CAVITY SPOT OF CARROT (*PYTHIUM* SPP.): ETIOLOGY, EPIDEMIOLOGY AND CONTROL

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MARY RUTH MCDONALD

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ABSTRACT

CAVITY SPOT OF CARROT (PYTHIUM SPP.): ETIOLOGY, EPIDEMIOLOGY AND CONTROL

Mary Ruth McDonald
University of Guelph, 1994

Advisor:
Professor Lloyd V. Edgington
1986-1989

Professor John C. Sutton
1989-1994

Several Pythium spp. were recovered from cavity spot lesions and pieces of asymptomatic periderm and lateral root scars from tap roots of carrots grown in organic soil in the Holland-Bradford Marsh. Isolates of Pythium violae, P. ultimum and P. irregulare recovered from lesions caused characteristic cavity spot lesions on carrots grown in infested growth medium and were re-isolated from the lesions. The frequency of Pythium recovery from lesions and asymptomatic root pieces was not closely associated with days after seeding, rainfall or soil temperature.

The development of cavity spot throughout the growing season was examined in relations to time (days after seeding), several rainfall parameters and soil temperature at 5 cm depth. Disease incidence and area under the disease progress curve (AUDPC) increased with increasing days after seeding (r^2=0.014-0.82). Incidence reached a maximum between 4 August and 27 October (62 to 159 days after seeding) on 24 of 27 disease progress curves recorded over six years. Disease incidence decreased in November or December on four of the 24 disease progress curves. Cavity spot often increased in association with increasing cumulative rainfall and decreasing soil temperatures but effects of these parameters could not be determined because both were highly correlated with days after seeding (r^2=0.74-0.99).

Increases in incidence followed nine to thirty nine days after a day with rainfall $\geq$ 20 mm or four consecutive days with total rainfall $\geq$ 20 mm

weight). Decreases in incidence followed periods of a minimum of thirteen days where there was no rainfall or rainfall < 5 mm per day. Large AUDPC's occurred in years when soil temperatures were low (16-17.5°C) in the six to eight weeks after seeding and cumulative rainfall was moderate (550 mm per season).

The use of the resistant cultivar Six Pak was the most effective method of suppressing cavity spot. Application of metalaxyl as a granular formulation at seeding or as a drench, in combination with mancozeb, applied within six weeks of seeding, was also effective. Metalaxyl plus mancozeb, fosetyl-Al and phosphorous acid reduced disease incidence when applied as a foliar spray 12 or 17 weeks after seeding but were not as effective as an early-season drench application of metalaxyl plus mancozeb. A drench application of metalaxyl plus mancozeb was effective on Six Pak when disease levels were high (3780 incidence days) but not when disease was moderate (1485 incidence days). Application of metalaxyl plus mancozeb to susceptible cultivars such as Chanton and Huron reduced AUDPC to that of untreated Six Pak.

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CHAPTER 1

GENERAL INTRODUCTION

The disease cavity spot affects carrots in all regions of Canada where carrots are grown (Odermatt and Snow 1991, Valk et al. 1988) and has also been observed on parsnip (Guba et al. 1961). It is widely distributed in carrot-producing areas of the world and has been reported from North America (Guba et al. 1961, Vivoda et al. 1991), Europe (Lyshol et al. 1984, Perry and Harrison, 1979a), Israel (Soroker et al. 1984) and Australia (Walker 1991). A similar disease, called brown blot, has been reported from Japan (Nagai et al. 1986). In some accounts, cavity spot is referred to as "horizontal lesions" (Valk et al. 1986). Also, a disease of carrot roots caused by Rhizoctonia solani Kuhn has been referred to as "cavity spot" (Mildenhall and Williams 1970), but is not included in this study.

Cavity spot occurs on carrots grown in both organic (Valk et al. 1986, Odermatt and Snow 1991) and mineral soils (White 1986, Walker 1991, Vivoda et al. 1991). While the disease rarely reduces harvested tonnage, carrots with more than a few superficial cavities are not acceptable for the fresh market or for processing, so marketable yield can be substantially reduced. In extreme cases, fields of carrots in Ontario with severe cavity spot have been disked under rather than harvested.

