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Feature, Function, and Nature of <u>Pratylenchus</u> <u>penetrans</u> and <u>Verticillium</u> dahliae Interactions Associated with <u>Solanum</u> <u>tuberosum</u>

presented by

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has been accepted towards fulfillment of the requirements for

Ph.D. degree in Entomology

reg Major professor

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FEATURE, FUNCTION, AND NATURE OF PRATYLENCHUS PENETRANS AND VERTICILLIUM DAHLIAE INTERACTIONS ASSOCIATED WITH SOLANUM TUBEROSUM

by

Jianjun Chen

A DISSERTATION

Submitted to Michigan State University in partial fulfillment of the requirements for the degree of

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Department of Entomology

ABSTRACT

FEATURE, FUNCTION, AND NATURE OF PRATYLENCHUS PENETRANS AND VERTICILLIUM DAHLIAE INTERACTIONS SSOCIATED WITH SOLANUM TUBEROSUM

Ву

Jianjun Chen

Potato (Solanum tuberosum) is one of the most important food crops in the world. Potato Early-Die (PED) is the most important disease currently limiting potato production in North America. Penetrans/Dahliae Disease Complex (PDDC), a component of PED, was caused by an interaction between the penetrans root-lesion nematode, Pratylenchus penetrans, and the soil-borne fungus, Verticillium dahliae. PDDC was growth studied under chamber, greenhouse, and field ecosystem environments to add new insights about the growth and development of the below ground system components of S. tuberosum associated with PDDC, and the individual and concomitant effect of P. penetrans and V. dahliae interactions on the below-ground system of S. tuberosum. The study was assisted by use of the computer simulation, agroecosystem experimentation, and manipulation of the plant below-ground architecture. Data and results were quantitatively and graphically analyzed using classical statistics and geostatistics.

The below-ground system of S. tuberosum was divided into basal roots, nodal roots, stolon roots, tuber roots, stolons, tubers, below-ground stems, and a seed piece. A computer model written in C++ Language was developed to simulate the growth and development of the below-ground system components under the PFE (Pathogen-Free Environment) or PIE (Pathogen-Impacted Environment). A maximum of 28.7% tuber weight loss (P = 0.05) was found in S. tuberosum when the stolon system was exposed to P. penetrans. The impact of P. penetrans and V. dahliae on the stolon system of S. tuberosum was about equal. P. penetrans was equally pathogenic on the basal-nodal root system and stolon system of S. tuberosum. V. dahliae was much more pathogenic on the basal-nodal root system than the stolon system of S. tuberosum.

The synergistic, additive, and antagonistic joint influence of *P. penetrans* and *V. dahliae* interactions associated with an *S. tuberosum* below-ground system occurred once, nine times, and twice, respectively. A biological twoon-one interaction concept was introduced. Kriging from 100 samples and a spherical semivariogram model ($r^2 = 0.902$) provided means of interpolating 676 points not physically sampled. The three-dimensional soilborne-organism distribution imaging was computer stereopercepted. Copyright by JIANJUN CHEN

DEDICATION

To my two precious sons Larry and Allen

With love, respect, and great pride

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1.0 Introduction

Potato (Solanum tuberosum) is one of the ten most important food crops on a world-wide basis. Its volume of production ranks fourth in the world (Horton et al., 1985). Premature vine death and declining vields are a limiting factor in potato production in Michigan, Wisconsin, Ohio, Idaho, and the Red River Valley (Rowe, et al., 1987). Similar symptoms are observed in the Pacific Northwest (Rowe, 1983). In the existing literature, this syndrome is frequently called Potato Early-Die (PED) (Riedel, et al., 1985). Surveys ranked PED as the most important disease of commercial potato crops in North America (National Potato Research Proposal, 1987; Slack, 1991). In this dissertation, one component of PED will be studied. It will be referred to as the Penetrans/Dahliae Disease Complex¹ (PDDC), caused by an interaction between the root-lesion nematode, Pratylenchus penetrans functioning as a predisposition agent², and the soil-borne fungus, Verticillium dahliae functioning as a secondary pathogen³.

^{1.} Disease complex: An infectious disease (detrimental physiological process), caused by the continued interaction of a predisposition agent and a secondary pathogen. 2. Predisposition agent: A living organism which alters the physiology of a host which is not usually susceptible to a specific pathogen at specific population densities. The predisposition agent renders the host susceptible to the pathogen. 3. Secondary pathogen: A biological causal agent which is not normally a primary pathogen⁴ of a specific host, but can cause an infectious disease after the host has been properly altered by a suitable predisposition agent. 4. Primary pathogen: An organism that can cause an infectious disease. (Bird, MSU ENT 870 Syllabus).

There is extensive literature on PED and various aspects of PDDC (Bird, 1990; Riedel et al., 1985; Rowe et al., 1987; etc.); however, there is still a distinct need for additional research on this topic. The research for this dissertation employs science and a philosophy of reductionism, interaction, and synthesis. The below-ground system of S. tuberosum is defined in this study as a multi-component system consisting of basal roots, nodal roots, stolon roots, tuber roots, stolons, tubers, below ground stems, and a seed piece. The goal of this research was to add new insights about the understanding of the PDDC system, the multiple below-ground system components of S. tuberosum, and the individual and concomitant effect of P. penetrans and V. dahliae interactions on the below-ground system of S. tuberosum. System science, interaction biology, and landscape ecology were used to provide a framework for the growth chamber, greenhouse and field studies. Both classical statistics and geostatistics were applied to quantitatively analyze the research results. The computer simulation, agroecosystem experimentation, and manipulation of the plant below-ground architecture added valuable technologies for the research. A proposed biological interaction concept and associated systems were discussed in relation to their potential value in helping to understand biological systems. The results should lead to a significantly

enhanced understanding of the feature, function, and nature of *P. penetrans* and *V. dahliae* interactions associated with the below-ground system of *S. tuberosum*.

The dissertation consists of eight chapters: Introduction; Goal, Objectives, and Research Approach; Literature Review; Experimentation; General Discussion; Summary and Conclusion; Potato Computer Simulation Model Appendix, and Bibliography.

2.0 Goal, Objectives, and Research Approach

2.1 Statement of the Problem

Tuber formation in *S. tuberosum* is considered to be the summation of the stolon development and tuberization at the stolon tip (Booth, 1963). To understand the impact of PDDC on tuber production, it is necessary to have a comprehensive understanding of its impact on the stolon system, the ontogeny of the stolon system, and other aspects of the below-ground components of this plant species.

The below-ground architecture of *S. tuberosum* includes a shoot system and a root system. The below-ground shoot system contains the seed piece, below-ground stems, stolons, and tubers. The root system consists of basal roots, nodal roots, stolon roots, and tuber roots (Kratzke and Palta, 1985). In evaluating the impact of PDDC on *S. tuberosum*, it is necessary to account for the specific type, time and sequence of roots affected.

PDDC is caused by interactions of two pathogens, *P.* penetrans and *V. dahliae*. To evaluate the impact of PDDC on *S. tuberosum*, it is also necessary to have an understanding of the potential of the individual and concomitant effects of these organisms on tuber production, and the nature of the concomitant effect of *P. penetrans* and *V. dahliae*

interactions.

Pratylenchus penetrans and V. dahliae interactions occur in an agroecosystem. From a practical perspective, it is necessary to evaluate the impact of PDDC on S. tuberosum with an understanding of its linear, spatial, and space features in an agroecosystem.

2.2 Science and Philosophy

2.2.1 Reductionism

The most successful and influential way of thinking ever introduced into the field of science is often named after Isaac Newton. According to Newtonian thinking, if an entity or phenomenon is to be understood, it needs to be reduced into its most basic elements or building blocks, which are simpler, more easily understandable, and often measurable (Schwartzman, 1984). Once these elements and their properties are known, an understanding of the whole can be achieved by recombining the elements.

2.2.2 Interactions

In the Newtonian mode of thinking, the elements are viewed as connected and interacting with each another through causality and objective observation (Colapinto, 1979). The search for the truth about complex phenomena should not only follow objectivity of observation, but also be dependent of the way they were observed.

Pratylenchus penetrans and V. dahliae interactions associated with an S. tuberosum ecosystem is conceptually introduced in this dissertation research in Figure 2.1. The nature of the proposed system is illustrated as a triangular interaction among P. penetrans, V. dahliae and S. tuberosum, coupled with the other 19 triangle interactions, and numerous other linear and polygonal interactions. Biological interactions in an agroecosystem are complex and extensive studies are needed.

2.2.3 Synthesis

As more and more fields of scientific inquiry encountered issues of increasing complexity, understanding the whole by means of a synthesis of the parts became increasingly difficult (Maturana, 1975). Dealing with more complicated phenomena in nature, scientists attach importance to the method of synthesis in an effort to better understand the whole as science proceeds into the 21st century. It is very significant to add new insights to the means of a synthesis of the parts to understand the whole for the Newtonian mode of science. For the science of General Biology, studies of the two-on-one interaction becomes significantly important.

2.3 Objectives

The main objective of this research was to identify and evaluate basic elements of the target bio-systems, the below



Figure 2.1. Pratylenchus penetrans and Verticillium dahliae interactions associated with a Solanum tuberosum ecosystem.

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ground system of *S. tuberosum* and the Penetrans/Dahliae Disease Complex system, study features and function of *P. penetrans* and *V. dahliae* interactions associated with *S. tuberosum* in an agroecosystem, and explore the nature of the concomitant effect of *P. penetrans* and *V. dahliae* interactions on the below ground system of *S. tuberosum*.

Research objectives were:

1. Determine the impact of PDDC on root and stolon systems through a split root-stolon culture system, a manipulation of the below ground system architecture of S. tuberosum.

2. Determine the impact of PDDC on specific below-ground system components of *S. tuberosum* by individually assessing the growth and development of basal roots, nodal roots, stolon roots, tuber roots, stolon, tuber, and below-ground stem; and simulating the multi-component below-ground system through the use of a computer model.

3. Determine linear, spatial, and space features of *P*. *penetrans* and *V*. *dahliae* interactions associated with *S*. *tuberosum* ecosystems through classical statistics, geostatistics, and multi-dimensional approaches, including conditional simulation of the interaction components of the system.

4. Determine individual and concomitant effect of P.

penetrans and V. dahliae on S. tuberosum tuber production through individual and concomitant infection of P. penetrans and V. dahliae; and explore nature of P. penetrans and V. dahliae interactions associated with S. tuberosum.

2.4 Biological Systems

2.4.1 Penetrans/Dahliae Disease Complex System

PDDC is caused by an interaction between the penetrans root-lesion nematode, P. penetrans functioning as а predisposition agent, and the soil-borne fungus, V. dahliae functioning as a secondary pathogen (Bird, ENT 870 Syllabus). The nature of injury caused by the lesion nematodes makes roots mechanically and biochemically suitable for invasion and development by the wilt fungus. It is found that infection of S. tuberosum by P. penetrans increased symptom expression and reduced wilt-fungus incubation period (Burpee and Bloom, 1978). Pratylenchus penetrans and V. dahliae interactions are documented through experiments that the PED disease complex has been successfully controlled by soil fumigation or application of aldicarb to control P. penetrans (Mai et al., 1981).

2.4.2 Below Ground System of Solanum tuberosum

The plant architecture of *S. tuberosum* is composed of an above-ground shoot system, a below-ground shoot system, and a root system (Figure 2.2). The above-ground shoot system

contains flowers, leaves, and above-ground stems. The below ground-shoot system contains the seed piece, below-ground stems, stolons, and tubers. The root system consists of basal roots, nodal roots, stolon roots, and tuber roots. A total of eight components in the below-ground shoot system and root system constitute the below-ground system of *S. tuberosum* (Figure 2.3).

Basal roots, nodal roots, stolon roots, and tuber roots are four types of adventitious functional roots in an *S. tuberosum* plant (Kratzke and Palta, 1985). The anatomy of the adventitious roots from tubers and stolons is similar to roots originating from other parts of the plant (Struchmeyer and Palta, 1986). Xylem connections exist from all four root types to the tuber as well as to the above ground part of the plant. Studies of the form and function of *S. tuberosum* root systems are few (Allen and Scott, 1992).

2.4.3 Split Root-Stolon System Architecture of Solanum tuberosum

Although relatively little is published about the architecture of the below ground stem and associated stolon and root configurations of *S. tuberosum*, this species appears to be ideally suited for research designed to evaluate the edaphic system architecture. Studies using split-root technique (Kotcon and Rouse, 1984) have demonstrated the


Figure 2.2. System levels of the plant architecture of *Solanum tuberosum*: with special reference to the below-ground system.



Figure 2.3. Conceptual illustration of the below-ground architecture of *Solanum tuberosum*.

synergistic interactions in peppermint (Faulkner, et al., 1970) and potato even when fungal and nematode pathogens were physically separated on halves of the same root system (Powelson and Rowe, 1993). The procedures have been successful in providing insight into the nature of disease complexes. The split root-stolon system architecture used in this research is a modification of the split root technique.

2.4.4 Agroecosystem

It is well known that the lack of consideration of the relationships between the root cause of a problem and the larger context of the overall system in which the problem exists can be misleading (Brown et al, 1976). An agroecosystem is viewed in this study as a diverse ecosystem where its spatial dynamics are captured in a grid-cell area of agricultural land. The grid approach represents the horizontal architecture of the ecosystem in two dimensions by using a grid of squares distributed over the area. Use of the gridsystem facilitates comparison of the results with theoretical models of the crop and pest system; provides a suitable method for for model mapping systems that can be used parameterization, verification, and validation; permits application of statistical methods; and allows modeling of agroecosystem patterns, distances between patches, and biological movements in a straightforward and realistic fashion.

2.5 Modeling and Assessment Technologies

2.5.1 System Science

System science is a discipline providing a framework for the study of interactions among related entities (Bird et al., 1985). For the term "system science" Sandquist (1985) designated "the total collection of knowledge, methods, and skills available for the identification, abstraction, modeling, quantification, analysis, synthesis, evaluation, and control of rational systems and their behavior." The major emphasis in system science is on the quantitative modeling and analysis of measurable systems. The causality principle should be translated into a quantitative mathematical model for systems. Use of system approaches, which have been successful dealing with complex military operations and space exploration development, is imperative and of significant value in scientific studies. Patil (1979) pointed out that for systems assessment activities to be meaningful and defensible, they need: (i) a conceptual and philosophical basis, (ii) a theoretical framework, (iii) methodological support, (iv) a technological toolbox, and (v) administrative management. It is necessary to discuss and develop a constructive interface between quantifiable problems in ecology and relevant quantitative methods.

2.5.2 Quantification

When you cannot measure it, when you cannot express it in numbers, your knowledge is of a meager and unsatisfactory kind: it may be the beginning of knowledge, but you have scarcely, in your thoughts, advanced to the stage of science.

- Quoted from Lord Kelvin

The rigorous formulation of a quantitative scientific concept requires, and in a sense creates, empirically measurable quantities. Conversely, the scientific validity of the concept is totally dependent upon the measured values of those quantities (Cairns, et al., 1979). This is a capsule version of the feedback process known as the "scientific method." The first procedure may be labeled as "modeling" and the second as "curve-fitting." These two processes must converge - more quantification must be used in concept validation and more concepts must be incorporated into the methodology of quantification. There are interdisciplinary needs of statistics and ecology at advanced instructional level.

2.5.3 Dimensionality

A physical and mathematical continuum of n dimensions is a set of n coordinates, that is, a set of n quantities capable of varying independently from one another and of assuming all the real values which satisfy certain inequalities (Poincare, 1963). The number of dimensions can be increased if other

senses are introduced into the combination. Space is a threedimensional continuum about which we would have a clear intuition. A space coupled with time is a four-dimensional continuum.

2.5.4 Simulation

Simulation modeling of agroecosystems, when coupled with appropriate data sources, have a great potential for bringing agricultural research and development into the age of information technology (Ritchie, 1986). Conditional simulation produces a simulation that generate the set of values, one each for a set of spatially dependent random variables, with the estimate coincides with the sample value at the sample locations (Warrick et al., 1986).

2.5.5 Computer Programming

FORTRAN was one of the first and most common machineindependent high-level computer languages. FORTRAN stands for FORmula TRANslation. Developed originally in 1954, this language was first designed to provide easy solutions to algebraic-type problems (Nickerson, 1975). Its popularity and ease of use has resulted in its being applied to a wide variety of computer problem-solving situations. In the early 1970s, Dennis Ritchie at Bell Labs designed a language he called C (Adams, 1995). With the availability of inexpensive C compilers for microcomputers, C has become the language in which most microcomputer applications are written. In the late 1970s, a new approach to programming called Objected-Oriented Programming (OOP) was becoming increasingly popular. Bjarne Stroustrup, another researcher at Bell Labs, added OOP features and new capabilities to C that eliminated many of the difficulties C posed for beginning programmers (Adams, 1995). The resulting language was first called C with Classes, but by 1983, more improvements had been added and the language was renamed C++.

