2188 ab	0.91 a	285 d	0.20 d	1.46 abc
oxamyl	4.4	L Sp	2769 ab	1635 abc	0.69 a	209 d	0.15 d	0.93 bcd
oxamyl	2.2 2.2	E Sp L Sp	3899 a	668 c	0.36 a	92 d	0.19 d	1.76 ab
Check	-	-	2678 ab	2879 a	1.15 a	1982 ab	0.95 abc	0.43 d

Means followed by the same letter do not differ significantly (P = 0.05) according to Duncan's Multiple Range Tests

* Timing: Fall = applied on September 12, 1979
E Sp = applied on April 7, 1980
L Sp = applied on May 14, 1980

** root pop. = P. penetrans/ gm fresh root weight

\# pop. change = March 1980 P. penetrans density divided by the September 1979 population density

\#\# pop. change = June 1980 P. penetrans density divided by the March 1980 population density loam. These differences are reflected in both nematode density and crop responses following nematicide applications.

June 10 population densities were significantly (P=0.05) less than checks with the two highest oxamyl rates (2.2 and 4.4 kg a.i./ha) at both locations and 1.1 kg a.i./ha in Marion County trials. Population change from pretreatment densities illustrate similar trends at Marion County (Table 14). Post-harvest P. penetrans densities (August 25) were significantly higher in check plots than in the two highest oxamyl rates (2.2 and 4.4 kg a.i./ha) and the highest rate in Marion and Linn counties, respectively. However, August P. penetrans densities in all treated plots at the Marion County site equaled or exceeded pretreatment densities. Resurgence was less dramatic in the Linn County plots.

Stand growth response to nematicide treatments also varied between locations (Table 13). Linn County trials did not demonstrate significant yield response, even though check plots did produce the lowest mean hay yield. Conversely, in Marion County plots all treatments yielded significantly (P=0.05) more hay than check plots and hay yields relected June 10 P. penetrans densities. Three oxamyl treatments, 4.4, 2.2, and 1.1 kg a.i./ha produced significantly greater yields than 0.6 kg a.i./ha. However, this lowest rate produced mean a yield twice that of check plots in Marion County trials. In both locations, treatment yields fell within the range of Willamette Valley peppermint stands without nematode damage observed during a 5 year, 5 county survey.

Table 13. Effect of 1981 oxamyl treatments on yield in two Willamette Valley peppermint fields with different edaphic and stand characteristics.

Rate	Marion County site			Linn County site		
kg a.i./ha	kg hay/m^{2}*	kg oil/ha #	crop value + (dollars)	kg hay/m^{2}*	kg oil/ha #	crop value + (dollars)
0.6	2.71 b	73.9	1626	2.53 a	69.0	1518
1.1	3.08 a	84.0	1848	2.58 a	70.4	1549
2.2	3.19 a	87.0	1914	2.95 a	80.5	1771
4.4	3.37 a	91.9	2022	2.47 a	67.4	1483
check	1.36 c	37.1	816	2.28 a	62.2	1368

Means followed by the same letter do not significantly differ ($P = 0.05$) according to Duncan's multiple range tests.

* kg fresh hay weight/ m^2

Oil yield calculated by: (kg fresh hay weight/m^2 x 10^4) = kg fresh hay/ha
(kg fresh hay/ha x 0.22) = kg dry hay/ha
(kg dry hay/ha x 0.0125) = kg oil/ha

+ crop value = (kg oil/ha x $ 22.00 / kg oil)

Table 14. Effect of 1981 oxamyl treatments on Pratylenchus penetrans densities in two Willamette Valley peppermint fields with different edaphic and stand characteristics.

Rate	Marion County site					Linn County site				
	April 2*	June 10*		August 26*		April 2*	June 10*		August 26*	
kg a.i./ha	root root pop. #	root root pop. #	pop. pop. change +	root root pop. #	pop. pop. change +	root root pop. #	root root pop. #	pop. pop. change +	root root pop. #	pop. pop. change +
0.6	1957 a	2660 a	3.81 a	3556 a	4.27 a	1648 ab	1238 ab	1.07 ab	943 a	0.74 a
1.1	2735 a	943 b	0.53 a	1964 ab	1.29 a	1336 ab	1215 ab	1.06 ab	933 a	0.79 a
2.2	1129 a	470 b	0.40 a	1877 ab	1.87 a	1947 ab	415 c	0.34 b	319 b	0.26 a
4.4	1694 a	395 b	0.36 a	1030 b	0.97 a	3014 a	203 c	0.10 b	182 b	0.09 a
-	1114 a	4215 a	3.79 a	3236 a	3.37 a	1045 b	1689 a	2.42 a	711 ab	0.76 a

Means followed by the same letter do not differ significantly (P = 0.05) according to Duncan's Multiple Range Tests

* Population sampling date

\# root pop. = P. penetrans/ gm fresh root weight

\+ pop. change = P. penetrans population density at indicated sampling date divided by the pretreatment (April 2) nematode density.

Discussion

Three cambamate nematicides, oxamyl, sulfone and carbofuran, were evaluated for *P. penetrans* management in peppermint during 1979 and 1981. Only sprayable formulations were selected for the following reasons; growers have access to large volume spray equipment, sprays give uniform coverage with low concentration broadcast applications, several of these compounds are reported to be basipetally translocated from foliage and granular nematicides must be tilled into the soil, a process that can increase *Verticillium* wilt severity and damage established plants.

In 1978, oxamyl was granted a section 18 emergency use peppermint on peppermint in Oregon for control of *Longidorus elongatus* damage. Some growers also applied oxamyl at 4.4 kg a.i./ha on *P. penetrans* damaged stands during early July that year, but no stand improvements were observed. Similarly, no plant response was recorded in blocks that we treated with 6.6 kg a.i./ha oxamyl at that time. These failures led us to set 5.5 kg a.i./ha as the base rate with multiple applications during 1979. Subsequent crop growth response and *P. penetrans* density reducation was greatest with oxamyl, even though all nematicides tested significantly increased yields in 1979 trials. Since multiple applictions produced no better yields than single applictions, we decided to limit 1980 trials to lower rates of oxamyl and include fall carbofuran treatments. Carbofuran was included because at this timing it could fit into insect management programs and avoid residue accummulations in peppermint oil that are present with spring applications (Dr. R. Berry. Department of Entomology, Oregon State University, personal communication.). In 1981, we observed that oxamyl rates as low as 0.6 kg a.i./ha produced hay yields double those harvested in untreated check plots (Table 13). Therefore, timing of applications and oxamyl prophylactic mode of action (2,34,88,164) can account for the discrepancy observed between the failure of oxamyl to produce increased plant growth in 1978, ,when rates as high as 6.6 kg a.i./ha were applied, and the dramatic yield increase with 0.6 kg a.i./ha in 1981.