Cavity spot is characterized by blackish, sunken lesions that develop on the surface of the carrot root (Guba et al. 1961). The lesions or "cavities" are roughly elliptical, elongated in a horizontal plane, and penetrate a few millimetres into the root (Perry and Harrison 1979a) (Figure 1). Vertical cracks are sometimes associated with the lesions (Scaife et al. 1983). There are no foliar symptoms of disease (Guba et al. 1961). To determine the severity of cavity spot, carrots must be lifted from the soil and the roots washed.

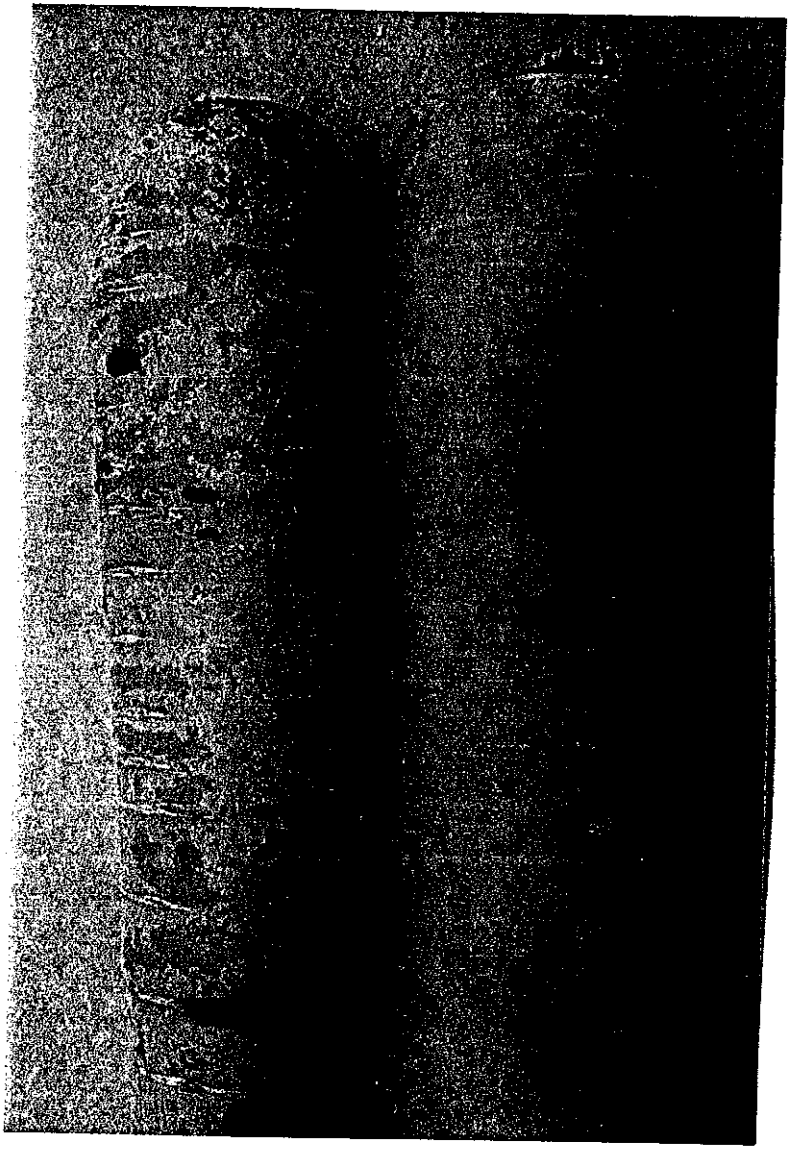

Figure 1. Cavity spot lesions on carrot roots

The symptoms first appear under intact periderm as sunken areas that are either normal in colour or gray. As the lesions develop, the periderm ruptures and darkens. Lesions vary in size, and secondary organisms may infect the carrot, causing rapid rotting (Perry and Harrison 1979a). Growers report that lesions increase in size while the carrots are in cold storage, but whether this can be attributed to primary causal agents or to secondary invasion is not clear.