2.5.6 MSTAT-C Classical Statistics Program

Classical statistics assumes that 1) sampling unit mean is an expected value everywhere in the unit; 2) variability about the mean is random; and 3) estimation error is expressed by within-unit variance. MSTAT-C, written in the C Language, is an integrated microcomputer program which can be used to assist scientists in most of the steps involved in agricultural and biological research. MSTAT can be used to generate experimental designs, manage and transform data and analyze experimental results from both a biological and economical perspective.

2.5.7 GS* Geostatistics Software

Geostatistics assumes that the distribution of the object of concern is spatially dependent. GS⁺ is designed to provide researchers in the biological, environmental, and agronomic sciences with the statistical tools needed to identify and quantify spatial relationships in geo-referenced data, and to use this information as desired to create optimal maps or isopleths of the variate examined. GS⁺ uses kriging to derive interpolated map values and associated variance estimates.

2.6 Cyberspace Advance

A comprehensive investigation guided by information highway and CD-ROM Databases can be used to examine all existing scientific information related to a research subject. The databases and networking are helpful at finding references to journal articles, books, governmental documents, research reports, newspaper articles, and other publications in particular subject areas. Some of the databases located in the Michigan State University Libraries contain the full-text of an article, and others the abstracts. They include 1) AGRICOLA: worldwide coverage of agriculture publications from 1984 to present; 2) AGRIS: all aspects of agriculture publications from 1975 to present; 3) CRIS/ICAR: current U.S., Canadian, and state-supported research in agriculture and related fields; and 4) Cambridge Lifescience: indexes over journals in biology and life sciences.

3.0 Literature Review

3.1 Pratylenchus penetrans

The penetrans root-lesion nematode (*P. penetrans*) is an important migratory endoparasite of roots, stolons, and tubers of *S. tuberosum* (Dickerson, *et al.*, 1964). All stages of *P. penetrans* are vermiform and migratory. The life cycle can be completed within 28-65 days. This nematode is commonly found in soils cropped to potato in the northeastern U.S.A. and Canada. At least 15 species of *Pratylenchus* spp. have been reported to be associated with potato culture (Brodie, 1984). *Pratylenchus penetrans* (Cobb, 1917) Filipjev & Schuurmans-Stekhoven, 1941, is the most highly pathogenic of these species to *S. tuberosum* (Brodie, 1984).

In 1938, Hastings and Bosher reported that *P. penetrans* retarded the growth of potato plants. The pathogenicity of this host-parasite relationship was confirmed by Oostenbrink (1954, 1956) and Dickerson et al. (1965). A linear relationship between initial population density of *P. penetrans* and tuber yield was found by Oosternbrink (1966), and was expanded by Olthof et al. (1973) and Olthof and Potter (1973). The pathogenic threshold of *P. penetrans* was estimated at 1.0 per gram of soil (Steinhorst, 1950). A range of 0.4 to **1.0** *P. penetrans* per gram in sandy soil and 0.7 to 2.0 per

gram soil in loam and organic soils was identified by **Oostenbrink** in 1966. A pathogenic threshold of 2.0 per gram of soil was established by Olthof and Potter in 1973. The effect of high populations of lesion nematode on plant growth and development sometimes resembles the above-ground symptoms of typical plant stress. Pratylenchus penetrans is capable of causing an overall growth inhibition of ca. 50% and a tuber yield inhibition of 10-50% under high population. Superior was the most susceptible of five cultivars to P. penetrans, and Russet Burbank was the most tolerant cultivar tested in an investigation of the ecology and economics of P. penetrans associated with potato production in Michigan (Bernard, 1973, and Bernard & Laughlin, 1976). The early potato nematology research in Michigan was summarized in 1981 (Bird, 1981). It is likely that some of these research projects did not adequately exclude Verticillium fungi from the research environment.

Penetration and movement of *P. penetrans* through the root tissues is both inter and intracellular. *Pratylenchus penetrans* colonizes, feeds, and reproduces in root cortex and other parenchymatous tissue. When necrosis becomes severe, this nematode tends to leave infected tissue in search of nonnecrotic roots. Entry may occur on other unsuberized surfaces of roots, rhizomes, and tubers (Hooker, 1981). Four

of the 15 Pratylenchus spp., including P. penetrans, have been known to attack both roots and tubers (Brodie, 1984). Stolon tissue of S. tuberosum can be infected with P. penetrans as early as 28 days after planting and can remain infected throughout the entire growing season. Nematodes inside roots usually excrete substances causing necrosis of plant cells. Lesions are not of the magnitude of those observed in the field where other organisms are present although lesion nematodes alone are fully capable of destroying plant cells and causing lesions (Brodie, 1984). Lesion formation and root death usually occur ahead of the invading nematodes. Faulkner et al. (1970) implied that the root-lesion nematodes not only provided a court for entry, but also modified the physiology of the plant to make host suitable for increasing the impact of other pathogens. P. penetrans reproduced faster in Verticillium-infected S. tuberosum than in S. tuberosum free of fungus infection (Schnathorst, 1981).

3.2 Verticillium dahliae

Verticillium wilt of potato was first described by Reinke and Berthold (1879) and Orton (1914). The term "early dying" was first used by Pethybride (1916) to describe the symptoms associated with this detrimental physiological process. The primary cause of potato early-die was identified as the soil fungus Verticillium, and the term "early dying" was reported

by Isaac and Harrison. Two species, V. dahliae and V. alboatrum, are known to be pathogens of S. tuberosum. Verticillium dahliae appears to be the more dominate species in the north central states and the Pacific northwest where average summer temperatures frequently exceed 25 C (Rowe et al., 1987). They also differ in that V. dahliae forms true microsclerotia as survival structures within infected tissues, whereas V. alboatrum forms melanized hyphae.

Verticillium is a monocyclic pathogen, and can be present in soil at planting. Verticillium produced in roots and stems during disease development becomes available for infection of subsequent crops. There are several ways for Verticillium to colonize noninfested fields. These include introduction on the surface or within tissue of infected seed tubers, by wind or mechanical movement of soil particles containing viable propagules, and occurring naturally in some areas in association with roots of native vegetation (Rowe et al., 1987). Once established in a field, Verticillium spp. can survive in soil for many years in a dormant state as microsclerotia or melanized hyphae (Powelson, et. al., 1993). It appears that V. dahliae is capable of survival in dried artificial cultures or field soils for about 13 years (Wilhelm, 1955). Verticillium spp. can be free or embedded in organic debris. Because of its wide host range, this fungus

can also maintain itself at low levels on roots of many symptomless crop and weed species.

Effects of V. Dahliae on potato plants include toxins, which are secreted in vessels by the fungi and carried upward in water, affecting living parenchyma cells adjacent to the xylem. Talboys (1958) concluded that in either the acute or mild syndrome necrosis of leaf tissue results from a toxigenic action of the pathogen. The toxins may also be carried to the leaves where they cause reduced chlorophyll synthesis along veins and thus reduced photosynthesis. Toxins disrupt the permeability of cell membranes and their ability to control water loss by transpiration and thereby result in leaf epinasty, wilting, interveinal necrosis, browning and death. The oxidation and translocation of some breakdown products are also responsible for the brown discoloration of affected vascular tissues. Wilts occur due to presence and activities of the fungus in xylem vascular tissues. Entire plant or parts of plants may die in weeks.

Symptoms of Verticillium wilt in cross sections of infected stems appear as discolored brown vascular areas. The fungus was found in xylem vessels of *S. tuberosum* infected with *V. dahliae* (Rudolph, 1931). The plant defense mechanisms include callose deposition, gel and gum formation in the xylem vessel, and possibly enzymes and enzyme inhibitors (Francl and Wheeler, 1993). Early senescence of infected plants occurs. Leaves become pale green or yellow and die prematurely, an "early dying" or "early maturity" (Hooker, 1981). Plants may lose their turgor and wilt during the growing season, especially on sunny hot days. Infected tubers often present a light-brown or darkgrey discoloration in the vascular ring. Cavities can develop inside tubers.

3.3. PDDC (Penetrans/Dahliae Disease Complex)

Although nematodes cause plant diseases by themselves, most of them live and function in the soil, where they are constantly surrounded by fungi and bacteria, many of which also cause plant diseases. In many cases an association develops between nematodes and certain of the other pathogens. Nematodes then become a part of an etiological complex. The interactions resulted in a combined pathogenic potential greater than the sum of the damage either of the pathogens can produce individually (Sikora and Carter, 1987).

Pratylenchus penetrans feeds as an endoparasite. Inside root tissue, P. penetrans causes necrosis of root cells. The nature of injury caused by P. penetrans makes the roots particularly suitable for invasion by other organisms (Brodie, 1984). The necrosis usually occurs ahead of the area penetrated and serves as an infection court for secondary root invaders (Mai et al., 1981). Pratylenchus penetrans and V. dahliae are two of the documented causal factors for PED (Riedel, et al., 1985). Infection of S. tuberosum by P. penetrans increases symptom expression and reduces the incubation period of V. dahliae and V. albo-atrum. In some cases V. albo-atrum infection suppresses the number of P. penetrans in potato roots (Burpee and Bloom, 1978).

Interactions between nematodes and fungi in disease complexes have been reviewed in detail by N.T. Powell (1971), and Sikora and Carter (1987). Plant parasitic nematodes interact with Verticillium spp. in potato production (Jacobsen et al., 1979). In 1985, researchers at Ohio State University and the University of Wisconsin confirmed this through their research with P. penetrans and V. dahliae (Rowe et al., 1985 and Kotcon et al., 1985). A research on disease complexes showed that predisposition with nematodes caused a significant increase in fungal infection (Porter and Powell, 1967). An increase in Verticillium wilt in potatoes was also noted in the presence of high densities of lesion nematodes (Cetas and Harrison, 1963). Large numbers of nematodes in the soil usually increased the incidence of wilts, presumably by providing more effective penetration points. The role of nematodes as predisposition agents can involve mechanisms more complex than root wounding. The S. tuberosum-Pratylenchus spp. biochemical interactions may alter overall physiology of

plants that affect response to infection and/or colonization by Verticillium (Rowe, et al., 1987).

The progression of wilt disease was logically deduced into well-defined spatial and temporal components (Beckman, fungus-nematode 1987). Possible interaction mechanisms considered were that nematodes could cause a number of physiological changes that limit structural responses, reduce the quantity and timing of biochemicals released, and provide additional substrate for the invader so that a systemic invasion proceeds (Beckman, 1989). The P. penetrans and V. dahliae interactions may involve effects of the nematode feeding on S. tuberosum that alter the plant's susceptibility to infection by the fungus or facilitate more rapid invasion by V. dahliae (Powelson, et al., 1993).

3.4 Solanum tuberosum

Potato (Solanum tuberosum L.), is a solanaceous cultivated plant, with its origin in the highlands of South America (Burton, 1989). Evidence indicates that two separate introductions of potato appeared in Europe during the sixteenth century, and then spread throughout the world (Brodie, 1984). The first route and earliest date that potato arrived in North America was from England via Bermuda to Virginia in 1621 (Hawkes, 1978). By 1980 the potato was grown in 126 countries, with a global production of 66 kg per capita

(Horton, 1982). The U.S. alone produces in excess of 20 million metric ton annually with an annual worth of over 1.2 billion dollars (U.S. Department of Agriculture, 1980).

Milthorpe (1963) assigned three phases of potato growth: pre-emergence, haulm growth and tuber growth. Tuber formation in the potato plant can be regarded as the summation of two separate processes: stolon development and tuberization at the stolon tip (Booth, 1963). Stolons of potato plants represent modified lateral shoots which arise from the nodes of underground stems. Stolons differ from normal stems in having elongated internodes, hooked tips, and small scale-leaves. Stolons lack chlorophyll and a diageotropic habit (Kumar and Wareing, 1972). There appears to be a significant relationship between stolon emergence and root growth (Booth, 1963). Stolon emergence was retarded in excised plants and occurred initially only at the basal nodes which carried adventitious roots. The first-formed and longest stolon developed at the lowest node. Katzke and Palta (1986) demonstrated the presence of functional tuber and stolon roots and their roles in transporting water to tubers under field conditions. These roots may play a role in tuber calcium uptake which is thought to move primarily with the water in the xylem. Iwama (1979) assumed that the relationship between root system and tuber yield was not due to the direct contribution of the root system, but due to the pleiotropic expression of the

earliness. Iwama et al. (1981) reported that clones with larger root, stem and leaf dry weights tended to have longer growing periods and higher yields. A tuber is formed at the stolen tip, with a 64-fold cell division and enlargement volume of lateral proliferating storage tissue increasing. A tuber consists of 1) medullary tissue; 2) cortical regions, filled with starch; 3) vascular ring; 4) storage parenchyma; 5) lateral/apical bud, etc. A tuber contains water (>50%), carbohydrates, protein, fat, vitamins, etc. Tuber initiation begins with the production of a small structure on a stolon of the mother plant. Cessation of stolon growth results in the initiation of tubers (Booth, 1963).

Basal roots originate at the base of the below ground stem. They supply water primarily to the above-ground vegetative portion of the plant (Kratzke and Palta, 1985). Basal roots do not appear to transport water to the tuber under field conditions (24 h period) though there is a xylem connection from the basal roots to the tuber. They do not contribute to Ca accumulation in the potato tuber (Kratzke and Palta, 1986).

Nodal roots arise from nodes on the below ground stem at the junction of the stolon to the mainstem (Stem-stolon junction roots). They supply water primarily to the aboveground vegetative portion of the plant (Kratzke and Palta,

1985). They do not appear to transport water to the tuber under field conditions.

Stolon roots are adventitious roots found at the nodes of stolons. They have normal root anatomy (Struckmeyer and Palta, 1986). Under field conditions, stolon roots transport water to the vegetative parts of the plant, including tubers. Stolon roots are capable of supplying water and perhaps some inorganic nutrients to the tuber (Kratzke and Palta, 1985). Tubers produced on longer stolons with numerous stolon roots may be larger since they have more access to water and nutrients. Sixty percent of the tuber Ca enters through stolon roots. Dixon (1922) estimated the area of phloem in a stolon and observed a high rate (50 cm h^{-1}) of carbohydrate flow. The tuberosum stolon is clearly an organ capable of and S. structurally adapted for unusually efficient translocation. It has been shown that the growth rates of individual tubers are correlated with the cross sectional area of stolon tissue.

Tuber roots are roots growing directly from the base of the buds on the tuber (Struckmeyer and Palta, 1986). Many tubers have small roots growing directly out of the tubers. They are capable of supplying water and perhaps some inorganic nutrients to the tuber. They transport water to the tuber under field conditions. Stolon and tuber roots may, in part, transport water to the tuber, since basal and nodal roots failed to transport water to the tuber during a 24 h period; whereas, tuber and stolon roots were able to provide water to this tuber within two hours (Kratzke and Palta, 1985). The occurence of tuber roots varies among cultivars. Russet Burbank and Superior were found to have 34% and 18% of tubers with tuber roots (Kratzke and Palta, 1992).

Early tuber ontogeny was anatomically described by Hayward (1938, 1967). The stolon tip enlarges radially after ca. 3-4 inch elongation of the stolon. The first region to grow actively is the pith. The coincidental compensating growth takes place in the cortex with tangential enlargement and radial divisions of cells to fill with starch. Pericyclic cells surrounding the outer groups of primary phloem divide, enlarge rapidly, and become filled with starch. The endodermis constitutes a line of demarcation between cortex and outer pericyclic zone in early ontogeny, and disappeared later as a distinct layer.

A tuber-forming stimulus appears to be formed by active growing points or entire plants subjected to *ca*. 14 short-day (9-hr. photoperiod) cycles (Chapman, 1958). Booth (1963) described the influences of growth substances such as GA, IAA, KIN, IAA/GA, IAA/KIN, etc. on the lateral growth. There was an inverse relationship between stem diameter and lateral shoot length because they are competing for a limited supply of

nutrients or a more specific growth factor (Booth, 1963). Kumar and Wareing (1972) showed that darkness and a moist atmosphere favor stolon emergence, and raised the question as to whether normal stolon development is regulated through endogenous hormones.