The observed effects of nematicide rates and timing can be better understood if they are related to peppermint phenology (Figure 20). Peppermint is a perennial which overwinters as dormant runners and rhizomes. The previous season's roots die during the fall and there is little new root growth until late March to early April the following season. Root growth corresponds to top growth during the spring. Since these nematistatic compounds are transient in the soil (21), they are most effective when applied during periods of new root growth and prior to nematode invasion (67).

In 1978, high oxamyl rates applied in mid-summer were ineffective because these shallow-rooted, water and nutrient stressed plants could not capitalize on release from nematode parasitism. Peppermint flowering commences as day length decreases in early summmer and this reduces the phytosynthates available for root and vegetative growth. Furthermore, endoparasitic nematodes within the root are less affected by oxamyl than are early season soil populations which are attempting

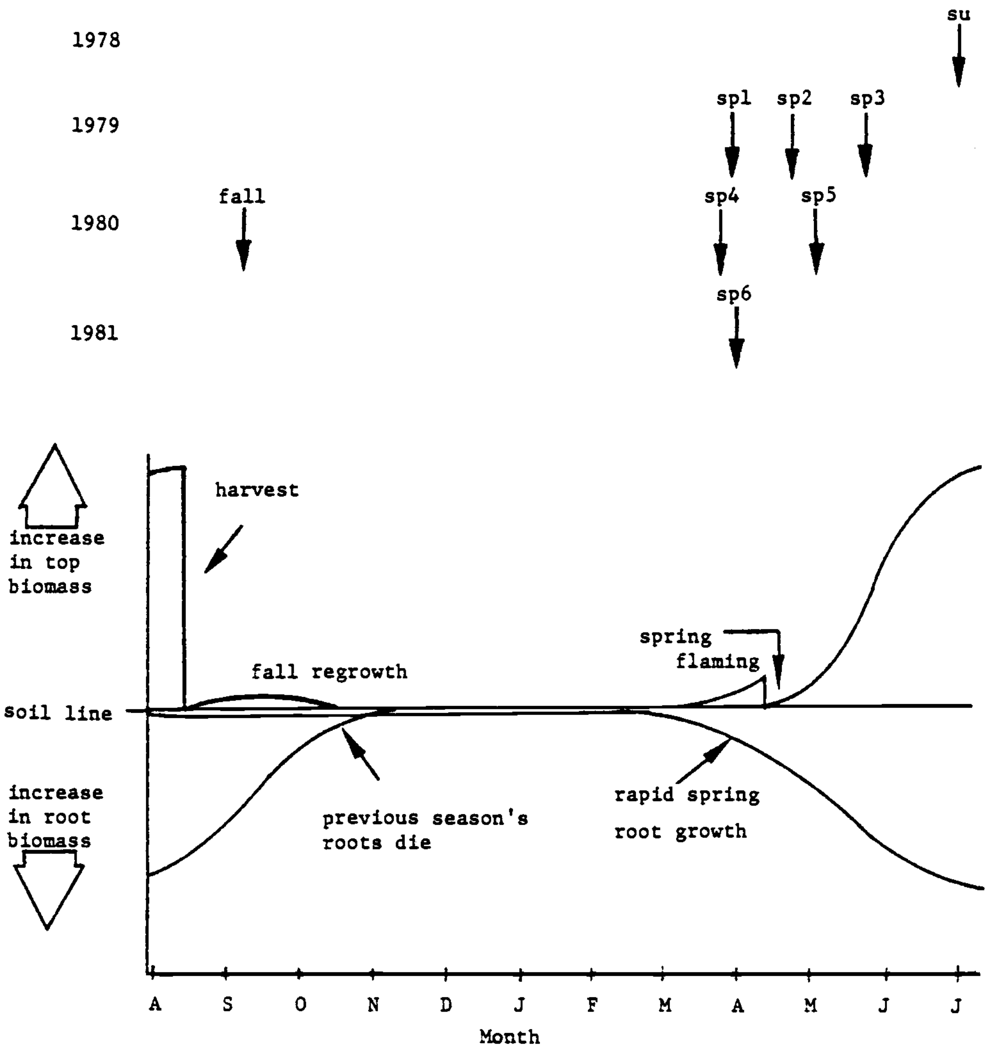


Figure 20. Nematicide application timing in field trials during 1978 to 1981 in relation to peppermint phenology.

1978 su = summer oxamyl applications which demonstrated no plant growth response

1979 sp1 = 5.5 kg a.i./ha of nematicide applied on April 5

sp2 = 5.5 kg a.i./ha of nematicide applied to 2/3 of sp1 plots on May 3 (total of 11.0 kg a.i./ha)

sp3 = 5.5 kg a.i./ha of nematicide applied to 1/2 of sp2 plots on June 2 (total of 16.5 kg a.i./ha)

1980 fall = nematicide applied on September 12, 1979

sp4 = oxamyl applied on April 7

sp5 = oxamyl applied on May 13

1981 sp6 = oxamyl applied on April 2

to penetrate roots (36,88,99). Finally at best, July treatments would only shift the plant growth curve in figure 20 to the right which would not provide ample time for hay growth prior to the August harvest.

Similarly, fall treatments were ineffective in increasing plant vigor and reducing P. penetrans densities in the succeeding season. Plant phenology also can account for these results. Root lesion nematodes are confined to the current season's roots which die in the fall and contribution mimimumally to plant function. Since old roots are relatively inactive, they do not sequester oxamyl from soil nor do they act as sinks for basipetally translocated nematicide. Therefore, endoparasitic P. penetrans remain protected in old root tissues well into the fall. Although there is some new root growth during fall, these roots are not heavily invaded during the cold winter period when nematode activity and densities are depressed.

Conversely, spring treatments significantly reduced P. penetrans root populations and the reduction was accompanied by significant yield increase, except for 1980 plots. Even though nematode population density reduction was not significantly different between early and mid-spring oxamyl applications, we believe that earlier treatments are best. Applications made shortly after spring growth commences will protect new roots for three to four weeks, the active life of oxamyl. These vigorous roots penetrate deeply and can supply nutrients and water during summer stress periods. Early spring vigor also aids plant recovery from stress caused by flaming for control of Puccina mentha. These data illustrated that a single early spring application of oxamyl as low as 0.6 kg a.i./ha temporarily protected peppermint plants and resulted in significant yield increase, even though _P. penetrans_ root densities exceeded pretreatment levels by mid-season.