In the Holland/Bradford Marsh area of Ontario, cavity spot is one of the most serious diseases affecting carrots, and few measures are available to manage the disease. No fungicides are registered in Canada for use against cavity spot (Ontario Ministry of Agriculture and Food 1992b). Field observations indicate that a three year rotation with onions is ineffective for reducing disease potential in a field. Avoiding infested fields can be difficult. Moderate to severe cavity spot was reported the first year that carrots were grown on newly broken muck soil and on carrots grown on mineral soils where carrots had never previously been grown. Thus, growers are in need of effective techniques for managing this disease. Effective control measures and a disease forecasting system to predict the optimum time of application could improve disease management.

Some methods of managing cavity spot which have shown potential in other countries include resistant carrot cultivars, (National Institute of Agricultural Botany 1991, British Columbia Department of Agriculture and Fisheries 1991) and the application of selective fungicides (Lyshol et al. 1984, Davis et al. 1991). The bacterization of seed with selected plant growth-promoting rhizobacteria can provide control of Pythium diseases of certain vegetable crops (Hadar et al. 1983) but these have not been tested on carrots.

Several commercial carrot cultivars that are partially resistant or tolerant to cavity spot have been identified through the cultivar evaluations at the Muck Research Station in Ontario (Valk et al. 1986 and

1988, McDonald et al. 1989, 1991), in British Columbia (British Columbia Department of Agriculture and Fisheries 1991) and in Britain (National Institute of Agricultural Botany 1991). The identification of this resistance has aided growers in the selection of cultivars, but the levels of resistance are often insufficient to prevent economic losses. Some cultivars with high yield or desirable characteristics such as high carotene content, (i.e. cv. Luck B) are susceptible to the disease (McDonald et al. 1991).

Fungicides, such as metalaxyl and fosetyl-Al, that are selective for fungi in the class Oomycetes were shown to reduce cavity spot (Lyshol et al. 1984, Walker 1991). However, neither of these products are registered for use on carrots in Ontario (Ontario Ministry of Agriculture and Food 1992b) and reports vary as to the optimum rate for metalaxyl (Lyshol et al. 1984, White 1988, Davis et al. 1991) and fosetyl-Al (Lyshol et al. 1984, Walker 1991) as well as optimum timing of the fungicide applications (Gladders and McPherson 1986, Davis et al. 1991, Walker 1991).

Certain plant growth-promoting rhizobacteria (PGPR) have been identified that provide biological control of many soil-borne diseases, including those caused by Pythium spp. (Kloepper et al. 1988). The PGPR are well-suited to control diseases such as seedling rots and damping off because the period of host susceptibility is short and the bacteria are placed directly on the seed (Parke 1990). The application of these bacteria to wheat seed has effectively controlled Pythium root rot (Weller and Cook 1986). Application of fungicides within the four weeks after seeding provides the most effective control of cavity spot even though symptoms develop later (Sweet et al. 1989). Thus, protection of the seedling root from Pythium infection appears to be an important factor in disease control and PGPR applied to the carrot seed may provide this protection.

The epidemiology of cavity spot, is poorly understood but high soil moisture was found to favour high levels of cavity spot (Guba et al. 1961,

Perry and Harrison 1979a, Jacobsohn et al. 1984). No studies on the progress of cavity spot in relation to plant age or environmental factors have been reported.

Several reports have confirmed that a number of Pythium spp. can cause cavity spot. White (1986) in England observed that Pythium violae Chesters and Hickman and Pythium sulcatum Pratt and Mitchell were the most pathogenic on carrots, while Vivoda et al. (1991) found that P. violae and P. ultimum Trow were the two most important species associated with cavity spot in California. Montfort and Rouxel (1988) in France, reported that P. violae was the major species involved, and in Israel, P. irregulare was shown to cause the disease (Shlevin et al. 1987). Nagai et al. (1986) found that P. sulcatum was the causal agent of brown blotting, a disease that may be synonymous with cavity spot.