Wurr (1977) suggested that the development of potato tubers followed an approximately sigmoidal curve, but some grew linearly. The allometric relationships between number of cells, the volume of the individual cells and tuber weight indicate that cell multiplication was the factor most responsible for an increase in size of the tuber (Plaisted, 1958). Plaisted (1958) reported that the number of subterranean nodes producing stolons on the potato plant increased upward as the plant became older, but the largest tubers were produced on the lower, older stolons of the plant. Wurr (1977) found that the tested potato varieties formed similar numbers of stolons but different numbers of tubers, and more tubers were formed at the first node.

3.5 Engineering Solanaceous Plants

Engineering is the science of making practical application of knowledge in any field (Webster, 1961). Manipulation of plant genetic information produces a genetically engineered plant. Manipulation of plant architecture results in an architecturally engineered plant.

Kotcon and Rouse (1984) employed a split root technique to study the impact of pathogens associated with PED on root deterioration. The procedures are helpful in providing insight into the nature of disease complexes.

The potential of utilizing tomato-potato hybrids for breeding will not be fully realized without a development of new techniques such as DNA transfers, engineering solanaceous plants, etc. (Taylor, 1987). Studies involving interspecific crosses with Solanum species have been widely reported (reviewed by Magoon, Ramanujani, and Cooper, 1962). Solanum-Lycopersicon interrelationships have generated much interest amongst systematists, geneticists, and plant breeders (Rick, et al., 1986). Potato genotypes grafted onto PVY-infected tomatoes showed reactions with extreme resistance or systemic hypersensitivity. Recent success in generating progeny from crosses between Cycopersicon and Solanum offers exciting new possibilities (Rick et al., 1986). It has been shown by further grafting experiments that the foliage of a tomato scion cannot induce tuber formation in a potato stock, but can support the development of tubers which have been previously induced (Madec and Perennec, 1959). Some features of the below-ground system of a potato-tomato grafting plant appear similar to that of the split root-stolon culture system of S. tuberosum used in this research.

3.6 Simulation modeling

A model is something that imitates relevant features of the situation being studied. An M is a model of an N if 1) Some of the components of M correspond in a one-to-one manner with some of the components of N; and 2) For at least some relationships, the relation between the components of M is analogous to that between the corresponding components of N (Eisen, 1988).

Agricultural crops, pests and the environment interact on in a dynamic manner. each other Simulation models of agricultural systems can be highly significant research tools. They must, however, be able to accurately simulate the dynamics of the system, including the impacts of pests. Nematologists have developed simulation models. For example, a model of Heterodera schachtii infecting Beta vulgaris was established (Caswell et al., 1986). There are, however, relatively few nematode simulation models. Agricultural scientists have developed a number of simulation models. For example, SUBSTOR is a sister simulation model of potato growth and development from the CERES grain models. Only a few of the crop models that predict yield include the influences of pests (Ritchie, 1986). A systems approach to achieving additional knowledge useful for interpreting the soil inoculum/disease and yield loss relationships has been initiated using a potato

plant growth model (Rowe et al., 1987). A Verticillium submodel, which includes independent functions for both infection and colonization, has been coupled to the growth model. Environmental variables can be incorporated to influence each of the components of the disease cycle separately. Additionally, other pathogens or pests can be coupled to the plant growth model, thus modifying growth and yield in the presence of *Verticillium*. Environmental effects on the plant itself are accounted for by the plant growth model. Additional experimental data are being developed to allow proper empirical relationships to be inserted into this model.

3.7 Interaction Biology

The importance of disease in population dynamics is increasingly being suggested and confirmed (Myers, 1988). It is also becoming apparent, however, that it is dangerous to consider the interaction between parasites and hosts as though there are only two components to the interaction. The influence of a parasite on its host may well be to change its response to competitors and mutualists, alter its reaction to physical conditions of the environment and damage its ability to garner resources (Begon, Harper, and Townsend, 1990). Models of host-parasite interactions are increasingly having to incorporate the behavior of at least a third biological

entity in order to increase their realism and predictive value (Holt and Pickering, 1985; Anderson and May, 1986). It is apparent that the development of a Verticillium wilt epidemic can be retarded or accelerated depending on which interactions are favored (Schnathorst, 1981). The complexity arises when one considers the possibilities of triple and quadruple interactions.

3.8 Landscape Ecology

A landscape is a portion of territory that can be viewed at one time from one place (Webster, 1988).

Landscape ecology is the study of the horizontal physical-biological relationships that govern the different spatial units of a surface area. A vertical physicalbiological relationship is a relationship among plants, animals, air, water, and soil within a relatively homogeneous spatial unit. It deals with the broad field of ecology. A horizontal physical-biological relationship is a relationship among spatial units that makes landscape ecology unique (Forman, 1986).

Landscape ecology focuses on three basic characteristics of the landscape: structure, function, and change. The seven general principles of landscape ecology are: landscape structure and function, biotic diversity, species flow, nutrient redistribution, energy flow, landscape change, and

landscape stability (Forman, 1986).

Development of the science of landscape ecology can be traced to the writings of scholars in every period of history. The outlines of a distinct discipline or field of study were provided by a series of pioneering geographers and biogeographers, primarily during the 1960s. Landscape ecologists recognize the relevance of work in several sister disciplines, such as geography, ecology, biogeography, environmental ecology, geographical ecology, community ecology, geographical population, planning and landscape architecture, etc (Jongman, 1987).

There are examples of landscape ecology research related to pests. The susceptibility of forests in a Douglas-fir region to selected insect and fungal pests was studied on a landscape ecology basis, and highly species specific responses of pests and pathogens to a developing patchwork was found (Franklin *et al.*, 1987). A concept of the landscape as the spatial dimension of the biotically-driven episodes that alter landscape structure is represented in a conceptual model linking insect-host and landscape mosaic interactions (Rykiel et al., 1988).

One of the purposes of landscape ecology applications is to use information about a system in the design of procedures to optimize landscape management. These systems should provide

spatial balances, high resistance to disturbance, high biotic diversity, low energy maintenance, and high harvestable productivity (Forman, 1986). There is a relationship between cropping systems and landscape heterogeneity/monogeneity in farming areas which cover large parts of the USA. It is, therefore, possible to provide new insights about PDDC by studying it through the use of the principles and approaches of landscape ecology.

Nematode distributions are generally aggregate or clumped (Ferris, 1984). Little work, however, has been done to quantify or describe that clumping (Ferris, 1984). Validation of nematode distributions is important for meeting assumptions of certain parametric statistical tests, for adding in the development of sampling techniques, for assessing temporal changes in density and distribution, and for comparing interspecific distribution patterns. No working hypotheses with landscape ecology, however, has been previously generated to address nematode problems in general and the PDDC system in specific. Certainly, exploration is needed to establish this research area for nematology and potato pest management. The possibility of a better understanding of the PDDC system on a landscape ecology base will increase opportunities to identify attractive options for novel methods of management of plant parasitic nematodes and other potato pests.

3.9 Geostatistics

Geostatistics consists of a set of statistical tools which offers a way of identifying, quantifying and analyzing spatial relationships in geo-referenced data (Isaaks, 1989). A geo-referenced datum exists when a sample is geographic in nature and a non-zero spatial autocorrelation is present; and should have to do with the relative location of the areal unit under study (Griffith, 1988). Classical statistics (e.g., classical sample mean) is not sufficient for geo-referenced data; since it fails to embrace any locational information. One of the fundamental assumptions of classical statistics is that the elements of a population take on numerical values in an independent fashion (Griffith, 1980). However, it has long been recognized that conditions of independent random sampling are rarely met in practice (Smith, 1980). The assumption of frequently violated in geo-referenced independence is situations. Moreover, the value of some phenomenon in a given areal unit tends to be related to those values of this phenomenon taken on by juxtaposed areal units. The spatial autocorrelation viewpoint does not ignore randomness. Rather, it maintains that a geographic distribution is composed of both pattern (a spatial structure component) and random error independent noise component). Violating classical (an independence of observations assumptions uncovers

complications that tend to lie dormant in classical statistical analysis (Griffith, 1980).

Geostatistics is one of the most rapidly growing areas of statistics. If geostatistics becomes as mature as classical statistics, it seems certain that we will understand nature much better (Griffith, 1988). As a young discipline, spatial statistics has components of all the classical areas of statistics. Classical statistics and spatial statistics are equally efficient if zero spatial autocorrelation is present. Autocorrelation refers to the pairwise correlation of univariate observations. A plot of the autocorrelation values laq (distance of separation) is called versus the an autocorrelogram (Trangmar et al., 1985). Traditionally science has been concerned, in part, with the study of structure amongst variables. More recent attention has been turned to the study of structure among observations of a single variable. Considerable attention has been focused on this spatial autocorrelation approach in recent years. More recent extensions and developments, especially in terms of kriging, offer far more promise (Griffith, 1988). The strength of geostatistics over more classical statistical approaches is that it recognizes spatial variability at both the "large scale" and the "small scale", or in statistical parlance, it models both spatial trend and spatial correlation.

4.0 Experimentation

The research consists of three major topic areas:

- * Initial ontogeny of the below-ground system of S. tuberosum in the presence and absence of microorganisms associated with potato production
- * Joint impact of *P. penetrans* and *V. dahliae* on *S. tuberosum*, with special reference to interactions in an etiological complex
- * Linear, spatial, and space feature of an S. tuberosum ecosystem: with special reference to P. penetrans and V. dahliae

4.1 Simulation modeling of the Solanum tuberosum below-ground system associated with Pratylenchus penetrans and Verticillium dahliae

4.1.1 Introduction

Development of mechanistic computer models to simulate *S*. tuberosum growth and development associated with pests has made a new approach available for development of IPM strategies and procedures (Bird, 1990). Models are able to be coupled to identify reference on healthy *S*. tuberosum yields, pest-infested crop yields, and firm-level estimates of tuber yield losses. In 1987, an empirical potato model of moderate

complexity, POTATOPEST, was converted to MICROPOTATOPEST using Microsoft FORTRAN Version 3.2 (Bird, 1990). It was calibrated for simulation of the growth and development of *S. tuberosum* cv Russet Burbank using 1985 Michigan State research data.

Studies of the form and function of S. tuberosum root systems are few (Allen and Scott, 1992). Root development, expansion, and death is much less understood that plant top development and growth. Computer simulation models, however, are only as accurate as is the information contained within them (Ritchie, 1986a). There are four types of S. tuberosum function roots: basal, nodal, stolon, and tuber roots (Kratzke and Palta, 1985 and 1992; Struckmeyer and Palta, 1986). Although these specific types of S. tuberosum roots were reported, extensive literature involving S. tuberosum have been associated with a very general concept of roots. The below-ground system of S. tuberosum in this research was reduced to eight basic components, which are basal roots, nodal roots, stolon roots, tuber roots, stolon, tuber, belowground stem, and seed piece. The main objective of this study was to construct a computerized model simulating S. tuberosum cv. Superior growth and development using C++ programming language, with special reference to seven of the eight below ground components associated with P. penetrans and V. dahliae. The seed piece was not included in the model. The related

objectives of the research consisted of:

* Identifying and demonstrating individual growth and development of *S. tuberosum* basal roots, nodal roots, stolon roots, tuber roots, stolons, tubers, and below-ground stems.

* Displaying and detecting best-fit linear, polynomial, logarithmic, or exponential function indicating trends, correlations, or forecasting of the growth and development of *S. tuberosum* basal roots, nodal roots, stolon roots, tuber roots, stolons, tubers, and below-ground stems.

* Determining and simulating growth and development of *S*. *tuberosum* basal roots, nodal roots, stolon roots, tuber roots, stolon, tuber, and below ground stems under a pathogen-free environment (PFE) and a pathogen-impacted environment (PIE) associated with *P. penetrans* and *V. dahliae* interactions.

4.1.2 Materials and Methods

4.1.2.1 Growth and development of a multi-component S. tuberosum below-ground system

1. A conceptual potato plant model system driven by water, with special reference to seven components of the below ground system, is proposed in Figure 4.1.1. The eighth component, the seed piece, is not included in the model.





2. Biomass production. Biomass production is a continuous time process in the plant system. The net change in biomass at a given time interval is $W(t+\Delta t) - W(t)$. The biomass production of the below-ground system of *S. tuberosum* system included: 1) basal roots; 2) nodal roots; 3) stolon roots; 4) tuber roots; 5) stolons; 6) tubers; and 7) below-ground stems. The sum of the two or more components included 1) basal-nodal roots; 2) stolon and stolon roots; 3) all roots in total; and 4) below ground system in total. The above ground *S. tuberosum* biomass production included leaves and above ground stems.

3. Biomass Partitioning. For any organ of a plant, such as roots, leaves, tuber, etc., the biomass accumulation for that organ at a given time interval is a function of the proportion of new biomass partitioned to the organ and the attribution to remobilization of the assimilate stored in it. Biomass produced is partitioned between organs. Weight of roots, for example, is allometric to the weight of the whole plant. The *S. tuberosum* biomass partitioning included the root/shoot ratio, the below-/above-ground ratio, etc. The biomass partitioning of the *S. tuberosum* below-ground system included: 1) the basal-/nodal-/stolon-/tuber root ratio; 2) the roots/stolon ratio; and 3) the root/tuber ratio.

4. Curve fitting. Curve fits are a visual way of

indicating trends or correlations in plotted data, and can also be used as a method of forecasting data. Curve fitting was applied to scatter graphs of the *S. tuberosum* growth and development in this research using microcomputer software of Cricket (Graph 1.3.2). Curve fits of linear function and equation with r² values were generated for the growth and development of the basal roots, nodal roots, stolon roots, tuber roots, stolon, tuber, below-ground stem, root system, below-ground system, above-ground system, and whole plant in PFE and PIE.

4.1.2.2 Experimentation

1. Experiment. Two soil environments were used in the greenhouse experiment of the computer simulation model The PFE (Pathogen-Free Environment) development. soil environment was created by planting S. tuberosum cv. Superior, susceptible to P. penetrans, and V. dahliae, in steamsterilized (2 hours, 98 C) Montcalm sandy loam soil. The PIE (Pathogen-Impacted Environment) was created by using field soil from a site where a high incidence of PED was observed throughout the previous 10 years. The site is located at the Michigan State University Potato Research Farm at Entrican, Michigan. Both soils were loamy sand (75.3% sand, 13.7% silt, 11.0% clay). The experiment was conducted in a randomized design with five replications each in PFE and PIE.

2. Growth and development assessment of the below ground system of S. tuberosum. Plants were destructively sampled 10, 15, 20, 25, 30, 35, 40, and 45 days after planting. Five plants from each of two soil environments were randomly selected. The 30.5 cm pot was first submerged in a water tank for 30 min. Soil was then removed from the plant by careful washing with a strem of water. The growth and development of the S. tuberosum production system, with special reference to the below-ground system, were recorded as 1) basal root weight and number; 2) nodal root weight and number; 3) stolon root weight and number; 4) tuber root weight and number; 5) stolon weight and number; 6) tuber weight and number; 7) below-ground stem weight and number; 8) above-ground stem weight and number; 9) leaf weight and number; 10) above-ground plant height; and 11) seed tuber weight. The plant dry weights were also measured 30, 35, 40, and 45 days after planting.

3. Population density assessment of *P. penetrans* and *V. dahliae.* The soil assay method for *P. penetrans* used a modified centrifugation-flotation technique. The root assay method for *P. penetrans* employed a shaker technique (Bird, 1971). The soil assay method for *V. dahliae* utilized a dilution plating technique. *Verticillium dahliae* population density in soil was assessed at planting. *Pratylenchus penetrans* population density under the PIE was assessed in
soil at pre-planting and 45 days after planting in soil, and in root and stolon tissues 15, 20, 25, 30, 35, 40, and 45 days after planting. The presence or absence of *P. penetrans* under the PFE was validated by sampling soil at planting, and a gram of root and stolon tissue randomly selected every five days.

4.1.2.3 Simulation Models

The potato simulation model was compiled and linked in the UNIX computing environment by Mr. Joseph Alexander at Michigan State University Computer Department using GNU g++ Compiler v.2.4.5. The potato model can also be developed in the DOS environment using Turbo C++ Compiler v.3.0. Figure 4.1.2 shows the flow chart of the computer model simulating the growth and development of *S. tuberosum* basal roots, nodal roots, stolon roots, tuber roots, stolon, tuber, and belowground stem under a pathogen-free environment (PFE-Clean Soil) and a pathogen-impact environment (PIE-Field Soil) associated with *P. penetrans* and *V. dahliae* interactions. The outputs included plant fresh weight in PFE and PIE, plant dry weight in PFE and PIE, and *P. penetrans* population dynamics. The program written in C++ Language is enclosed in appendix 7.0.