Plant vigor entering a growing season is critical to peppermint growth within the season. In two seasons, 1979 and 1981, plots were established in stunted stands with uniform crop coverage. These plots demonstrated excellent yield response following nematicide applications. Only in the two 1980 plots did nematicides fail to produce significant plant growth improvement. Prior to treatment, these stands with few overwintering runners and rhizome were less vigorous than 1979 and 1981 stands. Plants in these 1980 plots had little reserves for spring growth and could not captialize on the cessation of nematode feeding following nematicide applications. Even though individual plants did have improved growth after oxamyl treatments, these plants produced few runners and large barren areas persisted in the stand through the season. A follow-up treatment in spring 1981 possibly could have promoted rhizome production from these improved plants and resulted in yield of the magnitude observed in 1979 and 1981 plots. Unfortunately one stand was plowed under and the second was not retreated, so this hypothesis remains untested.

Rejuvenated stands following 1979 nematicide applications maintained crop vigor and produced yields greater than check plots for three years. This illustrates durability of rejuvenated plant to withstand _P. penetrans_ root densities which exceed extremely damaging pretreatment densities. Plants in 1979 treated plots were so vigorous during 1979 and 1980 that their rhizomes encroached widely into adjacent check plots by 1981 and obscured nematicide treatment effects. These data suggest that alternate year oxamyl applications at high ratess (2.2 kg a.i./ha or greater) or low rate of oxamyl (0.6 to 1.1 kg a.i./ha) applied annually should be adequate to maintain good hay production after a stand has been rejuvenated. Rate of stand decline after an oxamyl treatment should follow a two to four year pattern observed in newly established peppermint on infested sites.

Soil texture has been demonstrated to influence _P. penetrans_ population dymanics and plant damage (77). In 1981, plots in a silty loam demonstrated no significant plant growth response following oxamyl treatments, even though nematode population densities were significantly reduced. However, plots established in a sandy loam with equal pretreatment _P. penetrans_ densities had yield responses corresponding to population density decreases. A comparison of these two sites (Table 13) indicated that the nematode significantly reduced plant growth in sandy loam (Marion County), while in silty loam (Linn County) nematodes were much less damaging. The water retention capacity in a silty loam is greater than in sandy loam. Therefore, plants experience less drought stress during mid-summer and retain vigor longer in fine textured soil, although nematode densities will finally increase to equal levels in both soils. Furthermore, _P. penetrans_ populations increase less rapidly in heavy soils as illustrated by slower resurgence in silty loam following oxamyl treatments compared with sandy loam (Table 14). These data agree with greenhouse studies of _P. penetrans_ population dynamics in a range of soil types and *P. penetrans* distributions across soil textural gradients within peppermint fields. Additional research is needed to determine if nematicide applications are cost effective in *P. penetrans* infested peppermint in fine textured soils.

Declining peppermint stands in sandy soils with high *P. penetrans* densities can be treated cost effectively with early spring applications of carbamate nematicides. In 1979, single 5.5 kg a.i./ha oxamyl and carbofuran treatments produced projected returns of $1500/ha and $1423/ha, respectively, while untreated plots had an estimated return of $444/ha. Two years later, these 1979 treatments still produced estimated returns of $1027/ha and $1111/ha, respectively. Similarly, 1981 oxamyl treatment of 0.6, 1.1, 2.2, and 4.4 kg a.i./ha produced projected oil values of $1626, $1848, $1914 and $2029, respectively, while untreated plots oil value was estimated to be $816/ha at the Marion County site. Since these data were obtained in different seasons and from two stands with different management histories, direct comparrison of data is inappropiate. However, single applications of 1.1 to 5.5 kg a.i./ha oxamyl produced yields equal to those from plot where higher rates and multiple treatments were applied. *P. penetrans* management stategies in peppermint must consider the interaction between crop vigor, soil type, and nematode population density. Nematicide applications will be cost effective on stands of moderate or low vigor, but not on vigorous nor severly damaged stands. Once a declining stand is rejuvenated, nematicide treatments in subsequent years should be applied when nematode population resurgence is accompanied by declining stand vigor.

DEVELOPMENT OF ECONOMIC THRESHOLDS AND MANAGEMENT GUIDELINES FOR CONTROL OF *PRATYLENCHUS PENETRANS* DAMAGE IN PEPPERMINT

Preface

Historically pest control recommendations have been based on spray schedules or subjective evaluation by trained persons. Calander spray schedules, which are not based on pest and host phenologies, pest population density, or changing pest damage potential over a range of environmental conditions are still widely used. However, pest management programs in which population densities are monitored to maximize treatment efficacy and profit are presently being developed for many crops. Field and greenhouse studies conducted with *P. penetrans* on peppermint have provided data required for developing control recommendations based on nematode density, edaphic parameters, stand vigor, and nematicide efficacy. These aspects of current research have been amalgomated to produce management guidelines for aiding peppermint growers in reducing losses from *P. penetrans*.

Pest management decisions should be based on economic injury levels and economic thresholds derived from sampling pest populations and quantifying the relationship between pest density and crop value. Headley (64) defined economic injury level as the pest " population that produces incremental damage equal to the cost of preventing the damage". When control measures are applied at the economic injury level, a lag period between treatment and pest supression can result in unnecessary crop loss as population density briefly exceeds the economic injury level. However, this loss can be prevented if control measures are applied at the economic threshold level, which is "the density at which control measures should be applied to prevent an increasing pest population from reaching the economic injury level" (130).

Ferris (45) has applied these concepts in his discussion of the derivation, requirements and theoretical considerations in developing economic thresholds for nematode diseases of plants. He defined the economic threshold as the point which maximized the difference between a nematode damage function (where dollar crop value was plotted against nematode population density) and a control function (where dollars expended for nematode control were plotted against nematode density which remained after control measures were applied). Therefore, two components, a control cost function and a damage function, are required for estimating an economic threshold. Ferris' derivation is illustrated graphically in figure 21. The economic threshold is the nematode population density determined by intersection of derivatives of control-cost and nematode damage functions.