Identification of Pythium spp. associated with cavity spot in Ontario is necessary for making comparisons of etiology and disease development elsewhere. In addition, an investigation of the relationship between environmental factors and the frequency of Pythium recovery over time may provide more information on the factors that favour infection.

Field trials were conducted over a seven year period to study the etiology, epidemiology and control of cavity spot and to provide a basis for a disease forecasting and management program for cavity spot on carrots grown in organic soil in Ontario. The first objective was to investigate the association of Pythium species with cavity spot, to determine whether one or more species of Pythium were the primary cause of cavity spot in Ontario, and to establish whether plant age, rainfall parameters and soil temperature affected the frequency of Pythium recovery from various parts of the root, specifically asymptomatic periderm, lateral root scars or cavities. The second objective was to study the relationship between plant age, rainfall and soil temperature, and disease progress in order to determine which host and environmental factors were associated with symptom development. The final objective of this research

was to investigate methods of controlling cavity spot, including resistant cultivars, selective fungicides and plant growth-promoting rhizobacteria (PGPR) and to determine whether cultivar resistance interacts with fungicide and PGPR efficacy. Analysis of the effects of these control measures on disease progress could reveal some information about the nature of cultivar resistance and the mode of fungicide action. A series of recommendations were developed for managing cavity spot in commercial carrot fields and the important parameters for a disease forecasting system were identified.

CHAPTER 2

LITERATURE REVIEW OF CAVITY SPOT OF CARROT

THE CULTIVATED CARROT

The cultivated carrot, Daucus carota L. has its centre of diversity in Afghanistan where Daucus carota ssp. carota is found (MacKevic 1929). This wild carrot is morphologically variable and coloured in varying degrees by anthocyanin (Banga 1976). The western carotene carrot was derived from this eastern anthocyanin carrot. The first carrots grown in Europe were either purple or yellow until around 1600 when selection was initiated in the Netherlands to derive a more orange-coloured type from the yellow. A cultivar, Long Orange, was established and by 1763, three orange cultivars had been differentiated. These were Late Half Long (the biggest), Early Half Long, and Early Scarlet Horn (the smallest). All present cultivars have been developed from these four closely related cultivars (Banga 1963). Holland continued to play a leading role in carrot breeding during the seventeenth and eighteenth centuries; France took over as the major developer of carrot cultivars in the nineteenth century (Banga 1976).

The wild carrot Daucus carota ssp. carota is a biennial plant with a dormant winter survival period and is distributed mainly in cool temperate regions of the world. Cultivated carrots are grown in a wide range of climates, including the subtropics, but carrot roots usually are stored only in cool temperate regions (Lewis and Garrod 1983).

The edible portion of the root is a fleshy storage organ made up of the merged hypocotyl and tap root which consists mainly of secondary vascular tissues. Lateral roots are arranged in four longitudinal rows on the underground portion of the plant. As the plant grows, the root and hypocotyl thicken and the cortex is sloughed off (Esau 1940). The outer part of the mature root consists of pericyclic parenchyma with oil ducts covered by periderm. The outermost cells of the periderm are dead (Lewis and Garrod 1983).

In temperate regions, the development of the carrot plant slows as the temperature starts to fall during autumn and finally growth ceases. Root tissues remain capable of wound repair and active defense under conditions of high humidity and temperatures near the freezing point (Lewis and Garrod 1983).

All cultivated carrots are diploid with 2n=2X=18. All carrot breeding was accomplished through mass selection until the mid-twentieth century when the development of mechanical harvesting led to a greater demand for uniformity and hybrid plants were developed using male sterile lines. The objectives of carrot breeding are largely to improve yield, shape, colour, earliness, resistance to bolting, and quality characteristics. In the future, breeding for resistance to pathogens may become more important (Banga 1976).