Figure 4.1.2. Flow chart of the computer model simulating the growth and development of *S. tuberosum* basal roots, nodal roots, stolon roots, tuber roots, stolon, tuber, and below-ground stem under a pathogen-free environment (PFE-Clean Soil) and a pathogen-impact environment (PIE-Field Soil).

4.1.3 Results

4.1.3.1 Running of the potato simulation model

The potato simulation model was run in a UNIX system at Michigan State University Computer Laboratories. An IBM-PC DOS version of the model can be made to run in microcomputers.

4.1.3.2 The growth and development of the Solanum tuberosum below-ground system.

Root System. The S. tuberosum cv. Superior basal root, nodal root, stolon root, and tuber root were first observed 10, 10, 30, and 40 days after planting under the PFE soil environment, respectively. A similar sequence of events took place in the PIE except for the tuber root which was not observed until 45 days after planting (Figure 4.1.2-5).

Below-Ground Shoot System. The *S. tuberosum* cv. Superior below-ground stem, stolon, and tuber were first observed 10, 20, and 35 days after planting under the PFE soil environment, respectively. A similar sequence of events took place in the PIE except for the tuber which was not observed until 45 days after planting (Figure 4.1.6-8).

Soil Environment. Differences between S. tuberosum cv Superior growth and biomass production under the PFE soil environment and that under the PIE were observed as early as 10 days after planting. They were consistent throughout the growing period. Basal root, nodal root, stolon root, tuber

root, stolon, tuber, below-ground stem, root system, belowground system, above-ground system, and whole plant exhibited more growth throughout the growth period under the PFE compared to the PIE soil environment (Figure 4.1.2-12). The growth of the basal root and tuber were impacted to a much greater extent than that of other *S. tuberosum* below-ground system components (Figure 4.1.2, 4.1.7).

Biomass Production. Linear curve fitting was associated with the growth of *S. tuberosum* system components (Figure 4.1.2-12). The average r^2 value under the PFE was 0.818, compared to 0.739 under the PIE.

Significantly higher dry weights of basal roots, nodal roots, stolon roots, and tuber roots under PFE were observed 30, 30, 45, and 40 days after planting, compared to that under PIE, respectively (Table 4.1.1). Significantly higher dry weights of stolon, tuber, and below-ground stem under PFE were observed 40, 35, and 40 days after planting, compared to that under PIE, respectively (Table 4.1.1).

Biomass Partitioning. The average root/tuber, root/shoot, root/stolon, and below-ground/above-ground system ratios of *S*. *tuberosum* during the growing period under the PFE were 0.26, 22.2, 2.96, and 0.45, respectively. Those ratios under the PIE were 0.24, 16.6, 95.65, and 0.42, respectively (Figure 4.1.13). The average biomass partitioning under the PFE were that the basal roots accounted for ca. 5%, nodal roots accounted for 12%, stolon roots accounted for 0.1%, tuber roots accounted for 0.001%, stolons accounted for 1%, tubers accounted for 6%, below-ground stems accounted for 7%, and above-ground system accounted for 69%. The average biomass partitioning under the PIE were that the basal roots accounted for ca. 1%, nodal roots accounted for 14%, stolon roots accounted for 0.1%, tuber roots accounted for 0.0001%, stolons accounted for 1%, tubers accounted for 0.2%, below-ground stems accounted for 14%, and above-ground system accounted for 71%.

4.1.3.3 Pratylenchus penetrans population biology in PIE

P. penetrans was recovered from the basal root, nodal root, stolon root, and tuber root of the *S. tuberosum* 15, 15, 35, and 45 days after planting under the PIE. This nematode was also recovered from the stolon 30 days after planting under the PIE (Figure 4.1.15). No *P. penetrans* was recovered under the PFE.

Second-stage juveniles and male adults of *P. penetrans* were recovered from the basal root, nodal root, stolon root, and stolon. Female adults of *P. penetrans* were recovered from the basal root, nodal root, stolon root, tuber root, and stolon. A second-stage juvenile with body length of 0.211 mm was recovered from the stolon 45 days after planting.

Observations from randamly selected root samples showed that about 70% and 40% of *P. penetrans* were counted for the second-stage juveniles 25 and 45 days after planting, repectively. About one thirty of *P. penetrans* were counted for the male adults 45 days after planting.

The population density of this nematode in basal roots, nodal roots, stolon roots, and stolons continued to increase throughout the growing period of *S. tuberosum*. By 45 days after planting, Fifty-six, 53, 33, 20, and 5 *P. penetrans* per gram of plant tissue were recovered from the basal roots, nodal roots, stolon roots, tuber roots, and stolons, respectively (Figure 4.1.14). A linear curve was observed better-fitted for *P. penetrans* population dynamics in basalnodal roots (Figure 4.1.15-16).

4.1.4 Discussion

This research reduced the below-ground system of *S*. tuberosum into basal roots, nodal roots, stolon roots, tuber roots, stolon, tuber, and below-ground stem. Results showed that there were significantly less basal roots of *S*. tuberosum under the PIE than that under the PFE soil environment. Additional research is needed to explore its significance.

The recovery of a young second-stage juvenile with body length of 0.211 mm from the stolon tissue suggested that the reproduction of *P. penetrans* could be accomplished in the *S*.

tuberosum stolon.

With a validation of this potato simulation model, it should be incorporated into the SUBSTOR. SUBSTOR is a potato simulation model developed at Michigan State University as part of the CERES crop model system.

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Table 4.1.1. Dry weights (g/plant) of the below-ground system components of *Solanum tuberosum* under the Pathogen-Free Environment (PFE) and Pathogen-Impacted Environment (PIE).

		I	Days aft	er	plant	ing		
Plant S	Soil	30	35		40	4	15	
Basal roots	PFE PIE	0.22 0.03	0.48 * 0.02	*	0.53 0.03	*	0.88	*
Nodal roots	PFE PIE	0.78 0.43	1.55 * 0.72	*	1.74 0.92	*	2.20 1.18	*
Stolon roots	PFE PIE	<0.01 <0.01	<0.01 <0.01	< <	0.01 0.01		0.02	*
Stolons	PFE PIE	0.03 0.04	0.10 0.06	*	0.36 0.11	*	0.26 0.15	*
Tuber roots	PFE PIE	0.00 0.00	0.00 0.00	<	0.01	< * <	0.01	
Tubers	PFE PIE	0.00 0.00	0.03 0.00	*	1.63 0.00	*	3.69 0.03	*
Below-ground stems	5 PFE PIE	0.58 0.57	1.06 0.84		1.52 1.10	*	2.13 1.05	*
Note: "*" indicate	es tha	t the c	dry weig	rht	(q/p)	lant	und	Pr

Note: "*" indicates that the dry weight (g/plant) under the PIE is significant (P = 0.05) lower than that under the PFE by t-test.



Figure 4.1.3. Basal root growth of *Solanum tuberosum* associated with the linear function under PFE and PIE.



Figure 4.1.4. Nodal root growth of *Solanum tuberosum* associated with the linear function under PFE and PIE.



Figure 4.1.5. Stolon root growth of *Solanum tuberosum* associated with the linear function under PFE and PIE.



Figure 4.1.6. Tuber root growth of *Solanum tuberosum* associated with the linear function under PFE and PIE.



Figure 4.1.7. Stolon growth of *Solanum tuberosum* associated with the linear function under PFE and PIE.



Figure 4.1.8. Tuber growth of *Solanum tuberosum* associated with the linear function under PFE and PIE.



Figure 4.1.9. Below-ground stem growth of *Solanum* tuberosum associated with the linear function under PFE and PIE.



Figure 4.1.10. Root system growth of *Solanum tuberosum* associated with the linear function under PFE and PIE.



Figure 4.1.11. Below-ground system growth of *Solanum* tuberosum associated with the linear function under PFE and PIE.



Figure 4.1.12. Above-ground system growth of *Solanum tuberosum* associated with the linear function under PFE and PIE.



Figure 4.1.13. Plant growth of *Solanum tuberosum* associated with the linear function under PFE and PIE.



Figure 4.1.14. Solanum tuberosum biomass partitioning under PFE and PIE.





Figure 4.1.15. Pratylenchus penetrans population densities in basal roots, nodal roots, stolon roots, tuber roots, and stolons of Solanum tuberosum under the PIE 40 and 45 days after planting.

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Figure 4.1.16. *Pratylenchus penetrans* population dynamics in basal-nodal roots, stolon roots, tuber roots, and stolons of *Solanum tuberosum* under the PIE.

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Figure 4.1.17. Linear, polynomial, logarithmic, and exponential *Pratylenchus penetrans* population dynamics associated with *Solanum tuberosum* under the PIE.

4.2 Effect of Pratylenchus penetrans and Verticillium dahliae on isolated below-ground system components of Solanum tuberosum

4.2.1 Introduction

Tuber formation in *S. tuberosum* is regarded to be the summation of the stolon development and tuberization at the stolon tip (Booth, 1963). Field studies have shown that stolon tissue of *S. tuberosum* can be infected with *P. penetrans* as early as 32 days after planting and can remain infected throughout the entire growing season (Bird, 1987). A field nematicide trial has demonstrated that stolon tissue from plants grown in nematicide treated soil can have significantly greater biomass as early as 28 days after planting. This trend can continue throughout the growing season, resulting in greater tuber yield. Hence, there is a distinct need to learn more about the nature of the interactions between *P. penetrans* and *Verticillium* fungi with specific reference to the impact of phytopathogenesis on the ontogeny of stolon tissue and tuber production.

Although relatively little is published about the belowground system architecture and associated stolon and root configurations of *S. tuberosum*, this plant appears to be ideally suited for research using a modification of the split root technique. The split root technique was effective in providing insight into the nature of disease complexes, and was used by Kotcon and Rouse (1984) to assess the impact of pathogens on root deterioration. This study presented a split root-stolon culture system architecture. The below-ground system of *S. tuberosum* was architecturally manipulated into isolated root system and stolon system. The root system consists of basal roots and nodal roots. The stolon system consists of stolon and stolon roots. The technique and results of research should lead to a significant improvement in the understanding of the nature and potential concomitant impacts of *P. penetrans* and *V. dahliae* on tuber production.

4.2.2 Material and Methods

Architecturally isolated below-ground system of S. tuberosum: Microtubers of S. tuberosum cv Superior (average 15 grams) were incubated in vermiculite in a growth chamber programmed at 24 ± 2 °C until the stolon tissue of the uppermost node of the below-ground stem had elongated to 6-10 cm. The stolon tissue of the uppermost node, nodal root tissue of lowermost nodes of the below-ground stem, and basal root tissue were selected. All other root and stolon tissue were excised. Isolated basal-nodal root and stolon tissues were individually inserted into opposite chambers of two-chamber growth containers (Figure 4.2.1).

Experiments: The isolated S. tuberosum below-ground

system was inoculated with individual and concomitant inocula of *P. penetrans* culture from peas, and a highly-virulent isolate (H2) of *V. dahliae*. There was a total of 12 treatment combinations using a randomized block design with four replications. Randomly selected *S. tuberosum* plants, with special reference to basal-nodal root system and stolon system, were photographed (Figure 4.2.2-11). Tubers were harvested 55-60 days after the below-ground system was architecturally isolated into basal-nodal root system and stolon system. Differences in tuber yields among treatment means were tested for significance (P = 0.05) using Duncan's multiple range test procedure. Experiment A was repeated in Experiment B.

4.2.3 Results

The architecturally isolated S. tuberosum below-ground system without the impact of the P. penetrans and V. dahliae interaction exhibited normal, healthy, and optimal growth of the basal roots, nodal roots, stolon roots, stolons, and tubers (Figure 4.2.2). The individual and concomitant effect of P. penetrans and V. dahliae on S. tuberosum resulted in less plant growth and development, below-ground system biomass, and tuber production, compared to that in the absence of individual or both pathogen. (Figure 4.2.3-11)

Stolon systems exposed to individual or both pathogens

resulted in significantly (P = 0.05) less tuber weight in each experiment than that in the absence of those organisms (Table 4.2.2). Seventeen to 29% (P = 0.05) less tuber weights were found in *S. tuberosum* infected with *P. penetrans* in the stolon system than in the control. Eighteen to 25% (P = 0.05) less tuber weights were found in *S. tuberosum* infected with *V. dahliae* in the stolon system than in the control. Twenty-eight to 42% (P = 0.05) less tuber weights were found in *S. tuberosum* infected with *P. penetrans* and *V. dahliae* in the stolon system than in the control.

The basal-nodal root system exposed to either V. dahliae or P. penetrans or in combination resulted in significantly (P = 0.05) less tuber weight in Experiments A and B. Twenty-five to 30% (P = 0.05) less tuber weights were found in S. tuberosum infected with P. penetrans in the basal-nodal root system than in control. About 45% (P = 0.05) less tuber weights were found in S. tuberosum infected with P. penetrans in the basal-nodal root system than in the control. About 60% (P = 0.05) less tuber weights were found in S. tuberosum infected with both P. penetrans and V. dahliae in stolon system than in control (Table 4.2.2).

The basal-nodal system exposed to *P. penetrans* and stolon root system exposed to *V. dahliae* resulted in about 34% (P = 0.05) less tuber weight than in control. The basal-nodal system exposed to V. dahliae and stolon root system exposing to P. penetrans resulted in about 50% (P = 0.05) less tuber weight than in control. The basal-nodal system exposing to both pathogens and stolon root system exposing to both pathogens resulted in about 64% (P = 0.05) less tuber weight than in the control (Table 4.2.2).

4.2.4 Discussion.

This method of isolating the stolon from the basal-nodal root system makes it possible to demonstrate that *P. penetrans* could have a significant (P = 0.05) impact on tuber yield through parasitism of the stolon system. A maximum of 29% tuber weight loss (P = 0.05) could occur when only the stolon system was exposed to *P. penetrans*. This result places an increased emphasis of the role of stolons in tuber development, and justified the incorporation of a stolon system component into the *S. tuberosum* development simulation model.

More studies are needed on the nature of the pathogenic stolon system such as: 1) influence of necrotic injury, 2) influence of fungal toxin; 3) decreased water transport from stolon roots to mainstem and aerial part of the plant, and tuber, 4) decreased water transport from tuber roots to tuber, and 5) increased wilt-fungus spread. Table 4.2.1. Twelve experimental combinations of individual and concomitant infestation of *Pratylenchus* penetrans and *Verticillium* dahliae in isolated root system and stolon system of *Solanum* tuberosum in Experiments A & B.

Treatment	Basal-Nodal Root System	Stolon System
1	Ck ¹	Ck
2	Pp ²	Ck
3	Ck	Рр
4	Рр	Рр
5	Vd ³	Ck
6	Ck	Vd
7	Vd	Vd
8	Рр	Vd
9	Vd	Рр
10	PpVd⁴	Ck
11	Ck	PpVd
12	PpVd	PpVd

Note:

1. Noninfested Solanum tuberosum.

2. S. tuberosum infested with Pratylenchus penetrans.

3. S. tuberosum infested with Verticillium dahliae.

4. S. tuberosum infested with P. penetrans and V. dahliae

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Basal-Nodal Root System	Stolon System	Exper. Tuber	iment A Loss(%)	Experim Tuber Lo	ent B ss(%)
CK	CK	46.6 g		41.2 g [•]	
P. penetrans	CK	32 . 8 g	29.6	31.1 g	24.5
CK	P. penetrans	38 . 5 g	17.4	29.4 g	28.6
P. penetrans	P. penetrans	29.1 g	37.6	22.6 g	45.2
V. Dahliae	CK	25.5 g	45.3	23.1 g	43.9
CK	V. dahliae	38.1 g	18.2	30 . 8 g	25.2
V. dahliae	V. dahliae	22.8 g	51.1	18.2 g	55.8
P. penetrans	V. dahliae	30 . 8 g	33.9	27.4 g	33.5
V. dahliae	P. penetrans	22.3 g	52.2	21.2 g	48.5
P. penetrans + V. dahliae	CK	18.8 g	59.7	15.7 g	61.9
СК	P. penetrans + V. dahlić	ae 33.4 g	28.3	24.0 g	41.8
P. penetrans + V. dahliae	P. penetrans + V. dahlid	ae 17.5 g	62.5	13.9 g	66.3
* Duncan's multiple rang tuber weight in the cont:	e test showed that there rol than in any of the fo	was sign: ollowing 1	ificant treatmen	(P = 0.05)t combinat:	less ions.



Figure 4.2.1. Experimental unit used for separating the below-ground system of Solanum tuberosum.



Figure 4.2.2. Architecturally isolated below-ground system of Solanum tuberosum: basal-nodal root system and stolon system.