Cost analysis of P. penetrans damage in peppermint

Nematode damage functions have been developed from greenhouse (123), microplot (7) and field studies (58). Experiments conducted under a narrow set of controlled conditions in microplots or

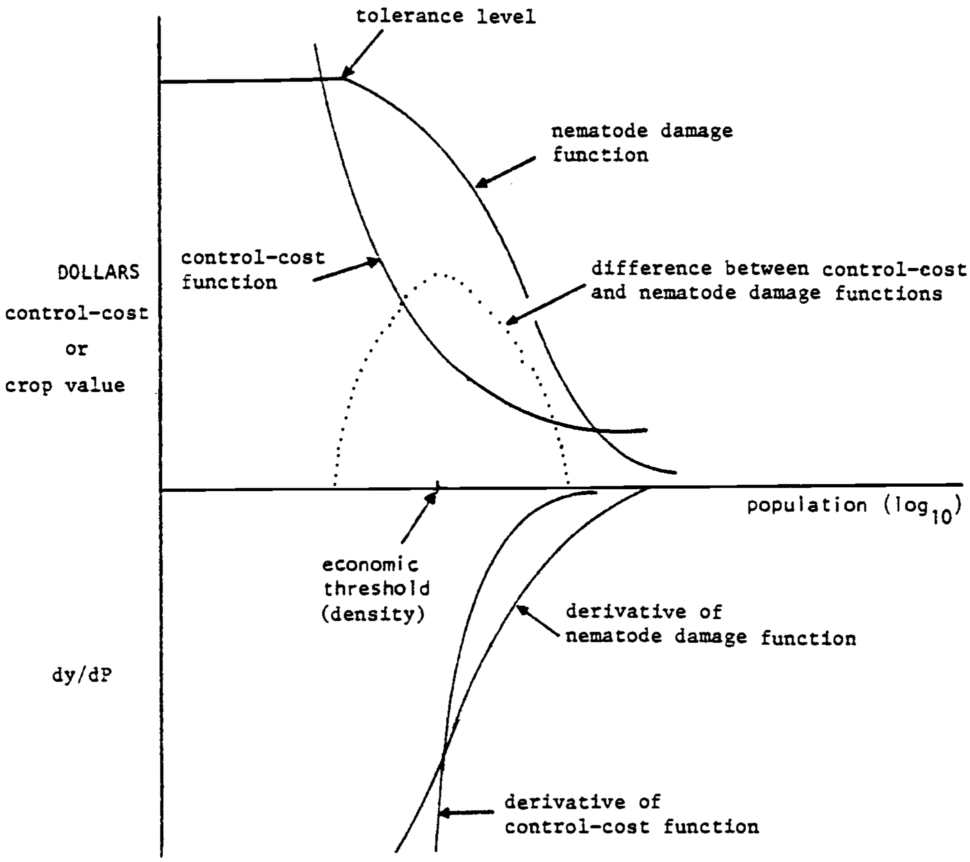


Figure 21. Determination of the economic threshold by maximizing the difference between control-cost function and nematode damage function or by the intersection of the derivatives of the two functions (after Ferris (45)).

greenhouse pots have produced data which statistically fit damage functions more closely than data from field experiments. However, field generated yield loss models may be of more immediate use to growers because they integrated variability found under actual production conditions. The damage function developed in this *P. penetrans* -peppermint study should be well adapted for Willamette Valley peppermint fields.

Two-year field studies demonstrated that post-harvest *P. penetrans* root densities provided an excellent diagnostic criterion for making spring treatment recommendations. Relationships between yield and nematode density were not significantly different between locations or seasons. Figure 22 illustrates relationship between estimated dollar crop value over variation in *P. penetrans* densities collected at three locations during the two-year study. These estimations are based on $22.00 per kg oil and a conversion factor where kg oil/ha = kg green hay/ha x .22 (for dry hay conversion) x .0125 (for oil content) (Dr. C. E. Horner, Department of Botany and Plant Pathology, Oregon State University, personal communiction). Utilizing these figures, the mean 100 percent yield level in two years at three locations was estimated at $ 1968/ha based on mean maximum yields of 88 and 91 kg oil/ha in 1979 and 1980, respectively. Tolerance level or damage threshold, the *P. penetrans* density required to produce measurable yield loss, was estimated to be 1450 *P. penetrans* per gram dry root weight for the two years. Based on this regression model (figure 22), a predicted $ 730/ha yield loss will result from a ten fold increase in nematode density above the