CARROT PRODUCTION AND PROTECTION IN ONTARIO

Carrots are produced on both organic and mineral soils in Ontario. In 1990, there were 5,615 acres (2,444 hectares) of carrots grown in Ontario, (Ontario Ministry of Agriculture and Food 1991a). In 1992, 3,097 acres (1,239 ha) were grown in the Bradford and District Marsh area and another 485 acres (194 ha) of carrots were grown on mineral soil in the surrounding area (Appendix I). The farm gate value of carrots produced in Ontario was $17.1 million in 1989, $14.5 million in 1990 and $17.8 million in 1991 (Ontario Ministry of Agriculture and Food 1991a, 1992a).

In the Bradford area, carrots are seeded from late April until late June, at a rate of approximately 92-120 seeds/m for packaging carrots and 40 seeds/m for processing carrots.

Under ideal growing conditions (16-20°C) and adequate moisture, carrots germinate and emerge within four days of sowing. The first true leaf emerges approximately 14 days after seeding (Esau 1940).

Hand-harvesting of bunching carrots begins in early to mid-July in the Bradford area. Carrots for packaging and processing are machine-

harvested beginning in late July or early August and ending in November or occasionally early December. The carrots are stored in pallet boxes or are washed and stored in bulk storages. Rapid cooling of harvested carrots is recommended for disease control in storage. The ideal storage conditions for carrots are temperatures at 0-1°C and 95% relative humidity (Ontario Ministry of Agriculture and Food 1992b).

DISTRIBUTION AND IMPORTANCE OF CAVITY SPOT

Cavity spot is a widely distributed disease and causes economically important losses in most carrot producing areas of the world. It has been reported in Britain (Groom and Perry 1985), Norway (Lyshol et al. 1984), France (Montfort and Rouxel 1988), Israel (Soroker et al. 1984), Australia (Walker 1991) and the United States (Guba et al. 1961, Vivoda et al. 1991). In Canada, the disease has been found on carrots in British Columbia (Odermatt and Snow 1991), Ontario (Valk et al. 1988), and on samples received from Manitoba, Quebec and Prince Edward Island. The disease has also been observed on parsnip (Guba et al. 1961).

While cavity spot rarely reduces harvested yield, carrots with lesions are not acceptable for the fresh market or for processing, and marketable yield may be severely reduced (Groom and Perry 1985, Montfort and Rouxel 1988, Lyons and White 1992).

In the Bradford and District Marshes of Ontario, cavity spot has resulted in a higher proportion of cull carrots and increased costs for grading carrots. In some cases, fields or portions of fields have been abandoned and the carrots disked because the high incidence of cavity spot would make the crop uneconomical to harvest. Truckloads of carrots have been rejected by the packing houses and processors because of high levels of cavity spot.

There has been no attempt to estimate the financial losses caused by this disease in the Bradford area, but cavity spot is the most widespread field disease of carrot roots and is second only to sclerotinia rot in

importance and potential for reducing marketable yield.

There has been some confusion as to the identification and correct name for this disease. In some reports, cavity spot has been referred to as "horizontal lesions" (Valk et al. 1986, 1988, Odermatt and Snow 1991). A root disease of carrot caused by Rhizoctonia solani Kuhn was also called "cavity spot" (Mildenhall and Williams 1970).

SYMPTOMS OF CAVITY SPOT

Cavity spot is easily seen on freshly washed tap roots of carrot. One or more lesions may occur on any part of the surface of a mature root (Perry and Harrison 1979a). Initially, lesions are sunken elliptical areas oriented across the breadth of the root. They form under the intact periderm and are either not discoloured or gray (Perry 1967). The underlying tissue collapses to cause the cavity. Lesions enlarge as roots mature, the depression deepens and the periderm fractures, leaving a ragged edge. Invasion by saprophytic or weakly pathogenic fungi and bacteria may then occur, causing further enlargement and darkening (Perry and Harrison 1979a). Reports on size and frequency of lesions vary. Guba et al. (1961) described the lesions as 3-4 mm deep with openings 0.2 to 0.5 X 1.5 to 4 mm in diameter. He reported that some roots show an abundance of lesions, that were scattered and were usually more numerous on the upper than the lower part of the carrot. Perry and Harrison (1979a) noted that lesions were initially 2-15 mm long but later extended more than halfway around the circumference of the carrot and were up to 40 mm long on the vertical axis and up to 7 mm deep radially. Maynard et al. (1961) described smaller lesions that occurred at a frequency of up to 40 per root. In Scotland, this high frequency of lesions was never observed (Perry and Harrison 1979a). Vertical cracks were often associated with cavities (Scaife et al. 1983). Cavities may heal as the roots grow, leaving a shallow, clean, laterally elongated scar (Guba et al. 1961). There are no foliar symptoms of the disease (Guba et al. 1961).