Figure 4.2.3. Influence of *Pratylenchus penetrans* on the growth and development of the basal-nodal root system in an architecturally isolated below-ground system of Solanum tuberosum.



of the stolon system in an architecturally isolated below-ground system of Solanum Figure 4.2.4. Influence of Pratylenchus penetrans on the growth and development tuberosum below-ground system.



Figure 4.2.5. Influence of Verticillium dahliae on the growth and development of the basal-nodal root system in an architecturally isolated below-ground system of Solanum tuberosum.


the stolon system in an architecturally isolated below-ground system of Solanum Figure 4.2.6. Influence of Verticillium dahliae on the growth and development of tuberosum.



Figure 4.2.7. Influences of *Pratylenchus penetrans* on the growth and development of the basal-nodal root system and *Verticillium dahliae* on the stolon system in an architecturally isolated below-ground system of Solanum tuberosum.



the basal-nodal root system and Pratylenchus penetrans on the stolon system in an Figure 4.2.8. Influences of Verticillium dahliae on the growth and development of architecturally isolated below-ground system of Solanum tuberosum.



Figure 4.2.9. Influences of *Pratylenchus penetrans* and *Verticillium* dahliae on the growth and development of the basal-nodal root system in an architecturally isolated below-ground system of Solanum tuberosum.



Figure 4.2.10. Influences of *Pratylenchus penetrans* and *Verticillium dahliae* on the growth and development of the stolon system in an architecturally isolated belowground system of Solanum tuberosum.



Figure 4.2.11. Influences of Pratylenchus penetrans and Verticillium dahliae on the growth and development of the basal-nodal root system and stolon system in an architecturally isolated below-ground system of Solanum tuberosum. 4.3 Synergistic, additive and antagonistic nature of *Pratylenchus penetrans* and *Verticillium dahliae* interactions associated with *Solanum tuberosum*

4.3.1 Introduction

Interactions between nematodes and soilborne fungi have received considerable attention (Bergeson, 1963, Riedel, et al., 1985). Atkinson (1892) observed that infection by rootknot nematodes was shown to increase the severity of *Fusarium* wilt. The concept of interactions between nematodes and fungi in disease complexes was documented by Powell (1971). Synergism and antagonism are terms describing quantitative plant disease interactions in which the combined effect of a phytoparasite nematode and another plant disease organism is either greater or less than the sum of the effects of the individual organisms (Sikora and Carter, 1987). Joint effects of *P. penetrans* and *V. dahliae* have been shown to be affected by abiotic factors including temperature and moisture (Powelson and Rowe, 1993).

Synergistic interactions between *P. penetrans* and *V. dahliae* in PED disease development of potato yield inhibition were found (Martin, et al., 1982, Rowe, et al., 1985). Recent work has shown that the impact of *Meloidogyne hapla* on yield could be additive with *V. dahliae* (MacGuidwin and Rouse, 1990). There has been little research on the effect of

combined infection by these pathogens on tuber quality (MacGuidwin and Rouse, 1990). There is still a distinct need to learn more about the nature of the interactions between *P. penetrans* and the *Verticillium* fungi. Results of this research should provide insight into the nature of disease complexes and lead to a significant improvement in the understanding of potential concomitant impacts of *P. penetrans* and *V. dahliae* on tuber production, which could impact pest management for potato crops.

The main objective was to determine the qualitative and quantitative nature of *P. penetrans* and *V. dahliae* interactions associated with *S. tuberosum* through six growth chamber and greenhouse experimental studies, and a three-year *S. tuberosum* ecosystem study. The purpose was to explore 1) synergistic, additive, or antagonistic concomitant influence of *P. penetrans* and *V. dahliae* in six growth chamber and greenhouse experiments, and in a three-year agroecosystem; and 2) *S. tuberosum* basal-nodal root system and stolon system interactions associated with *P. penetrans* and *V. dahliae*.

4.3.2 Materials and Methods

Experiments A-F. Experiment A was conducted in the greenhouse using 1) *S. tuberosum* cv. Superior microtubers with average weight of 15 grams; 2) *V. dahliae* highly-virulent isolate H2; and 3) *P. penetrans* greenhouse culture maintained

on *Pisum sativum*. Experiment B was a repeat of A with the same experimental design (Table 4.3.1). Populations of *P. penetrans* on *Pisum sativum* cv. Sugar Ann were maintained under greenhouse conditions. The greenhouse was programmed for 26 ± 2 C with a 16-hour of photoperiod.

Experiments C-F were conducted with less treatment combinations and more variables to capitalize on what had been learned (Table 4.3.1). The modified experimental design includes 1) S. tuberosum cv. Superior microtuber average 27 grams; 2) V. dahliae mildly-virulent isolate 355; 3) P. penetrans growth chamber monoxenic Gamborg's B-5 culture on Zea mays cv. Iochief; 4) growth chamber environment; and 5) change of inoculum levels. The growth chamber was programmed for a 16-hour of photoperiod at ca. 26 C, and 8-hour night at 18 C. Isolates H2 and 355 of V. dahliae, and Gamborg's B-5 culture of P. penetrans were from the Nematology Laboratory at Ohio State University Department of Plant Pathology.

Ecosystem: The *S. tuberosum* ecosystem consisted of cropping schemes involving two leguminous crops, alfalfa (*Medicago sativa*) and yellow sweet clover (*Melilotus* officinalis), two grain crops, corn (*Zea mays*) and sudax (*Sorghum halupeuse x Sorghum sudanese*), and potato (*Solanum tuberosum* L. cv. Superior). The research was initiated at the Montcalm Potato Research Farm in 1989, and concluded in 1991.

A randomized block design with five replications of each of 10 treatments was implemented. Each 4-row plot was 15 m in length and consisted of a loamy sand soil. Seed pieces of *S. tuberosum* were machine-planted to a depth of ca. 10 cm on 21 May 1991, with 21-cm spacings within the row and 0.86 m between rows. The research site was irrigated and managed following soil test results for fertility, weeds, and pests, according to conventional recommendations for commercial production of potatoes in Michigan.

Pathogen population densities were transformed using ln(x+1) for ANOVA procedures and regression analyses. Appropriateness of linear regressions of the tuber yields of *S. tuberosum* over pathogens fitted for each cropping scheme was evaluated by r^2 values. A DWLS computer model was used to view the tuber yield response surface of *S. tuberosum*.

4.3.3 Results

Nature of P. penetrans and V. dahliae interactions associated with S. tuberosum. Synergistic, additive, and antagonistic influences of P. penetrans and V. dahliae on S. tuberosum occurred once (Table 4.3.2), nine times (Table 4.3.2-4) and two times (Table 4.3.2-4), respectively in this research.

Nature of S. tuberosum basal-nodal root system and stolon system interactions associated with P. penetrans and V. **dahliae.** Additive and antagonistic influences of *S. tuberosum* basal-nodal root system and stolon system on tuber yields associated with *P. penetrans* and *V. dahliae* occurred five times, respectively (Table 4.3.5-9). There was no occurrence of synergistic influences of *S. tuberosum* basal-nodal root system and stolon system associated with *P. penetrans* and *V. dahliae* in this research.

Additive joint influences of *S. tuberosum* basal-nodal root system and stolon system on tuber yields occurred when 1) both plant systems were associated with *P. penetrans;* and 2) both plant systems were associated with *V. dahliae* (Table 4.3.5-7). It also occurred when the basal-nodal root system was associated with *V. dahliae*, and stolon system was associated with *P. penetrans* in Experiment A, but it did not occur in Experiment B (Table 4.3.7).

Antagonistic joint influences of *S. tuberosum* basal-nodal root system and stolon system on tuber yields occurred when 1) basal-nodal root system was associated with *P. penetrans*, and stolon system was associated with *V. dahliae*; and 2) both plant systems were associated with *P. penetrans* and *V. dahliae* interactions (Table 4.3.7-8). It also occurred when the basalnodal root system was associated with *V. dahliae*, and stolon system was associated with *V. dahliae*, and stolon system was associated with *P. penetrans* in Experiment B, but it did not occur in Experiment A (Table 4.3.7-8).

Individual and joint influence of P. penetrans and V. dahliae. The impact of P. penetrans on the basal-nodal root system of S. tuberosum was less severe than V. dahliae (Table 4.3.10). The impact of P. penetrans and V. dahliae on the stolon system of S. tuberosum was about equal. The joint impact of P. penetrans and V. dahliae on the basal-nodal root system and stolon system of S. tuberosum was probably additive (Table 4.3.2-3).

Pratylenchus penetrans was equally pathogenic on the basal-nodal root system and stolon system of *S. tuberosum* (Table 4.3.11). Joint impact of *P. penetrans* on basal-nodal root system and stolon system was probably additive. Verticillium dahliae was much more pathogenic on the basalnodal root system than the stolon system of *S. tuberosum* (Table 4.3.11). Joint impact of *V. dahliae* on the basal-nodal root system and stolon system was probably additive, but might be antagonistic (less yield loss than the predicted).

Antagonistic responses (less inhibition than predicted) occurred when both below-ground components were exposed to joint impact of *P. penetrans* and *V. dahliae* (4.3.8). The impact of *P. penetrans* on the basal-nodal root system of *S. tuberosum*, plus the impact of *V. dahliae* on the stolon system, resulted in antagonistic responses (Table 4.3.7). The impact of *V. dahliae* on the basal-nodal root system of *S. tuberosum*,

plus the impact of *P. penetrans* on the stolon system, resulted in an additive or antagonistic response (Table 4.3.7).

P. penetrans and V. dahliae interactions associated with a three-year S. tuberosum ecosystem. The highest preplant population density of V. dahliae (34 cfu/g soil) coupled with P. penetrans population density of 12 per 100 cm³ of soil was observed in the sudax-sudax-potato rotation scheme which resulted in the lowest potato tuber yields. The highest preplant P. penetrans population density (54/100 cm³ soil) coupled with V. dahliae population density of 19.5 cfu per gram of soil was observed in the corn-corn-potato rotation scheme which resulted in the second lowest potato yield in 1991. Both the two-year legume and two-year grain rotations with potatoes resulted in significantly (P < 0.01) lower P. penetrans population densities at the end of the three year rotation compared to three years of continuous potato production. Average potato tuber yield responses over all cropping regimes provided a negative regression with the natural log of preplant V. dahliae population density (r^2 = 0.53), P. penetrans population density $(r^2 = 0.38)$, and both pathogens $(r^2 = 0.75)$ at end of the three-year rotation (Figure 4.3.1).

4.3.4 Discussion

The two pathogens have different pathogenic impacts on

different components of the below-ground system of *S*. tuberosum. At relatively high population densities and when *V*. dahliae is impacting something other than the basal-nodal root system, the joint impact is additive. When *V*. dahliae is at relatively high population densities, and associated with the basal-nodal root system, the reverse S curve theory applies and the resulting yield inhibition is significantly less than expected or antagonistic (Figure 4.3.2). Soil environmental conditions in relation to the activity of *V*. dahliae and the rate of development of *S*. tuberosum would have a major impact on the severity of PED in a specific growing season.

Basal-nodal root system impact appeared to be dependent on preplant population densities of *P. penetrans* and *V. dahliae*. High and low preplant population densities of these organisms resulted in less and more impact on *S. tuberosum* than predicted, respectively (Table 4.3.2-). The stolon system impact appeared to take the same trend (Table 4.3.3).

Synergism, additivity, and antagonism were introduced as terms describing the nature of the *P. penetrans* and *V. dahliae* interactions associated with *S. tuberosum* where the predicted concomitant influence of both pathogens on the third organism, *S. tuberosum*, is either greater, the same, or less than the sum of the effects of the individual organisms. This study developed a statistical testing procedure to test the

quantitative nature of the *P. penetrans* and *V. dahliae* interactions associated with *S. tuberosum*. A synergistic influence of *P. penetrans* and *V. dahliae* on *S. tuberosum* occurs when the predicted joint impact of these organisms is greater significantly (P = 0.05) than the actual joint impact of these organisms. An additive joint influence of *P. penetrans* and *V. dahliae* on *S. tuberosum* occurs when the predicted joint impact of these organisms is the same (P =0.05) as the actual joint impact. An antagonistic joint influence of *P. penetrans* and *V. dahliae* on *S. tuberosum* occurs when the predicted joint impact of these organisms is less significantly (P = 0.05) than the actual joint impact of these organisms. (Table 4.3.4).

In most of the growth chamber and greenhouse studies, the predominantly *P. penetrans* and *V. dahliae* interactions associated with *S. tuberosum* observed were additive. Most of the additive nature of *S. tuberosum* basal-nodal root system and stolon system interactions were associated with the same pathogen, *P. penetrans* or *V. dahliae*. Most of the antagonistic nature of *S. tuberosum* basal-nodal root system and stolon system interactions were associated with *P. penetrans* and *V. dahliae*. Additive or antagonistic nature of *S. tuberosum* basal-nodal root system interactions associated with *P. penetrans* and *V. dahliae*. Additive or antagonistic nature of *S. tuberosum* basal-nodal root system interactions associated with *P. penetrans* and *V. dahliae*. Additive or antagonistic nature of *S. tuberosum* basal-nodal root system interactions

independent nature of the plant systems.

The r^2 value of tuber yield in regression with the natural log of preplant densities of *P. penetrans* or *V. dahliae* alone in the three-year *S. tuberosum* ecosystem study is much lower than that of both pathogens. This may suggest a *P. penetrans* and *V. dahliae* interaction. Francl et al. (1987) constructed regression and discriminant models relating preplant soil population levels of both fungus and nematode to subsequent tuber yield. The minimum population of fungal propagules necessary to cause at least a 10% yield reduction in the absence of nematodes was 11-18 cfu/cm of soil. In most cropping regimes of this ecosystem study, *S. tuberosum* tuber yields were more highly correlated with *V. dahliae* than *P. penetrans*; and in all cases, the regressions produced the best-fit when tuber yields of *S. tuberosum* were regressed with both *V. dahliae* and *P. penetrans* population densities.

Strong interactions appeared to occur at preplant P. penetrans densities of less than ca. 30 nematodes per 100 cm³ of soil in the disease complex (Figure 4.3.2). There has been little research on the effect of combined infection by these pathogens on tuber quality. More small B-size tubers were recovered and were highly correlated with the presences of V. dahliae and P. penetrans at the beginning of the 1991 season. It is evidence that continued work is needed in this area.

A-F.	
Experiments	
for	
design	
Research	
4.3.1.	
Table	

	<i>Pratylenchus penetrans</i> culture	Verticillium dahliae isolate	Inoculum level	Seed tuber	Research location
A	Pisum sativum	H2	High	15 g	Greenhouse
Д	P. sativum	Н2	High	15 g	Greenhouse
υ	P. sativum	Н2	Low	15 g	Growth chamber
D	P. sativum	Н2	High	15 g	Growth chamber
ជ	P. sativum	355	High	27 g	Greenhouse
٤	Zea mays	355	High	15 g	Growth chamber

Table 4.3.2. Individual and joint influences of *Pratylenchus penetrans* and *Verticillium dahliae* on tuber fresh weight of *Solanum tuberosum* when basal-nodal root system is exposed to these organisms.

	μ	ber Yield	Inhibiti	on in Ex	periments	A-F
Pathogen	A	В	ບ	D	ធ	મિ
Inoculum level	(High)	(High)	(TOW)	(High)	(High)	(High)
Pratylenchus penetrans	13.8 g	10.1 g	4.6 g	5.1 g	13.5 g	6.4 g
Verticillium dahliae	21.1 g	18.1 g	6.1 g	14.2 g	17.2 g	10.7 g
Joint Influence (Predicted)	34.9 g	28.2 g	10.7 g	19.3 g	30 . 7 g	17.1 g
Joint influence (Actual)	27.8 g	25 . 5 g	16.4 g	15.1 g	25.8 g	19.5 g
Difference = Predicted - Actual	7.1 g	2.7 g	– 5.7 g	4.2 g	4.9 g	- 2.4 g
P value of t-test	> 0.05	> 0.05	0.05	0.05	> 0.05	> 0.05

99 . Table 4.3.3. Individual and joint influences of *Pratylenchus penetrans* and *Verticillium dahliae* on tuber fresh weight of *Solanum tuberosum* when stolon system is exposed to these organisms.