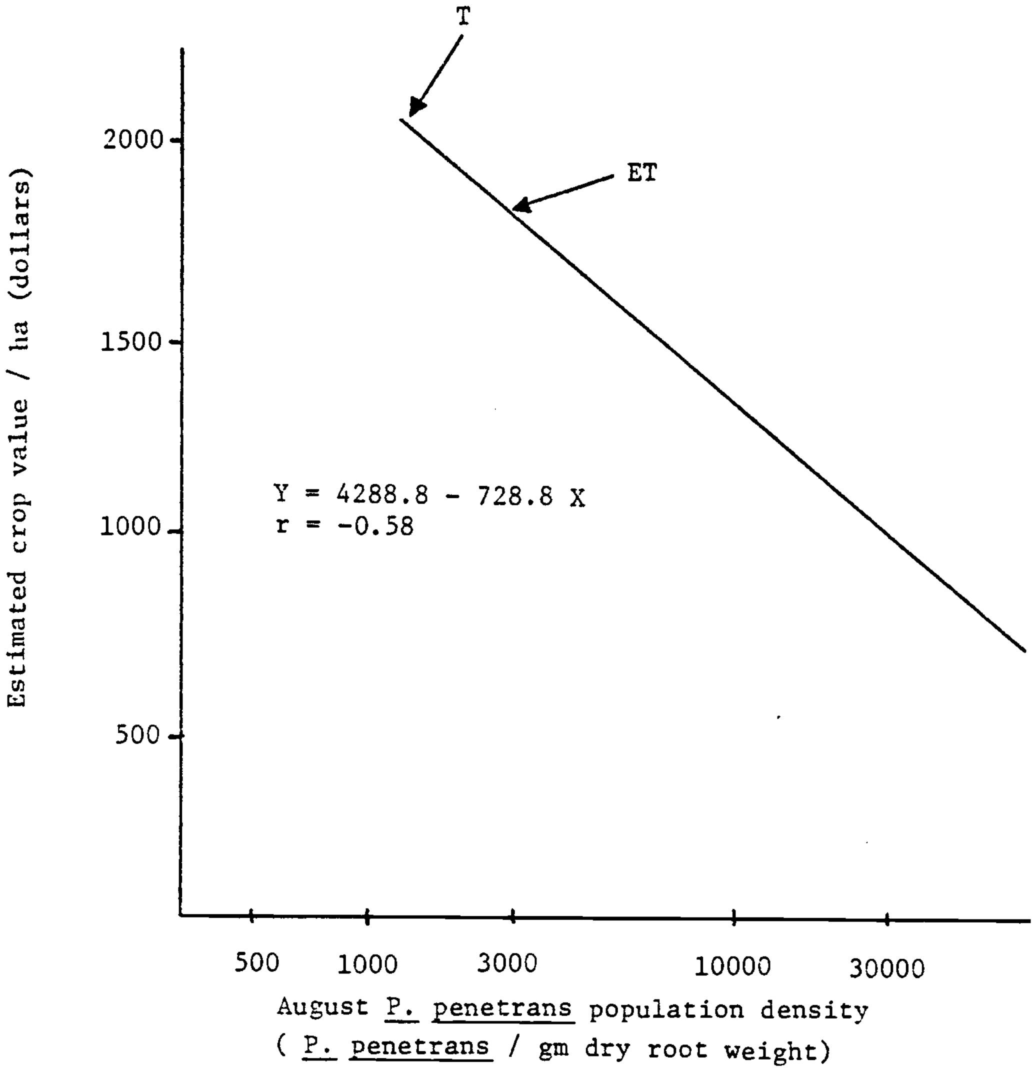


Figure 22. Relation between August *Pratylenchus penetrans* density and estimated crop value in three Willamette Valley Todd Mitcham peppermint fields during 1979 and 1980.

T = estimated tolerance level of 1450 *P. penetrans* / gm dry root weight .

ET = estimated economic threshold of 3000 *P. penetrans* / gm dry root weight based on a 2.2 kg a.i. / ha oxamyl treatment tolerance level.

The relationship between yield and *P. penetrans* density is also a function of past plant damage in addition to current nematode densities. Multiple regression models also indicate that evaluation of soil texture was necessary when predicting potential yield loss in the subsequent season. Therefore, nematode density data can be used quantitativly, while edaphic and plant vigor parameters can be used qualitativly in developing recommendations for specific peppermint fields.

Control-cost analysis of nematicide treatments

Ferris (45) proposed a mathematical function which described the relationship between cost of nematode control and final nematode density after control measures were implemented. The cost of removing additional nematodes from a population increases exponentially as nematode density decreases (figure 21). Even if it were possible to eradicate the nematode population, the cost of such treatments would greatly exceed crop value. Ferris' cost function was based on fumigation treatments which are lethal to nematodes. The relationship between non-volatile nematicide treatments and resulting nematode densities are not as straightforward as with fumigation. At field rates, systemic carbamate and organophosphates nematicides are nematistatic and arrest root penetration, feeding, reproduction and development of plant parasitic nematodes (62). As demonstrated with oxamyl rates of 0.6 and 1.1 kg a.i./ha (Tables 13 and 14), plant growth response following nematicide applications may not be accompanied by a nematode population decline, even though higher rates of 2.2 and 4.4 kg a.i./ha did suppress P. penetrans densities. Therefore, development of an economic threshold from oxamyl treatment data can not utilize Ferris' system. Economic threshold must be estimated solely on plant response over a range of oxamyl rates without directly utilizing nematode density change.

Oxamyl field trial results for 1978 to 1981 are compiled in Table 15. As previously discussed, no improved growth responses were obtained with 1978 and 1980 oxamyl treatments. I believe the July application, which occurred two months after maximum root growth and nematode damage, was ineffective in protecting roots during the 1978 season. The 1980 results demonstrated that no significant stand improvement was obtained when stands were extremely poor prior to oxamyl applications. Thus, oxamyl applications should be made when noticeable stand decline is first evident and not after decline has progressed for several seasons. The 1979 and 1981 data illustrate that properly timed oxamyl applications in early April were effective in increasing peppermint yields. In 1979, all three oxamyl rates, 5.5, 11.0 and 16.5 kg a.i./ha , produced significant yield increases. When considering net return based on an oil price of \$22.00/ kg oxamyl cost of \$70.00/kg a.i. and application cost of \$10.00/ha , the 1 x 5.5 kg a.i./ha treatment produced the best cost benefit projection (Table 15). Reduced oxamyl rates of 0.6 to 4.4 kg a.i./ha applied in 1981 trials produced significant yield improvement over non-treated check plots at the Marion County site. However, the 1.1 and 2.2 kg a.i./ha rates maximized the net return with $ 1756 and $1743ha, respectively. Similarly, the 2.2 kg a.i./ha rate produced the greatest net return at the Linn County site. Therefore, I recommend that 1.1 to 2.2 kg a.i./ha oxamyl treatments should be made in early spring five to ten days prior to flaming. These treatments protect the rapidly growing root system during the first three to four weeks of growth and improve plant recovery from flaming stress. Absence of nematode activity during this period appears to be adequate for plants to develop deeply penetrating roots systems which provide the basis for much improved yields.

Management guidelines

Economic thresholds are based on pest population densities and proper sampling procedures. The seasonal population dynamics studies compiled data necessary for developing a _P. penetrans_ sampling program. Post-harvest root samples collected in late summer or early fall provided diagnostic population density data for evaluating the contribution of _P. penetrans_ to yield depression. Soil sampling is also recommended for detection of ectoparasitic nematode populations. Each field should be partitioned into blocks no larger than 2.2 ha from which a minimum of 20 subsamples should be collected and bulked for nematode analysis. Partitioning of fields should be according to plant vigor, where estimated stand yields exceeding 68 kg oil/ha (60

Table 15. Oil and net return from oxamyl field trial during 1978 to 1981.