The sequence of events in lesion formation was described by Perry and Harrison (1979a). Initially the contents of the outer layer of cells of the phloem parenchyma aggregated and the walls collapsed. This effect spread until the periderm and pericycle cells disintegrated. A layer of wound periderm formed beneath the lesion. Lignin and subarin were present in the cell walls of the periderm and polyphenols were found in apparently healthy tissue surrounding the lesion but not in tissues of unaffected roots. No tannins were found. Cavities were not consistently associated with anatomical features such as oil ducts or lateral root origins.

ETIOLOGY OF CAVITY SPOT - A HISTORICAL PERSPECTIVE

Cavity spot was first described on carrots and parsnips in 1961 by Guba et al. (1961) in Massachusetts. Since this description, the disease has been attributed to numerous physiological causes including calcium deficiency (Maynard et al. 1961), soil ammonification (DeKock et al. 1980, Scaife et al. 1980), and anaerobic growing conditions (Perry and Harrison 1979b, Soroker et al. 1984). Biological agents that have been implicated in cavity spot formation included anaerobic bacteria, specifically Clostridium spp. (Perry and Harrison 1979b), fungus gnat larvae (Bradysia spp.) (Hafidh and Kelly 1982) and slow-growing species of Pythium, (Groom and Perry 1985, White 1986).

Guba et al. (1961) were unable to isolate a causal organism and concluded that the disease was physiological in origin. They noted a genetic variation in susceptibility to the disease. Cavity spot was observed to be worse on carrots growing in wet soils and those lacking fertility and humus.

Another disease of carrots, root scab, was reported to be very similar to cavity spot (Maynard et al. 1963, Hafidh and Kelly 1982), although Guba et al. (1961) considered the diseases to differ in etiology. Interestingly, Scaife et al. (1983) found that cavity spot and scab were strikingly dissociated, in that scab was most common in soils above pH 6.5

and cavity spot more frequent on carrots growing in soils below this pH.

A number of physiological factors have been implicated in the etiology of cavity spot. Initially, cavity spot was reported to be a symptom of calcium deficiency which could be induced by high levels of potassium (Maynard et al. 1961, 1963). Subsequent trials failed to find a relationship between calcium, potassium or Ca/K ratios and cavity spot (Perry and Harrison 1979a, Hafidh and Kelly 1982, Soroker et al. 1984, White 1988, Vivoda et al. 1991).

Another series of reports focused on the role of waterlogged soil and lack of aeration in symptom expression. Perry and Harrison (1979b) concluded that anaerobic bacteria of the genus Clostridium could induce cavity spot symptoms in carrots grown in pots and subjected to anoxic conditions. However, in field-grown carrots, they were only able to isolate the bacteria from 22% of lesions and from 6% of healthy tissues.

The role of anaerobic bacteria in cavity spot development was not confirmed by Soroker et al. (1984). Instead, they suggested that cavity spot was caused by physiological injuries to the carrot which resulted from environmental stress, specifically temperatures above 28°C, in conjunction with a minimum of six hours of flooding. Once cells collapsed and subepidermal cavities formed, then nonspecific bacteria proliferated and the plant responded by producing oxidized polyphenol compounds which accumulated and resulted in the formation of brown cavity spots. An attempt to find a specific physiological cause of cavity spot through studies of mineral nutrition in relation to cavity spot incidence yielded variable but mostly negative results.