	E	uber Yiel	d Inhibit	ion in Ex	kperiment	s A-F
Pathogen	A	а	υ	Q	ы	ĹŦŧ
Inoculum level	(High)	(High)	(Low)	(High)	(High)	(High)
Pratylenchus penetrans	8 . 1 g	11.8 g	5 . 3 g	5.6 g	12.3 g	7.5 g
Verticillium dahliae	8.5 g	10.4 g	4.7 g	8.4 g	12.1 g	9.2 g
Joint Influence (Predicted)	16.6 g	22.2 g	10.0 g	14.0 g	24.4 g	16.7 g
Joint influence (Actual)	13.2 g	17.2 g	12.4 g	15.2 g	17.8 g	18.6 g
Difference = Predicted - Actual	3.4 g	5.0 g	- 2.4 g	- 1.2 g	6.6 g	- 1.9 g
P value of t-test	> 0.05	> 0.05	> 0.05	> 0.05	0.05	> 0.05

Pratylenchus penetrans and Verticillium dahliae interactions associated with Solanum tuberosum. Statistical nature of Table 4.3.4.

Joint Influence	Predicted - Actual	P value	No. Occurrences in Experiments A - F
Synergistic	Z1 > Z2	0.05	1
Additive	Z1 = Z2	0.05	6
Antagonistic	Z1 < Z2	0.05	2

Z1 = Actual joint impact

Z2 = Predicted joint impact = X + Y

- X = Impact on tuber weight by *Pratylenchus penetrans*
- Y = Impact on tuber weight by Verticillium dahliae

Table 4.3.5. Individual and joint influences the basal-nodal root system and stolon system infected with *Pratylenchus penetrans* on tuber fresh weight of *Solanum tuberosum*.

		Tuber Yield Inhibiti	on in Experiments A&B
Plant Component	Pathogen	А	В
Basal-nodal root system:	P. penetrans	13.8 g	10.1 g
Stolon system:	P. penetrans	8.1 g	11.8 g
Joint Influence (Predicted	d)	21.9 g	21.9 g
Joint influence (Actual)		17.5 g	18.6 g
Difference = Predicted - 1	Actual	4.4 g	3.3 g
P value of t-test		> 0.05	> 0.05

stolon	erosum.
and	tube
system	Solanum
root	of
-nodal	weight
basal	fresh
of the	tuber
influences	dahliae on
al and joint	Verticillium
5. Individ	ected with
le 4.3.(tem inf
Tabj	syst

Plant Component	Pathogen	ruber Yield Inhibitio	on in Experiments A&B
Basal-nodal root system:	V. dahliae	18.1 g	21.1 g
Stolon system:	V. dahliae	10.4 g	8.5 g
Joint Influence (Predicted	d)	28.5 g	29.6 g
Joint influence (Actual)		23.0 g	23 . 8 g
Difference = Predicted - 1	Actual	5.5 g	5 . 8 g
P value of t-test	·	> 0.05	> 0.05

Table 4.3.7. Individual and joint influences of the basal-nodal root system and stolon system infected with Pratylenchus penetrans or Verticillium dahliae on tuber fresh weight of Solanum tuberosum.

		Tuber Y	ield Inhi	bition in Exp	eriments	A & B
Plant Component	Pathogen	A	В	Pathogen	A	В
Basal-nodal root system:	P. penetrans	13.8 g	10.1 g	V. dahliae	21.1 g	18.1 g
Stolon system:	V. dahliae	8.5 g	10.4 g	P. penetrans	8.1 g	11.8 g
Joint Influence (Predicted	d)	22.3 g	20.5 g		29.2 g	29 . 9 g
Joint influence (Actual)		15.8 g	13.8 g		24.3 g	13.8 g
Difference = Predicted - <i>I</i>	Actual	6.5 g	6.7 g		4.9 g	7.1 g
P value of t-test		0.05	0.05		> 0.05	0.05

weight of Solanum tuberosu	• •		
		Tuber Yield	Inhibition
Plant component	Pathogen	Experiment A	Experiment B
Basal-nodal root system:	P. penetrans + V. dahliae	27.8 g	25 . 5 g
Stolon system:	P. penetrans + V. dahliae	13.2 g	17.2 g
Joint Influence (Predicted)		41.0 g	42.7 g
Joint influence (Actual)		29 . 1 g	27.3 g
Difference = Predicted - A	ctual	10.9 g	15.4 g
P value of t-test		0.05	0.05

Table 4.3.8. Individual and joint influences of the basal-nodal root system and stolon system infected with *Pratylenchus penetrans* and *Verticillium dahliae* on tuber fresh

system interrelationships associated with Pratylenchus penetrans and Verticillium Table 4.3.9. Statistical nature of Solanum tuberosum basal-nodal root system and stolon dahliae.

Joint Influence	Predicted - Actual	P value	No. Occurrences in Experiments A & B
Synergistic	Z1 > Z2	0.05	0
Additive	Z1 = Z2	0.05	£
Antagonistic	Z1 < Z2	0.05	£

- Z1 = Actual joint impact
- Z2 = Predicted joint impact = X + Y
- X = Impact on tuber weight by Pratylenchus penetrans
- Y = Impact on tuber weight by Verticillium dahliae

on tuber fresh weight of <i>Solanum</i> t	uberosum.	
	Tuber Yiel	d Inhibition
- Plant Component	P. penetrans	V. dahliae
Basal-nodal root system:	12.0 g	20.0 g
Stolon system:	10.0 g	9.5 g
Both systems:	18.1 g	23.4 g

Table 4.3.10. Individual influences of Pratylenchus penetrans and Verticillium dahliae

107

6.0 g

3.9 g

Less

Yield inhibit than predicted

σ

18.1

Less

σ

23.4

29.4 g

22.0 g

Joint Influence (Predicted)

Joint influence (Actual)

Difference

	Tuber Yield Inh	libition
Pathogen	Basal-nodal root system	Stolon system
P. penetrans	8.9 g	8.4 g
V. dahliae	15.7 g	8.9 g
P. penetrans + V. dahliae	21.7 g	15.7 g
Joint Influence (Predicted)	21.9 g	17.3 g
Joint influence (Actual)	18.1 g	15.7 g
Difference	3.8 д	1.6 g
Yield inhibit than predicted	Less	Less

Table 4.3.11. Joint influences of *Pratylenchus penetrans* and *Verticillium dahliae* on tuber fresh weight of *Solanum* tuberosum.

		Tuber Yield]	Inhibition		1
<pre>Below-ground plant component:</pre>	Basal-nodal	root system	Stolon	system	1
Levels of pathogen inoculum:	High	Low	High	LOW	
P. penetrans	9.8 g	4.6 g	9.1 g	6.1 g	1
V. dahliae	16.8 g	10.1 g	9.4 g	7.4 g	
P. penetrans + V. dahliae	22.7 g	16.4 g	16.4 g	15.4 g	
**********************************				 	1
Joint Influence (Predicted)	26.6 g	14.7 g	18.4 g	13.5 g	
Joint influence (Actual)	22.7 g	16.4 g	16.4 g	15.4 g	
Difference	3.9 g	1.7 g	2.0 g	1.9 g	
Yield inhibit than predicted	Less	More	Less	More	

Table 4.3.12. Joint influences of *Pratylenchus penetrans* and *Verticillium dahliae* on tuber fresh weight of *Solanum* tuberosum at two inoculum levels.

frach		inf	luences (of	Pratylenc	chus p	enetrans	and Vert	Lici.		m da	<i>hliae</i> on research
-	JIIGTON	10	INDIDUCTOO	L CL			арестат	TOTOTOT	ר נ	ç		T COCAT CII

		Tuber Y	ield Inhibition	
Experiment Location:	Growt	ch Chamber	Gree	enhouse
Plant Component: Bas	al-Nodal Root	Stolon System	Basal-Nodal Root	Stolon System
P. penetrans	5.4 g	6.1 g	12.5 g	10.7 g
V. dahliae	11.7 g	7.4 g	19.7 g	10.3 g
P. penetrans + V. dahliae	17.0 g	15.4 g	26.4 g	16.1 g
Joint Influence (Predicted) I/.I g	13.5 g	32.2 g	21.1 g
Joint influence (Actual)	17.0 g	15.4 g	26.4 g	16.1 g
Difference	0.1 g	1.9 g	5.8 g	5.0 g
Yield inhibit than predict	ed Less	More	Less	Less

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V & N: Verticillium & Nematode

Figure 4.3.1. r Square values in regressions of potato yields with Pratylenchus penetrans and Verticillium dahliae disease complex under a three-year Solanum tuberosum ecosystem.



Disease Complex Severity Index

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Figure 4.3.2. Plant disease reverse S curve theory.

4.4. Linear, spatial, and space features of *Pratylenchus* penetrans and *Verticillium dahliae* interactions associated with *Solanum tuberosum* in an agroecosystem.

4.4.1. Linear Model

4.4.1.1. Introduction

P. penetrans and V. dahliae interactions associated with S. tuberosum in an ecosystem were analyzed several ways. First, each variable was analyzed separately, then the bivariate features of the interactions were analyzed. The univariate approaches are used to describe the distributions of individual variables. The bivariate approaches are used to describe the relationships and dependencies between variables in the interactions.

4.4.1.2 Materials and Methods

Field experiments with a 10 x 10 grid of an ecosystem associated with *S. tuberosum* stressed by *P. penetrans* and *V. dahliae* interactions were conducted at Michigan State University Montcalm Potato Research Farm, Entrican, Mid-Michigan in 1991, 1992, and 1993; and Jon Haindl's Farm, Cook, Upper Peninsula of Michigan in 1993.

The grid-ecosystem used in this study consists of several variables measured at each of one hundred sample points on the rectangular grid system. The continuous variables were the population densities of *P. penetrans* and *V. dahliae*, and tuber

yields of *S. tuberosum*. The discrete variable was viewed as a number that assigns each point to one of two possible categories, the presence or absence of PED symptoms and the presence or absence of the pathogens.

All S. tuberosum plants were uniformly distributed in a geo-referenced research site. A plant is located in the central spot of the area (34 x 34 inches, or 86.36 x 86.36 centimeters, or 0.8636 x 0.8636 meters). The 100 plants of the Loc 1 - Loc 100 are uniformly distributed 34 inches, or 0.8636 meters apart (Figure 4.4.1.1).

4.4.1.3 Results

Univariate features of P. penetrans and V. dahliae interactions associated with S. tuberosum.

The normal probability plot of 100 *P. penetrans* data resulted in a straight line, although some values departed from the trend. It indicated that the *P. penetrans* distribution had properties that favored its use in theoretical approaches to estimation (Figure 4.4.1.2). The straight line also exhibited a normal population density distribution between 10 and 50 *P. penetrans* per 100 cm³ soil. A lognormal probability plot of the same 100 *P. penetrans* data showed same trend (Figure 4.4.1.3).

Bivariate features of *P. penetrans* and *V. dahliae* interactions associated with *S. tuberosum*. A q-q plot indicated that there was a similarity in distributions of *P. penetrans* and *S. tuberosum* biomass (Figure 4.4.1.4)

The 100 pairs of *P. penetrans* and *S. tuberosum* interaction values were shown on a scatterplot in Figure 4.4.1.5). Though there was some scatter in the cloud of points, the larger values of the *P. penetrans* population densities tended to be associated with the smaller values of the *S. tuberosum* tuber yields.

The increase of the *P. penetrans* population density resulted in a decrease of the *S. tuberosum* tuber yields. The covariance was used as a summary statistic of the scatterplot. The covariance of *P. penetrans* and *S. tuberosum* interactions was -1788.94. The correlation coefficient was -0.496, where the scatterplot appeared as a cloud of points. A measure of the linear relationship of *P. penetrans* and *S. tuberosum* was provided by the correlation coefficient. The rank correlation coefficient was - 0.561 for *P. penetrans* and *S. tuberosum* interactions. A line was superimposed on the scatterplot for the linear relationship (Figure 4.4.1.6)

4.4.1.4 Discussion

A normal and lognormal probability plot of the 100 P. penetrans data indicated that the P. penetrans distribution and properties favored its use in theoretical approaches to

estimation. The shape of the plot clearly indicated that the values were distributed lognormally.

Some of the most important and interesting features of *P*. *penetrans* and *V*. *dahliae* interactions and pathogen-host interactions are the relationships and dependencies between variables including the comparison of the two distributions, scatterplots, h-scatterplots, moving window statistics, correlation, and linear regression.

A q-q plot of two identical distributions plot as the straight line x = y. For distributions that are very similar, the small departures of the q-q plot from the line x = y will reveal where they differ. For the biological distributions in the Montcalm Data Set, a q-q plot of two distributions is some straight line other than x = y, then the two distributions have the same shape but their location and spread may differ. The similarity of an observed distribution to any theoretical distribution model can be checked by the straightness of their q-q plot.

Scatterplot is the most common display of the bivariate feature of the biological interaction. It is necessary in the early stages of the study to check and clean the data; the success of any estimation method depends on the reliability of the data. The scatterplot can be used to help both in the validation of the initial data and in the understanding of later results.

A strong interaction between two variables can help us predict one variable if the other is known. The simplest way we can do is linear regression, in which we assume the dependence of one variable on the other. It can be described by the equation of a straight line. The slope is the correlation coefficient multiplied by the ratio of the standard deviations of *P. penetrans* and *S. tuberosum* interactions.
Geo-referenced Research Site 10 X 10 Grid of Ecosystem



Figure 4.4.1.1. Geo-referenced research site of 10 x 10 grid of Solanum tuberosum ecosystem.



Figure 4.4.1.2. Pratylenchus penetrans population normal probability plot.



P. penetrans/100 cm³ soil

Figure 4.4.1.3. Pratylenchus penetrans population lognormal probability plot.



q1

Figure 4.4.1.4. The q-q plot of *Pratylenchus penetrans* populations versus *Solanum tuberosum* tuber yields.



Figure 4.4.1.5. Scatterplot of *Pratylenchus penetrans* populations versus *Solanum tuberosum* tuber yields.



Figure 4.4.1.6. The linear regression line superimposed on the scatterplot of *Pratylenchus penetrans* and *Solanum tuberosum* interactions.

4.4.2 Spatial Model

4.4.2.1 Introduction

Geostatistics is a set of statistical tools which offer a way of identifying, quantifying and analyzing spatial relationships in geo-referenced data. One of the important characteristics of P. penetrans and V. dahliae interactions associated with S. tuberosum is that the interactions exist some locations in two-dimensions. The spatial description describes the degree of continuity, the overall trend, and the location of the extreme values. Spatial features of P. penetrans and V. dahliae interactions associated with S. tuberosum included the location of extreme values, the overall trend, and the degree of continuity. None of the univariate and bivariate descriptive tools capture spatial features. The objective of this study was to look at the spatial aspects P. penetrans and V. dahliae associated with S. tuberosum, including contour maps, indicator maps, correlation functions, covariance functions, and variograms.

4.4.2.2 Materials and Methods

Ecosystem. Biological information of *P. penetrans* and *V. dahliae* interactions associated with *S. tuberosum* in an ecosystem was derived from a 10 x 10 grid of ecosystems associated with uniform potato plants along with the presence of various *P. penetrans* and *V. dahliae* combinations at

Michigan state University Montcalm Potato Research Farm, and Jon Haindl's Farm. Organization and presentation were considered to in communicating the essential feature of *P. penetrans* and *V. dahliae* interactions associated with *S. tuberosum* in a large spatial agroecosystem. The spatial biological information obtained by the descriptive tools as desired was used later to perform semivariance analysis and create optimal isopleths of the variates examined, with the use of kriging to derive interpolated map values and associated variance estimates.

Autocorrelating Biological Data. Autocorrelation analysis provides a quantitative estimate of the degree to which sample points in space (or time) are correlated with one another by virtue of distance. Because samples taken closer together are typically more closely related than are points taken from locations farther apart, it is useful to calculate autocorrelation indices for pairs of points separated by a variety of "lag" distances. The resulting graph of autocorrelation vs. different lag distances yields a composite picture of spatial or temporal autocorrelation in biological interactions.

Semivariance is a type of spatial autocorrelation analyses are provided for quantifying spatial dependence. The plot of semivariance of lag distance class h vs. all h's evaluated is the semivariogram. Semivariance analysis includes a least squares algorithm for fitting viable semivariogram models. Semivariance analysis is relatively sensitive to skewed frequency distributions. Because a lot of biological data tend to be log-normally distributed, the data can be normalized by choosing an appropriate data transformation ln(z+1). Semivariance analysis can also be very sensitive to active step size and active lag distance. The smaller the step size, the greater the number of lag classes but the fewer the number of sample pairs in each class and thus the greater the "noise" in the semivariogram.

There are five potential isotropic models. They are linear, linear to sill, spherical, exponential, and Gaussian models, each of them defined in terms of nugget variance (Co), sill (structural variance C + Co), and range (Ao) parameters.