1978 No plant growth response observed with oxamyl applied at 6.6 6.6 kg a.i. / ha in early July.

1979

treatment	estimated yield (kg oil / ha)	net return * (dollars)
check	20.19	444
1 x 5.5 kg a.i. / ha	68.20	1093
2 x 5.5 kg a.i. / ha	62.20	566
3 x 5.5 kg a.i. / ha	72.57	398

1980 No plant growth response observed with 2.2 and 4.4 kg a.i. / ha oxamyl applied in September, April or June.

1981

Marion County site

Treatment	Estimated yield (kg oil / ha)	Net return * (dollars)
check	37.1	816
0.6 kg a.i./ha	73.9	1576
11 kg a.i./ha	84.0	1756
2.2 kg a.i./ha	87.0	1743
4.4 kg a.i./ha	91.9	1694

Linn County site

Treatment	Estimated yield (kg oil/ha)	Net return * (dollars)
check	62.2	1368
0.6 kg a.i./ha	69.0	1467
1.1 kg a.i./ha	70.4	1457
2.2 kg a.i./ha	80.5	1600
4.4 kg a.i./ha	67.4	1154

* net return = (value of oil / ha) - (cost of oxamyl treatment)

where treatment cost at: 0.6 kg a.i./ha = \$ 51/ha
1.1 kg a.i./ha = \$ 92/ha
2.2 kg a.i./ha = \$ 171/ha
4.4 kg a.i./ha = \$ 329/ha

lb) are rated strong, 47 to 68 kg oil/ha (40 to 60 lb) are rated moderate and estimated yields below 47 kg oil/ha (40 lb) are rated poor. Sampled blocks should also be evaluated for disease and insect problems. Fields should also be partitioned into blocks according to soil texture, with light soils (greater than 55 percent sand, ie. sandy loams, loamy sands, sandy clay loams and sands) sampled separately from areas of heavier soil texture. Since nematode distributions and plant damage follow edaphic gradients, partitioning will minimize the probability of applying nematicide in areas where nematode damage potential is slight. Growers are reluctant to invest money on correct sampling, but the modest cost of sampling 2.2 ha (estimated at $ 23.00; $18.00 for O.S.U laboratory processing of the sample and 0.5 hours at $ 10.00 per hour labor cost for collecting the sample) are minimal in comparison to $ 91 to $ 345 expended in treating 2.2 ha when no nematode problems exist.

Even when provided with adequate sampling data, it was not possible to develop a precise economic threshold from yield loss# and nematicide control aspects of this research. As with other perennial crops, a simple relationship does not exist between current pest population densities and predicted yields. Other factors, such as crop management and edaphic factors, also have a mitigating influence on nematode crop loss relationships. Similarly, systemic nematistatic compounds, such as oxamyl increase plant yield disproportionately to their effect on nematode density. Yields can not be predicted from oxamyl plot population data by using the regression models developed here. Therefore, economic thresholds can not be derived by Ferris' method. However, a series of management guidelines have been developed based on proper sampling methods, current value of peppermint oil ($22.00/ kg or $10.00/lb and current oxamyl treatment costs ($52, $91 and $171/ha for 0.6, 1.1 and 2.2 kg a.i./ha, respectively.

If 1) post-harvest P. penetrans root population densities exceed 3000/gm dry root weight (ca. 350/gm fresh root weight), 2) the soils have high potential for P. penetrans population increase and plant damage (sands, loamy sands, sandy loams and sandy clay loams) and 3) plant vigor at harvest is rated moderate or poor, then oxamyl applications at 1.1 to 2.2 kg a.i./ha are recommended in early April five to ten days before flaming. The higher rate is recommended under conditions where greatest potential yield loss exists, i.e., sandy soils with poor previous season stand vigor and nematode densities greatly above 3000/gm dry root weight. The lower rate is recommended in stands with less potential for yield loss, i.e., moderate previous season stand vigor. High variability and lack of significant yield differences between treated and check plots in silt loam (Linn County) plots made data difficult to interpret. Oxamyl treatments appear to be cost effective under the experimental conditions with high pretreatment P. penetrans densities (ca. 20,000/gm dry root), but further research is necessary before oxamyl recommendations can be developed for fine textured soil and vigorous stands.

Peppermint fields planted in light textured soils infested with P. penetrans should be monitored annually and a 0.6 kg a.i./ha oxamyl treatment should be applied as an annual maintainance program to prevent stand decline. As demonstrated in 1980 nematicide trials, when stand vigor is reduced to extremely low levels, then a single oxamyl application was not adequate to rejuvenate the stand to economically acceptable yield levels. Subsequent oxamyl applications the following year may be necessary to achieve acceptable yields. Therefore, one or more years of oil production may be severely reduced by neglecting P. penetrans control programs. Similarly, a rejuvenated stand will follow the gradual decline pattern which existed before oxamyl treatment, as illustrated by the 1979 nematicide trials where plant growth was evaluated for two additional years after stand treatment. Annual 0.6 to 1.1 kg a.i./ha applictions should maintain vigorous in rejuvenated stands and these treatments should be cost effective.

The preceeding recommendations are based on field studies with one peppermint cultivar, Todd Mitcham. Greenhouse experiments with three peppermint cultivars, Todd, Black, and Murray Mitcham indicated that Murray Mitcham is the least tolerant of P. penetrans injury while Black Mitcham was most tolerant. Therefore, recommendations for Todd Mitcham must be modified for other cultivars. The low tolerance Murray Mitcham planted in sandy soils may need to be treated annually with 2.2 kg a.i./ha oxamyl to prevent complete stand destruction. Conversely, vigorous Black Mitcham stands may succumb to other limiting factors, disease, weed or insect problems, before P. penetrans becomes economically damaging. Thus, Black Mitcham should be planted in fields infested with P. penetrans if the site is free of Verticillum dahliae. Conversely, Murray Mitcham should never be planted in fields infested with *P. penetrans*. Further research is necessary to evaluate these cultivars with five to ten year field experiments on a range of soil types infested with *P. penetrans* in order to develop cultivar selection and oxamyl treatment guidelines for each site type.

Finally, numerous factors outside the scope of the present research may have mitigating effects on recommendations developed here. Since these recommendation are based on plant vigor, any factor which reduce plant vigor will also be reflected in increased susceptibility to *P. penetrans* injury. Recommendations based on fall nematode densities must be modified after severe winters when rhizome survival is reduced. In these cases, oxamyl applications may be justified in areas which treatment decisions were previously borderline cases. Similarly, *P. penetrans* has been demonstrated to interact syngeristically with *Verticillium dahlia* to increase wilt severity and *Verticillium* soil inoculum density. Thus, controlling *P. penetrans* damage may reduce loss to *Verticillium* wilt and be expedient when both organisms are present in a peppermint stand. Although research has not been conducted to investigate insect and *P. penetrans* interactions on perppermint, insect feeding also depresses plant vigor and should reduce plant tolerance to nematode feeding. Finally, spring flaming for *Puccina menthe* in *P. penetrans* damaged stands will further reduce the plant's ability to withstand nematode injury. Thus, flaming intensity should be reduced, fertilization increased, and irrigation schedules modified in nematode damaged areas to increase stand recovery following oxamyl applications.