Larvae of the fungus gnat (Bradysia impatiens (Joh.)) were found in cavities of greenhouse-grown carrots. An application of the systemic insecticide aldicarb suppressed cavity spot and fungus gnats were identified as the cause of cavity spot (Hafidh and Kelly 1982). Fungus gnats can ingest and transmit oospores of Pythium aphanidermatum (Jarvis et al. 1993). These insects may be involved in cavity spot initiation as

a vector of Pythium propagules, rather than as causal agent. Insecticide applied to carrots growing in organic soil failed to reduce cavity spot (Valk et al. 1986).

The most significant development in the search for a causal agent of cavity spot was the discovery by Lyshol et al. (1984) that the disease could be reduced by applications of the fungicides metalaxyl, fosetyl-Al or propamicarb, but not by the fungicide iprodione or by the insecticide aldicarb. Metalaxyl applications also reduced the incidence of pythium root dieback on young plants. Once it became clear that fungicides which selectively controlled Oomycetous fungi controlled cavity spot, the Pythium spp. that caused the disease were soon identified.

TAXONOMY AND IDENTIFICATION OF PYTHIUM SPP. ASSOCIATED WITH CAVITY SPOT

The genus Pythium belongs to the Kingdom Fungi, Division Eumycota, Subdivision Mastigomycotina, Class Oomycetes, Order Peronosporales and Family Pythiaceae (Barr 1983, Hendrix and Campbell 1983). The Oomycetes are zoosporic fungi that have biflagellate zoospores; one flagellum is tinsel type and the other is a whiplash flagellum (Fuller 1987). The Oomycetes have an oogamous type of sexual reproduction which is their major distinguishing feature because there is no motile sexual stage; the oosphere is fertilized within the oogonium as a result of transfer of a gametic nucleus from an antheridium (Barr 1983). Meiosis occurs in the antheridia and oogonia to produce non-flagellate haploid gametes. Fertilization results in a diploid oospore. Oospores germinate and produce diploid vegetative hyphae that can reproduce asexually by means of the biflagellate zoospores (Fuller 1987).

The Oomycetes probably evolved from a heterokont algae. Their cell walls are composed primarily of B-glucans with a small amount of cellulose (Barr 1983).

The Peronosporales are the most specialized of the Oomycetes. This order consists of three families, the Pythiaceae, Peronosporaceae and

Albuginaceae. The Pythiaceae are the least specialized of the families; several of the member species are aquatic or saprophytic. The other two families are more specialized and are all obligate parasites. Members of the Peronosporales are unable to synthesize sterols and must obtain these from a host or culture medium to complete asexual and sexual reproduction (Fuller 1987).

Pythium species are ecologically versatile and physiologically unique fungi. They are ubiquitous in soil and aquatic environments and worldwide in distribution. They are among the most important and destructive plant pathogens and have a broad host range (Tsao 1974). However, Pythium spp. are rarely observed in natural habitats. In general, they are identified only after isolation and culture on laboratory media (Hendrix and Papa 1974).

The genus Pythium was first described by Pringsheim in 1858. Several monographs and keys describing various species have been published including those by Matthews (1931), Sideris (1932), Middleton (1943), Waterhouse (1968), Hendrix and Papa (1974), Van der Plaats-Niterink (1981) and Dick (1990). Hendrix and Papa (1974) grouped similar and possibly synonymous species into 15 groups. Van der Plaats-Niterink (1981) published a very complete and well illustrated monograph of 85 species with a dichotomous key. Dick (1990) edited and amended the key of Van der Plaats-Niterink, included 25 taxa and developed a Venn-diagram key.