Kriging Biological Data. Kriging provides a means of interpolating values for points not physically sampled using knowledge about the underlying spatial relationships in a data set to do so. Semivariograms provide this knowledge. Kriging is based on regionalized variable theory and is superior to other means of interpolation because it provides an optimal interpolation estimate for a given coordinate location as well as a variance estimate for the interpolation value. Two types of interpolation statistics are provided, block kriging and punctual kriging. Because the nematode samples were taken to represent an area around the actual sample point, the block kriging was more appropriate and selected. If samples were taken to represent point values in a field, or in time, however, then punctual kriging is more appropriate.

Mapping Biological Data. The spatial biological relationships in the geo-referenced *S. tuberosum* ecosystem was used to create optimal and kriged maps of the variate for the geographic area of interest.

Two-dimensional maps are presented as pattern isopleths with isopleth contour intervals. The map resolution for the nematode population and potato tuber yields was controlled by the interpolation interval at which the data were kriged. The minimum value for contour level 1 is always the minimum value for z within the range mapped; the maximum level for the highest contour level is always the maximum value for z within the range mapped. The automatic five levels of the contour was chosen for mapping *P. penetrans* population and *S. tuberosum* tuber yields.

4.4.2.3 Results

The overall trends for the distributions of *P. penetrans* distribution were described using a contour map generated by computer (Figure 4.4.2.1). The closeness of the contour lines in the southwestern corner indicated a steep gradient and drew

attention to the fact that the highest data value is very close to the lowest data value.

The *P. penetrans* population density ranges of less than 10, 30, 50, and 70 were used as thresholds rather than each individual value itself. Four classes of the *P. penetrans* population densities were designated. A grayscale map (Figure 4.4.2.2) provided an excellent visual summary of the data.

A series of six indicator maps corresponding to the six class boundaries from the symbol map were showed in Figure 4.4.2.3. Each map indicated in white the data locations at which the *P. penetrans* population density was less than the given threshold and in black the locations at which *P. penetrans* population density was greater than or equal to the threshold. This series of indicator maps recorded the transition from high *P. penetrans* population densities that tended to be aligned in an east to west direction to low nematode population densities.

The linear isotropic model described a straight line semivariogram, and was not appropriate for the *P. penetrans* population in this study. The linear/sill isotropic model had an r^2 value of 0.903 for *P. penetrans*. The spherical isotropic model had an r^2 value of 0.902 for *P. penetrans*, and was a modified quadratic function. The exponential isotropic model was found with a relatively low r^2 value of 0.601 for the *P*.

penetrans population. The Gaussian isotropic model was found with a r^2 value of 0.901 for *P. penetrans* population (Table 4.4.2.1).

Five anisotropic models were also used to evaluate geometric anisotropy, which presumed different C's and ranges for each direction examined but identical Co's. They were linear ($r^2 = 0.401$), linear to sill ($r^2 = 0.676$), spherical ($r^2 = 0.659$), exponential ($r^2 = 0.414$), and Gaussian ($r^2 = 0.669$) models.

4.4.2.4 Discussion

The contour map provided a helpful visual display. Some features that were not obvious from the data posting alone became more prominent. It is noted that the contour map may be useful in qualitative displays with questionable quantitative significance.

It is probable that nematode distributions in some locations are more variable than in others. Such anomalies may have practical biological implications. The calculation of a few summary statistics within moving windows can be used to investigate anomalies both in the average value and in the area is divided into several variability. The local neighborhoods of equal size and within local each neighborhood, or window, summary statistics are calculated. The uniformity in the local means indicates generally well behaved data values. If the uniformity does not exist, then we may look for what causes the big variations. Here we see that the mean *P. penetrans* population density ranges from 19 to 34, a 1.79- fold difference. The mean *S. tuberosum* tuber yields range from 783 to 1954 grams, a 2.5-fold difference. The standard deviations of *P. penetrans* population density range from 7 to 15, a 2.14-fold difference; and the *S. tuberosum* tuber yield standard deviations range from 194 to 376, a 1.93fold of difference. It is interesting to note that less anomaly of *P. penetrans* population resulted in more anomaly of *S. tuberosum* tuber yields.



Figure 4.4.2.1. Computer generated contour map of *Pratylenchus penetrans* at intervals of 10 nematode/100 cm³ soil.



Figure 4.4.2.2. Pratylenchus penetrans population grayscale map with 4 classes of densities: 10. 30, 50, and 70 nematode/100 cm³ soil.





≥ 10 P. penetrans/100 cm³ soil





Figure 4.4.2.4. Local means and local variability of 16 *Pratylenchus penetrans* population densities.



Figure 4.4.2.5. Semivariogram spherical model for *Pratylenchus* penetrans,



Estimated Pratylenchus penetrans population densities and Solanum tuberosum tuber yield maps (676 points/map developed from two-dimensional kriging of a best-fit spherical model. Figure 4.4.2.6.

4.4.3 Space Model

4.4.3.1 Introduction

A space model in this research and the spatial model presented in 4.4.2 were a three-dimensional and twodimensional study, repectively. The objectives of this threedimensional study were to 1) investigate stereo effects and distribution of *Pratylenchus penetrans* and *Verticillium dahliae* interactions associated with *Solanum tuberosum*; and 2) present a mathematical three-dimensional model of *S. tuberosum* tuber yield response surface associated with *P. penetrans* and *V. dahliae* interactions in an ecosystem.

4.4.3.2 Materials and Methods

An S. tuberosum field ladder-shaped polyhedron model representing a north-south field-row $(0.4 \text{ m}^2 \times 0.8 \text{ m}^2 \times 0.3 \text{ m})$ was used in this study (Figure 4.4.3.1). The ladder-shaped soil polyhedron was sampled in two dimensions, and then in the third dimension. Sixty samples were collected from the 6 x 10 sectors of upper zone (ca. 0.5 x 0.9 x 0.1 m), 80 from the 8 x 10 sectors of middle zone $(0.7 \times 0.9 \times 0.1 \text{ m})$, and 100 from the 10 x 10 sectors of lower zone (0.9 x 0.9 x 0.1 m) (Figure 4.4.3.2).

A computer-based three-dimensional imaging methodology was used to visualize numerical image representations, manipulate & display electronic biological and ecological

imaging, extract desired information from the threedimensional data set, and cognition and understanding of the image content and spatial relationships.

A three-year S. tuberosum ecosystem associated with P. penetrans and V. dahliae was used in this study to reveal a three-dimensional tuber yield response surface.

4.4.3.3 Results

P. penetrans population densities in the upper, middle, and lower zones were 1.8, 8.7, and 14.4 nematodes per 100 cm³ soil, respectively. *Verticillium dahliae* population densities in the upper, middle, and lower zones were 2.0, 0.6, and 0.7 cfu per 1.0 g dry soil, respectively (Table 4.4.3.1).

P. penetrans populations were distributed independently in the upper and middle zones, but in a spatially dependent distribution in the lower soil cuboid zone (Table 4.4.3.2). Verticillium dahliae distributions appeared to be independent.

Population densities of *P. penetrans* and *V. dahliae* were associated with the three-dimensional-visualizing sub-divided Solanum tuberosum polyhedron system (Table 4.4.3.3-4)

Three-dimensional distributions of the soilborne-organism imaging was computer-stereopercepted (Figure 4.4.3.3).

A three-dimensional S. tuberosum tuber yield response surface associated with P. penetrans and V. dahliae interactions was presented by a mathematical model (Figure 4.4.3.4).

4.4.3.4 Discussion

The three-dimensional soilborne-organism distribution imaging was useful in the computerized stereopercepting. Three-dimensional viewing & thinking may be a way of challenging nature in the future. A Potato Field Ladder-shaped Polyhedron Model



- * A north-south field-row (0.4m²x0.8m²x0.3m)
- 6x10 sectors of upper zone (0.5x0.9x0.1m)
- 8x10 sectors of middle zone (0.7x0.9x0.1m)
- 10x10 sectors of lower zone (0.9x0.9x0.1m)

Figure 4.4.3.1. Research site for a Solanum tuberosum field ladder-shaped polyhedron model associated with Pratylenchus penetrans and Verticillium dahliae.



- A Ladder-shaped Field-row Polyhedron -



- * Sampling in two dimensions, and then in the third dimension.
- 60 samples from the 6x10 sectors of upper zone
- 80 samples from the 8x10 sectors of middle zone
- * 100 samples from the 10x10 sectors of lower zone

Three-dimensional sampling methodology for space features of the Pratylenchus penetrans and Verticillium dahliae interactions. Figure 4.4.3.2.



Three-dimensional Pratylenchus penetrans distribution in a Figure 4.4.3.3. Three-dimensional Pratylenchus penetrans distributield at Montcalm Michigan State University Potato Research Farm.



response surface associated with Pratylenchus penetrans and Verticillium dahliae Figure 4.4.3.4. Three-dimensional presentation of Solanum tuberosum tuber yield interactions under cropping regimes in 1991.

 Table 4.4.3.1.
 Population
 densities
 of
 Pratylenchus
 penetrans
 and
 Verticillium

 dahliae
 in
 the
 sub-divided
 potato
 production
 polyhedron
 system.

Polyhedron Soil Zone	P. penetrans (100 cm ³ soil)	<i>V. dahliae</i> (cfu/1.0 g soil)
Upper	1.8	2.0
Middle	8.7	0.6
Lower	14.4	0.7

Table 4.4.3.2. Spatial relationship of the soilborne organism Pratylenchus penetrans and Verticillium dahliae.

V. dahliae	Independent	Independent	Independent
P. penetrans	Independent	Independent	Dependent
Polyhedron Soil Zone	Upper	Middle	Lower

Table 4.4.3.3. Population densities of *Pratylenchus penetrans*/100 cm³ soil in the sub-divided Solanum tuberosum production polyhedron system.

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9		16	
12		ω	
12		വ	
11		4	
10		ω	
7		11	
6		8	,
9	,	11	
2		12	1
1//-F		U-N	



Table 4.4.3.4. Population densities of Verticillium dahliae (cfu/g dry soil) in the sub-divided Solanum tuberosum production polyhedron system.

· ~
1.91 1.08



5.0 General Discussion

5.1 Implications of the manipulating Solanum tuberosum belowground system architecture and configuration.

The manipulating of the below-ground system of S. tuberosum below-ground system architecture and configuration was implemented in this dissertation research. The success of an in vitro excised root assay of this Solanaceous plant which accurately identified Lycopersicon esculentum Mill cultivars with known susceptibility and resistance to Meloidogyne incognita has been reported (Kofoi and White) Chitwood. The reported effectiveness of applying tissue culture in other S. tuberosum improvement efforts suggests that the application of an excised root assay for nematode resistance is feasible (Wang and Hu, 1985). A split root technique was employed to study the impact of pathogens associated with the PED on root deterioration (Kotcon and Rouse, 1984). The split root-stolon culture system used in this research enables us to study the impact of P. penetrans and V. dahliae on an isolated stolon system.

The potential of using tomato-potato hybrids for breeding will not be fully realized without a development of new techniques such as DNA transfers, engineering solanaceous plants, etc. (Taylor, 1987). It has been shown by further

grafting experiments that the foliage of a tomato scion cannot induce tuber formation in a potato stock, but can support the development of tubers which have been previously induced (Madec and Perennec, 1959). The isolated stolon system practiced in this research could be grafted into a tomato plant. The success in grafting a tomato-potato plant would offer exciting future for certain researches in nematology, plant pathology, and crop science.

5.2 Relationship between distances and the impact of Pratylenchus penetrans on Solanum tuberosum

It is practically impossible to sample every inch of the target area in biological field research. The impact of one biological population on another biological population over distances becomes a fascinating topic. The landscape ecology and geostatistics employed in this research may enable us to study relationship between distances and the impact of *Pratylenchus penetrans* on *Solanum tuberosum*. It can be studied using *P. penetrans* and *S. tuberosum* interactions as a model system. It can also be studied by applying statistical approaches and graphic approaches, such as the cross hscatterplot, correlation coefficient, rank correlation coefficient, distance weighted least squares smoothing, weighted quadratic multiple regression, and simple regression.

The concept of a cross h-scatterplot is developed through the idea of an h-scatterplot. Instead of pairing the value of one variable with the value of the same variable at another location, values of different variables at different location will be paired. It is obviously of an interest to nematologist, entomologists, and environmentalists due to the analysis of risk organisms and materials and their potential to damages in an area.

The correlation coefficient and the rank correlation

coefficient that we used to describe the spatial continuity of one variable, are also useful for describing the spatial continuity between two variables. The distance weighted least squares method was applied in this study (Figure 5.2.1) which is useful for a regression of one variable on another without being positive about the shape of the function.

In Figure 4.4.1.6, a cross h-scatterplot was superimposed between P. penetrans population densities and S. tuberosum tuber yields for h = (0, 0). More cross h-scatterplots (ht1-9) of the 100 P. penetrans and S. tuberosum yield data at various separation distances in the north-south direction were performed. The x-coordinate of each point is the P. penetrans population at a particular data location and the y-coordinate is the S. tuberosum yield data at a separation distance h to the north. Figure 4.4.1.6 could be considered as that the xcoordinate of each point corresponded to the nematode population and the y-coordinate to the potato yield data at the same location. A comparison between the ten h-scatterplots showed that as h increased, the relationship between the nematode population and potato yields over distances became weaker and appeared almost no correlation beyond some distances. There was a negative correlation between the nematodes and potato yields at the same location shown in Figure 4.4.1.6. The biological relationship between the nematode population and potato yields became progressively weaker over distance. There was almost no negative correlation occurred at a distance of 2.59 meters apart, and correlations fluctuated beyond a distance of 2.59 meters (Figure 5.2.1).

The Pearson correlation coefficients and Spearman rank correlation coefficients were calculated in this study. Figure 5.2.1 was produced by the calculated Pearson correlation coefficients over 7 distances. Distance weighted least squares fits a line through a set of points by least squares, and the surface is allowed to flex locally to fit the data better. Both Pearson correlation coefficients and Spearman rank coefficients could be used for the analysis and had a 2-3 time higher r^2 value in a *ca*. 7 m² area than in a *ca*. 9 m² area.

A simple linear regression model, with a multiple r value of 0.73, was temporarily used to analyze the impact of the nematode population on the potato tuber yields over distances:

Y = -0.295 + 0.062X

X: Separation distances between the analyzed nematode population and potato tuber yields. It ranges from 1 to 7 for this model, with a length of 0.8636 meter at each level.
Y: Correlation between the nematode population and potato yields over distances. A negative correlation means that nematode population have an impact of decreasing potato yield over distances.



Figure 5.2.1 The biological relationship between *Pratylenchus* penetrans population and *Solanum* tuberosum yields over distances.
5.3 Biological concept of two-on-one interactions

The dissertation research data had showed that combined effects of *P. penetrans* and *V. dahliae* on *S. tuberosum* could be synergistic, additive, or antagonistic. A biological concept of two-on-one interaction, other than one-on-one interaction, was then stimulated.

Reductionism asserts that if a phenomenon is to be understood, it needs to be reduced into its most basic elements. An understanding of the whole can be achieved by recombining the elements. Dealing with more complicated phenomena in nature, scientists attach importance on means of a synthesis of the parts to understand the whole as science proceeds into 21st century.

Plant pathologists, entomologists, and nematologist frequently note that a plant is attacked by two or more pests of the same or different kinds (Bird, 1981, Gage and Russell, 1987, Powell, 1971, Rowe, at al., 1985). In-depth studies in this area, like the effect of multiple-pest interactions on crops, help to drive the development of the disciplines of plant pathology, entomology, and nematology into a new stage. For the science of general biology, two-on-one interaction, other than one-on-one interaction, is yet to be explored.

The biological two-on-one interaction concept was developed in this research by exploring its qualitative and

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quantitative properties, with special reference to: 1) introduction of two-on-one interaction in nature; 2) construction of a Disease Complex Triangle model, 3) development of a statistical testing procedure, and 4) incorporation of mathematical functions.

Introduction of two-on-one interaction in nature. Synergism, additivity, and antagonism were proposed as terms describing the nature of two-on-one interactions that the predicted synthetic influence of two organisms on the third organism is either greater, same or less than the sum of the effects of the individual organism. Other related subjects of mode, model, mechanism, function, quantification, definition, flexibility, etc. could also be explored.