This research did not produce precise economic thresholds or predictive models. However, the guidelines developed to manage *P. penetrans* damage in Todd Mitcham can and are being utilized by western Oregon peppermint growers. As with any research project , the questions answered are balanced by new questions posed. Evaluation of seasonal decline rates in replicated plots planted with the three peppermint cultivars is needed. Such experiments would need to extend over a period of five to ten years and include a range of soil types and a variety of initial *P. penetrans* densities. Seasonal population dynamics could be observed and damage models based on *P. penetrans* densities could be developed for each season. Annual samples of hay, oil root and rhizome biomass could be utilized to quantify plant vigor each season and these data could be integrated into damage models. Split,split block experimental design with factorial analysis would be adequate to evaluate affects of nematicide treatments for maintaining economically acceptable yields and extending stand productive life. Carefully designed and monitored experiments utilizing the three cultivars could provide data on both the affects of nematicide treatments and nematode damage at very low *P. penetrans* densities, in fine textured soils and in vigorous stands. These conditions which were not satisfactorily evaluated in our research. This experimental approach would improve the precision of management guidelines developed in this current research.

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APPENDICES

Appendix A. Means and ranges of 1979-1980 nematode population, edaphic, and peppermint growth parameters measured Benton, Linn, and Polk County damage studies.

		Linn County		Benton County		Polk County	
		Range	Mean	Range	Mean	Range	Mean
	Yield (kg/10.25 m^2)	8.5-29.7	13.1	5.78-29.7	15.4	5.3-30.2	14.85
	P. penetrans/gm dry wt. root	1415-26720	6807	2411-17299	8669.6	3486-59538	20777
1979	*P. penetrans*/50 cm^3 soil	16-355	71.9	8-174	61.5	4-398	111.2
	% Sand	46-70.5	58.9	52-75.5	64.6	50-72.5	63.0
	% Silt	20-38.4	28.5	18.6-28.4	233	14.1-273	19.7
	Yield (kg/10.0 m^2)	5.0-33.9	15.3	2.0-31.8	12.1	1.8-25.1	11.9
	1979 Vigor (1-3)	1-3	1.89	1-3	1.84	1-3	2.0
	P. penetrans/gm dry wt. root 4/79	4400-33227	15417	909-24157	9015.7	533-51667	18347
	P. penetrans/50 cm^3 soil 4/79	16-260	105.6	2-269	90.6	8-256	78.6
	P. penetrans/gm dry wt. root 8/79	3073-19368	10358	1516-20827	10830	2012-21212	10387
	P. penetrans/50 cm^3 soil 8/79	16-257	80.5	8-269	64.3	30-813	158.0
	Paratylenchus/50 cm^3 soil	0-1349	29.0	0-759	12.4	0-5012	226.5
1980	*Longidorus*/50 cm^3 soil	0-5	1.4	0-6	1.8	0-0	0
	Trichodorus/50 cm^3 soil	0-71	2.2	0-85	3.4	0-21	1.2
	% Sand	46-71	62.0	48-73	63.4	48-70	61.8
	% Silt	20-38	26.8	17-38	24.2	-	-
	Soluble solids (ppm)	50-240	68.5	70-122	76.3	50-150	93.3
	Bulk density (gm/cm^3)	1.35-1.60	1.50	1.25-1.64	1.54	1.46-1.65	1.57
	pH	5.24-5.86	5.56	4.63-5.48	5.22	4.50-5.31	5.00

Appendix B. Benton county multiple regression yield loss models.
1) 1979 2) August 1980 population data 3) April 1980 population data

1

Constant	Root Population+	Soil Population+	Percent Sand+	Percent Silt+	R^2
379.67	-85.09*				.548
600.48	-171.49**	66.77			.7223
337.65	-42.61		-1.94		.6257
-112.84	-6.45			7.85*	.780
256.89		28.66		10.75***	.846
258.75		13.22	-3.68*		.591
599.05	-128.97	67.08		-1.96	.801
110.53	-92.37*	65.62**		-7.75**	.948

2

Constant	Root Population	Soil Population	Previous Season Vigor	Percent Sand	R^2
157.83	-31.00				.159
167.74	-37.24	8.17			.169
186.66	0.62			-2.43	.5370
-12.38			25.84***		.7210
17.58	-7.09		24.79***		.7281
47.26	-2.21		20.93**	-0.66	.7423
51.40	-5.96	4.47	21.08**	-0.62	.7450

3

Constant	Root Population	Soil Population	Previous Season Vigor	Percent Sand	R^2
100.83	-18.73		1		.235
85.42	-13.04	-3.85			.252
117.22	-8.03			-0.91	.307
-0.75			16.26***		.685
15.10	-3.57		15.35**		.691
14.62	-3.70		15.39**	-0.01	.692
59.20	-9.47	10.72	17.34**	-0.68	.758

*, ** and *** indicates the predictor variable is significant at the .05, .01 or .001 levels, respectively , for each predictor variable (+) entering the regression model.

Appendix C. Polk county multiple regression yield loss models.
1) 1979 2) August 1980 population data 3) April 1980 population data

1

Constant	Root Population^{+}	Soil Population^{+}	Percent Sand^{+}	Percent Silt^{+}	R^2
279.53	-56.60^{**}				.669
259.67	-42.02^{*}	-19.69			.708
330.98	-36.99^{*}		-2.10^{*}		.754
93.05	-31.89^{*}			4.29^{*}	.796
-7.69		-23.85		5.21^{*}	.7641
273.32		-27.32	-2.72^{*}		.7033
311.87	-29.41	-13.21	-1.86		.771
95.06	-24.69	-12.29		3.96^{*}	.810

2

Constant	Root Population	Soil Population	Previous Season Vigor	Percent Sand	R^2
335.22	-72.42^{***}				.576
326.76	-76.56^{***}	13.24			.601
425.68	-58.34^{***}			-2.38	.707
-7.28			25.81^{***}		.575
189.59	-43.93^{*}		15.60^{*}		.696
309.26	-46.17^{**}		9.23	-1.58	.735
300.84	-49.59^{**}	8.64	9.16	-1.49	.745

3

Constant	Root Population	Soil Population	Previous Season Vigor	Percent Sand	R^2
195.09	-37.16^{**}				.449
182.75	-40.04^{**}	11.20			.468
206.76	-35.99^{*}			-0.27	.450
1.13			19.88		.445
110.05	-22.07		11.57		.526
12.88	-23.15		15.82	1.50	.548
17.82	-24.66	3.65	15.10	1.42	.550

*, ** and *** indicates the predictor variable is significant at the .05, .01 and .001 levels, respectively , for each predictor variable entering (+) the regression model.