Construction of a Disease Complex Triangle model. In the discipline of plant pathology, a disease triangle is used to represent the interactions of three components of disease, which are pathogen, host, and environment (Agrios, 1988). This study introduced a disease complex triangle (Figure 2.1; 5.3.1) to visualize the two-on-one interactions of the disease complex. Each side of the triangle represents one of the three biological entities, which are *P. penetrans*, *V. dahliae*, and *S. tuberosum*. The shape and quantification of the triangle provided insights on the nature of two-on-one interactions and disease complexes. Major differences exist between the disease

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triangle and the disease complex triangle (Table 5.3.1).

Development of a statistical testing procedure. The quantitative plant disease interactions for synergism and antagonism are combined effect of a phytoparasite nematode and another plant disease organism is either greater or less than the sum of the effects of the individual organism. The study developed a statistical testing procedure using the PDDC as a model system (Table 4.3.4). A synergistic joint influence occurs when predicted joint impact of *P. penetrans* and *V. dahliae* on *S. tuberosum* is significantly (P = 0.05) greater than the actual joint impact. An additive influence occurs when predicted joint impact of *P. penetrans* and *V. dahliae* on *S. tuberosum* is the same (P = 0.05) as the actual joint impact. An antagonistic influence occurs when predicted joint influence occurs when predicted joint influence occurs when predicted joint influence occurs are the same (P = 0.05) as the actual joint impact. An antagonistic influence occurs when predicted joint impact. An antagonistic influence occurs when predicted joint impact of *P. penetrans* and *V. dahliae* on *S. tuberosum* is significantly (P = 0.05) less than the actual joint impact.

Incorporation of mathematical functions. An S-shaped curve (logistic function) differs from a geometric curve (exponential function) in two ways: 1) it has an upper asymptote, i.e., the curve does not exceed a certain maximal level; and 2) it approaches this asymptote smoothly, not abruptly (Krebs, 1989). The relationship between yield and tenderometer was described by a second-order polynomial (Steel and Torrie, 1980). The mathematical functions of exponential, logistic, and 2nd-order polynomial were hypothesized and linked with synergistic, additive, and antagonistic effects, respectively (Figure 5.3.2).

The development of a new biological concept of two-on-one interactions should lead us to provide insights into the nature of *P. penetrans* and *V. dahliae* interactions and disease complexes, potential concomitant impacts of *P. penetrans* and *V. dahliae* on the tuber production, and measure of control and pest management for potato crops. Potentials appear from existing pesticide researches to molecular biological studies.

Discussions showed, for example, that environment as the third side of the disease triangle was not a biological entity, but connected with the other two. Reduction of Newtonian mode of science might not be applied in the disease triangle for a disease in fields in which two or more pests are very likely involved.

Results should 1) add new insights on means of a synthesis of the parts to understand the whole for Newtonian mode of science; 2) help to drive the development of the disciplines of entomology, plant pathology, nematology, etc. into a new stage; and 3) fill a blank research area, two-onone interactions other than one-on-one, for science of general biology.

The two-on-one interaction is a triangle relationship

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among three entities. It is two-dimensional. It contains linear relationships between any two entities, and the one-onone interaction is influenced by the third entity. The joint effect of any two entities on the third entity is synergistic, additive or antagonistic. Numerous triangle and linear relationships exist when it is coupled with time, environment and society.

Although the one-on-one interaction is a fundamental way of thinking in science and human ecology, a new way of thinking and philosophy may be helpful and significant as we advance into 21st century. Discussions were optimistic that this new two-on-one concept could eventually rise to a law of nature, against or together with one-on-one interaction.



The Disease Complex Triangle

Figure 5.3.1. Graphical presentation of the disease triangle and the introduced disease complex triangle.



Figure 5.3.2. Mathematical functions of exponential, logistic, and 2nd-order polynomial associated with synergistic, additive, and antagonistic effects, respectively.

Table 5.3.1. Major differences between the disease triangle and the introduced disease complex triangle.

	m	Two-on-one	YES Reductionism	Reductionism by selection of one major pathogen	Easier measurement among three biological entities
Disease Triangle	N	One-on-one	No reductionism	No reductionism	Difficult measurement between environment and biological entity
	Biological Entities	Biological Interaction	Disease involving two pathogens	Disease involving more than two pathogens	Quantification

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6.0 Summary and Conclusion

The S. tuberosum below-ground system was divided into basal root, nodal root, stolon root, tuber root, stolon, tuber, and below-ground stem. A computer model was developed to simulate the growth and development of these below-ground system components under the PFE (Pathogen-Free Environment) and PIE (Pathogen-Impacted Environment). There were very significantly less basal root biomass and tuber yield of S. tuberosum under the pathogen-free environment than that under the pathogen-impacted environment. The computer simulation model was written in C++ language.

P. penetrans was recovered from all four types of roots. This nematode was recovered from the stolon as early as 30 days after planting. A young second-stage juvenile with a body length of 0.211 mm suggested that the reproduction of *P. penetrans* could be established in the stolon.

The exposition of stolon system to *P. penetrans* and/or *V.* dahliae resulted in significant tuber weight losses (P = 0,05). A maximum of 28.7% tuber weight loss (P = 0.05) was found in *S. tuberosum* when the stolon system was exposed to *P.* penetrans. The greatest tuber weigh loss of 66.2% occurred when both basal-nodal root system and stolon system of *S.* tuberosum were concomitantly exposed to *P. penetrans* and *V.*

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dahliae. The synergistic, additive, and antagonistic joint influence of *P. penetrans* and *V. dahliae* interactions associated with a *S. tuberosum* below-ground system occurred once, nine times, and twice in the growth chamber and greenhouse experiments, respectively.

P. penetrans was equally pathogenic on the basal-nodal root system and stolon system of S. tuberosum. Verticillium dahliae was much more pathogenic on the basal-nodal root system than the stolon system of S. tuberosum.

The impact of P. penetrans on the basal-nodal root system of S. tuberosum was less severe than V. dahliae. The impact of P. penetrans and V. dahliae on the stolon system of S. tuberosum was about equal. The joint impact of P. penetrans and V. dahliae on the basal-nodal root system and stolon system of S. tuberosum was probably additive.

The two pathogens have different pathogenic impacts on different components of the below-ground system of S. tuberosum. When V. dahliae is at relatively high population densities, and associated with the basal-nodal root system, the disease reverse S theory applied and the resulting yield inhibition is significantly less than expected or antagonistic. Soil environmental conditions in relation to the activity of V. dahliae and the rate of development of S. tuberosum would have a major impact on the severity of PED in a specific growing season.

Indicator maps were useful for illustrating *P. penetrans* population dynamics in space. Distributions properties of *P. penetrans & Solanum tuberosum* favored the used of theoretical approaches to estimation. A spherical semivariogram model ($r^2 = 0.902$) provided a quantitative estimate of the degree to which *P. penetrans* or *S. tuberosum* sample points in space are correlated with one another by virtue of distance. Kriging from 100 samples and a best-fit spherical model provided means of interpolating 676 points not physically sampled. There was very little negative correlation between *P. penetrans* and *S. tuberosum* at distances of equal or greater than 2.5 m. There was very little negative correlation between *P. penetrans* and *S. tuberosum* at distances ≥ 2.5 m.

Three-dimensional soilborne-organism distribution imaging was computer stereopercepted. Upper zones in the sub-divided S. tuberosum production polyhedron system resulted in less P. penetrans population densities than middle and lower zones. Upper zones in the sub-divided S. tuberosum production polyhedron system resulted in more V. dahliae population densities than middle and lower zones. Pratylenchus penetrans populations were in an independent distribution in the upper and middle zones, but in a spatial dependency distribution in soil cuboid Independent dahliae the lower zone. V.

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distributions were suggested.

The implication of manipulating *S. tuberosum* below-ground system architecture and configuration, relationships between distances and the impact of *P. penetrans* on *S. tuberosum*, and development of a new biological two-on-one interaction concept were discussed.

cout << "Please enter the type of soil that you wish to observe the\n"; cout << "Please enter the part of the Potato that'u"; cout << "11) Plant Growth and Development'n"; cout << "10) Above-Ground System'n"; cout << "9) Below-Ground System/n"; cout << "7) Below-Ground Stem'n"; cout << "is to be observedun"; cout << "8) Root System'n"; cout << "12) Main Menu/n"; cout << "2) Nodal Root/n"; cout << "3) Stolon Root'n"; cout << "1) Basal Root/n"; cout << "4) Tuber Root/n"; #Include "project.driver.h" cout << "2) Clean Sollun"; cout << "1) Field SollVn"; cout << "Potato in:\n"; cout << "5) Stolon/n"; #include <lostream.h> #include <lomanlp.h> cout << "6) Tuber\n"; double Growth, Day; int Option, Section; cin >> Option; cout << "\n"; cout << "h": cout << "\n": (plov) nisin р

cin >> Section;

while (Section == 12);

cout << "The growth of the Basal Root'n"; cout << "on the " << Day << " day after'n"; cout << "planting is " << Growth; cout << " grams.'n"; cout << "on the " << Day << " day after'n"; cout << "planting is " << Growth; cout << "u"; cout << "The growth of the Nodal Root'u"; cout << "to observe the particluar section ofu"; cout << "the Potato after it has been planted: \n"; cout << "Please enter the day that you wish'u"; Growth = Field_Nodal_Root (Day); Growth = Field_Basal_Root (Day); cout << "n"; switch (Section) { break; cout << "h": cout << "'n"; cin >> Day; switch (Option) case 1: case 1: case 2:

cout << "planting is " << Growth; cout << " grams.\n"; break;

case 3: Growth = Fleid_Stolon_Root (Day);

cout << """; cout << "The growth of the Stolon Rooth";</pre>

^{co}ut << "on the " << Day << " day aftervn"; **cout << "planting** is " << Growth;

case 4:

Growth = Field_Tuber_Root (Day);

cout << "on the " << Day << " day after\n"; cout << "The growth of the Tuber Root'n"; cout << "planting is " << Growth; cout << " grams.\n"; cout << "\n"; break;

case 5:

cout << "on the " << Day << " day after'n"; cout << "planting is " << Growth; cout << "The growth of the Stolon'n"; cout << " grams.\n"; cout << "\n"; Growth = Field_Stolon (Day); break;

case 6:

cout << "on the " << Day << " day after\n"; cout << "planting is " << Growth; cout << " grams.\n";</pre> cout << "The growth of the Tuberth"; cout << ""n": Growth = Field_Tuber (Day); break;

case 7:

cout << "The growth of the Below-Ground"; cout << " day after planting is " << Growth; cout << " Stem'n on the " << Day; cout << " grams.\n"; Growth = Field_Below_Stem (Day); cout << "\n"; break;

cout << " development on the " << Day << " day"; cout << "The growth of the Below-Ground"; cout << " System on the " << Day << " day"; cout << " after'n planting is " << Growth; cout << " System on the " << Day << " day"; cout << "The growth of the Root System'n"; cout << "The growth of the Above-Ground"; cout << "on the " << Day << " day after'u"; cout << " after/n planting is " << Growth; cout << " after'n planting is " << Growth; cout << "The growth of the Plant"; cout << "planting is " << Growth; cout << grams.\n'; cout << " grams.\n"; cout << " grams.\n"; cout << " grams.\n"; Growth = Field_Above_System (Day); Growth = Fleid_Below_System (Day); Growth = Field_Root_System (Day); Growth = Field_Plant_Growth (Day); cout << "n": cout << "n": cout << "n"; cout << "u": break; break; break; default: break; case 11: case 10: case 9: case 8:

cout << "Invalid Section'n";

break; }

break;

cout << "the Potato after it has been planted: \n"; cout << "to observe the particluar section ofun"; cout << "Please enter the day that you wish'n"; cout << "\n"; cout, << "\n"; case 2:

cin >> Day;

switch (Section) {

case 1:

Growth = Clean_Basal_Root (Day); cout << "\n";

cout << "on the " << Day << " day after h" cout << "The growth of the Basal Root'vi"; cout << "planting is " << Growth; cout << "grams.\n"; break;

case 2:

cout << "on the " << Day << " day after h"; cout << "The growth of the Nodal Root'n"; cout << "planting is " << Growth; cout << " grams.\n"; Growth = Clean_Nodal_Root (Day); cout << "\n"; break;

case 3:

Growth = Clean_Stolon_Root (Day); cout << "\n";

cout << "The growth of the Stolon Root'vn"; cout << "on the " << Day << " day after'n"; cout << "planting is " << Growth;

cout << " grams.\n"; break;

cout << "on the " << Day << " day after/n"; cout << "on the " << Day << " day after/n"; cout << "on the " << Day << " day after'n"; cout << "The growth of the Tuber Root'n"; cout << "The growth of the Stolon'u"; cout << "The growth of the Tuber/n"; cout << "planting is " << Growth; cout << "planting is " << Growth; cout << "planting is " << Growth; cout << " grams.\n"; break; cout << " grams.\n"; break; cout << " grams.'n"; Growth = Clean_Tuber_Root (Day); cout << "\n": cout << "u"; cout << "\n"; Growth = Clean_Stolon (Day); Growth = Clean_Tuber (Day); break; case 5: case 4: case 6:

case 7:

Growth = Clean_Below_Stem (Day); cout << "\n"; cout << "The growth of the Below-Ground"; cout << " Stem\n on the " << Day; cout << " day after planting is " << Growth; cout << " grams.\n"; break;

cout << " development on the " << Day << "day"; cout << " System on the " << Day << " day"; cout << " System on the " << Day << " day"; cout << "The growth of the Root System'u"; cout << "The growth of the Above-Ground"; cout << "on the " << Day << " day after'u"; cout << "The growth of the Below-Ground"; cout << " after/n planting is " << Growth; cout << " after'n planting is " << Growth; cout << " after/n planting is " << Growth; cout << "The growth of the Plant"; cout << "planting ls " << Growth; cout << "grams.'n"; cout << " grams.\n"; cout << " grams.\n"; Growth = Clean_Above_System (Day); Growth = Clean_Below_System (Day); Growth = Clean_Root_System (Day); Growth = Clean_Plant_Growth (Day); cout << "\n"; cout << "n"; cout << "\n"; cout << 'n' break; break; break; case 11: case 10: case 8: case 9:

break; default: cout << "Invalid Section'v"; break;

cout << " grams.\n";

break;

default: cout << "Irwalid Option\n"; break; }

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double Fleid_Basal_Root (double); double Fleid_Nodal_Root (double); double Fleid_Stolon_Root (double); double Fleid_Tuber_Root (double); double Fleid_Tuber (double); double Fleid_Below_Stern (double); double Fleid_Below_System (double); double Fleid_Above_System (double); double Field_Plant_Growth (double); double Clean_Basal_Root (double); double Clean_Nodal_Root (double); double Clean_Stolon_Root (double); double Clean_Stolon Root (double); double Clean_Stolon (double); double Clean_Root_System (double); double Clean_Below_Stem (double); double Clean_Below_System (double); double Clean_Plant_Growth (double); double Field_Basal_Root (double Day)

return -3.09520-2 + 1.52620-2*Day; } double Field_Nodal_Root (double Day) { return -.5.8408 + 0.45717*Day; } double Field_Stolon_Root (double Day) { return -5.6190e-2 + 2.9524e-3^{*}Day:

double Field_Below_System (double Day) double Field_Above_System (double Day) double Field_Plant_Growth (double Day) double Field_Root_System (double Day) double Field_Below_Stern (double Day) double Fleid_Tuber_Root (double Day) return -3.3338-3 + 1.6667e-4*Day; return -0.22333 + 1.11670-2[#]Day; } return -0.57512 + 3.7595e-2*Day; } return 8.4167e-2 + 0.22017*Day; } double Field_Stolon (double Day) double Field_Tuber (double Day) return -6.4124 + 0.74929*Day; } return -6.6729 + 0.53379*Day; return -44.843 + 2.8508*Day; } return -51.255 + 3.6001*Day; }

double Clean_Basal_Root (double Day)
{
 return -3.8048 + 0.30831*Day;
}
double Clean_Nodal_Root (double Day)
 return -13.000 + 0.89981*Day;
}
double Clean_Stolon_Root (double Day)
f
double Clean_Stolon_Root (double Day)
double Clean_Tuber_Root (double Day)

{ return -5.3571e-3 + 2.8571e-4*Day; } double Clean_Stolon (double Day)

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double Clean_Tuber (double Day)
{
return -14.393 + 0.74967*Day;
}
double Clean_Below_Stem (double Day)

double Clean_Root_System (double Day) {

return -1.6515 + 0.33424*Day;

return -18.568 + 1.3442*Day;

double Clean_Below_System (double Day) { return -33.674 + 2.3860*Day; double Clean_Above_System (double Day) { retum -101.34 + 6.2501*Day; }

double Clean_Plant_Growth (double Day) {

return -135.02 + 8.6360*Day; }

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