Appendix D. Correlation matrices of monthly root and soil *Pratylenchus penetrans* populations from August 1979 to August 1980.

1) Cluster 1 sites, soil populations
2) Cluster 1 sites, root populations
3) Cluster 2 sites, soil populations
4) Cluster 2 sites, root populations
5) Cluster 3 sites, soil populations
6) Cluster 3 sites, root populations

D1	8/79	10/79	11/79	12/79	1/80	2/80	3/80	4/80	5/80	6/80	7/80	8/80
8/79		.15	.48	.53	.17	.22	.22	.37	.37	.42	-.09	.18
10/79			.47	.15	.32	.40	.50	.18	.31	.34	.30	.04
11/79				.44	.09	.20	-.11	.17	.00	.19	.01	-.03
12/79					.19	.14	.58	.16	-.05	.00	-.07	.26
1/80						.36	.25	.52	.18	.14	-.16	-.18
2/80							.45	.53	.28	.29	.23	.19
3/80								.00	.39	.26	.20	.02
4/80									.01	.18	-.35	-.14
5/80										.74	.15	.26
6/80											-.09	.36
7/80												.07
8/80												

D2	8/79	10/79	11/79	12/79	1/80	2/80	3/80	4/80	5/80	6/80	7/80	8/80
8/79		.65	.56	.47	.49	.41	.20	.37	.74	.49	-.28	.00
10/79			.57	.60	.42	.66	.42	.59	.70	.23	-.14	-.39
11/79				.32	.16	.47	.64	.53	.39	.40	.35	-.10
12/79					.58	.38	.50	.16	.28	.11	.36	-.25
1/80						.54	.20	.34	.20	-.14	.21	-.17
2/80							.64	.67	.46	.09	-.15	-.31
3/80								.58	.01	-.04	-.09	-.25
4/80									.35	-.04	.18	-.14
5/80										.55	-.17	-.11
6/80											.23	.22
7/80												.31
8/80												

D3	8/79	10/79	11/79	12/79	1/80	2/80	3/80	4/80	5/80	6/80	7/80	8/80
8/79		.87	.60	.86	.77	.12	.37	.58	.31	.01	.48	.68
10/79			.77	.64	.70	.26	.48	.60	.44	-.19	.63	.72
11/79				.40	.65	.47	.63	.46	.55	-.05	.42	.77
12/79					.76	-.09	.23	.50	.32	-.10	.39	.64
1/80						.26	.48	.58	.21	-.38	.13	.84
2/80							.27	.03	-.14	-.15	-.12	.37
3/80								.74	.61	.11	.22	.56
4/80									.53	-.18	.23	.56
5/80										.31	.62	.48
6/80											.21	-.25
7/80												.17
8/80												

D4	8/79	10/79	11/79	12/79	1/80	2/80	3/80	4/80	5/80	6/80	7/80	8/80
8/79		.65	.61	.84	.86	.76	.76	.60	.66	.41	.51	.25
10/79			.84	.85	.86	.92	.68	.74	.38	.26	.28	.18
11/79				.59	.76	.84	.62	.74	.44	.05	.39	.44
12/79					.91	.86	.72	.68	.50	.45	.33	.08
1/80						.91	.61	.79	.66	.46	.33	.36
2/80							.72	.79	.62	.49	.49	.29
3/80								.37	.49	.19	.69	.12
4/80									.29	.22	.11	.06
5/80										.62	.59	.65
6/80											.37	.09
7/80												.36
8/80												

D5	8/79	10/79	11/79	12/79	1/80	2/80	3/80	4/80	5/80	6/80	7/80	8/80
8/79		.54	.33	.56	.10	.04	.72	.53	.04	.33	.32	.58
10/79			.25	.41	.60	.16	.47	.43	.05	.16	.39	.54
11/79				.88	.21	-.17	-.01	.43	.47	.60	.62	.26
12/79					.43	-.10	.39	.74	.55	.85	.32	.68
1/80						.45	.43	.69	.72	.51	-.11	.60
2/80							-.06	.48	.46	-.20	.09	.06
3/80								.51	.20	.53	-.31	.74
4/80									.70	.71	.00	.83
5/80										.63	-.03	.35
6/80											-.21	-.77
7/80												-.25
8/80												

D6	8/79	10/79	11/79	12/79	1/80	2/80	3/80	4/80	5/80	6/80	7/80	8/80
8/79		.54	.92	.50	.49	.40	.86	.92	.88	.91	.80	.49
10/79			.72	.39	.78	.46	.89	.32	.35	.55	.22	-.20
11/79				.34	.49	.61	.90	.77	.77	.83	.64	.46
12/79					.83	.21	.56	.64	.70	.66	.74	-.34
1/80						.29	.77	.43	.50	.56	.47	-.48
2/80							.45	.39	.51	.41	.40	.29
3/80								.70	.68	.84	.57	.10
4/80									.95	.94	.92	.36
5/80										.88	.98	.36
6/80											.81	.32
7/80												.29
8/80												

Appendix E. Particle distribution* of experimental soils

	Percent particle size		
Particle distribution (mm)	Newberg loam	Camas gravelly sandy loam	Cloquato silty loam
% 2>mm	.03	.03	5.05
2 - 1	0.1	0.1	0.1
1 - .5	0.7	1.0	0.2
.5 - .25	5.1	8.9	0.1
.25 - .1	29.3	43.4	2.2
.1 - .05	18.7	17.3	7.7
Total sand	59.9	70.7	10.6
0.05 - 0.02	11.9	7.2	15.6
0.02 - 0.002	20.2	13.4	47.3
Total silt	32.1	20.6	62.9
Total clay	14.0	8.7	26.5

* Analysis by pippet method

Appendix F. Nematicide trade names and manufacturers

oxamyl

Trade name:	Vydate
Manufacturer:	I. E. duPont de Nemours & Co. Biochemical Department Wilmington, Delaware

sulfone

Trade name:	Standak
Manufacturer:	Union Carbide Agricultural Products Co. Research Triangle Park, N.C. 27709

carbofuran

Trade name:	Furadan
Manufacturer:	FMC Corporation Agricultural Chaemical Division Middleport, N.Y. 14105