The characteristics of the genus Pythium include: a) an asexual stage comprised of sporangia of different sizes and shapes; b) zoospores which are released through a pore or evacuation tube into a vesicle where they mature and from which they are liberated; and c) a sexual stage consisting of an oogonium which usually contains a single oospore at maturity. The oogonia are fertilized by one to many antheridia which may be monoclinous, diclinous or hypogynous. There are many variations of these attributes among Pythium spp. Some species lack sporangia, while others have no known sexual stage (Hendrix and Campbell 1983). The hyphae

of Pythium spp. are hyaline, mostly five to seven and occasionally 10 μ wide. Septa are absent except in old hyphae or at the base of reproductive organs. Cytoplasmic streaming can often be seen in young hyphae.

Identification of Pythium spp. is largely based on the morphology of the sporangia, conidia, oogonia and antheridia, but the presence, size, shape, and number of these structures varies considerably depending on culture media, temperature, age of the culture and other environmental conditions. Therefore standard culture methods are essential for accurate identification (Van der Plaats-Niterink 1981).

Several Pythium spp. have been identified as causal agents of cavity spot. Those most often associated with the disease are the slow-growing species, Pythium violae Chesters and Hickman and P. sulcatum Pratt and Mitchell, although P. ultimum is reported to be an important causal agent of cavity spot in California (Vivoda et al. 1991). Other species, including Pythium sylvaticum Campbell and Hendrix, P. intermedium de Bary, P. ultimum de Bary, P. irregulare Buisman and P. aphanidermatum (Edson) Fitz. have also been isolated from cavities in carrots (White 1986).

Studies of Pythium taxonomy demonstrated that Pythium debaryanum Hesse could not be distinguished from P. irregulare based on morphology, host range or temperature requirements. Pythium sylvaticum was included in a species complex with P. irregulare following observations that the heterothallic condition of P. sylvaticum was comparable to P. debaryanum. Serological studies suggest that P. ultimum, P. irregulare and P. sylvaticium can all be included in the same species complex (Hendrix and Campbell 1983).

Identification of Pythium spp. by isolation on selective agar medium is time consuming and requires extensive expertise in mycological techniques and fungal morphology (Lyons and White 1992). Most keys are based on characteristics of the oogonia and antheridia (Van der Plaats-Niterink 1981, Dick 1990) and this prevents the identification of species

that do not produce sexual structures in culture, such as Pythium sp. "group G" (Huang et al. 1992). Other techniques to identify Pythium spp. are being investigated, such as isozyme analysis (Chen et al. 1992), electrophoresis of mitochondrial DNA (Huang et al. 1992) and competition ELISA (Lyons and White 1992). Chen et al. (1992) studied 204 isolates and concluded it was not feasible to use isozyme banding patterns for the conclusive identification of Pythium species.

PYTHIUM SURVIVAL STRUCTURES AND PRIMARY INOCULUM

Pythium violae readily forms oogonia and it is assumed that they are the means of survival and of infection (Phelps et al. 1991). Pythium ultimum also forms thick-walled oospores that allow the fungus to survive for long periods. While sporangia appear to be the principal functional inoculum, dormant oospores may convert to thin-walled spores and function like sporangia (Hancock 1977). Neither P. intermedium nor P. sylvaticum produce sporangia or zoospores and P. irregulare seldom produces sporangia (Van der Plaats-Niterink 1981). Lyons and White (1992) noted that both P. violae and P. sulcatum appear to lack an asexual reproductive stage in their life cycle, but Van der Plaats-Niterink (1981) describes P. sulcatum as having filamentous sporangia and zoospores which form at 20°C. Pythium aphanidermatum has lobate sporangia and zoospores are formed at 25-30°C (Van der Plaats-Niterink 1981).

Sporangia and oospores of Pythium spp. are capable of maximal germination (80-100%) in soil within one to three hours once stimulated by a substrate. Subsequently, there is rapid exploitation of the colonized substrate and conversion into numerous resting structures (up to 500/mm^2 root tissue). Dormant resting structures formed during pathogenic and/or saprophytic colonization of plant tissues have long been considered the primary sources of inoculum for succeeding crops, but the nonpathogenic colonization of other crops and weeds may provide an alternate or initial

INFECTION AND COLONIZATION

Species of Pythium usually enter the host directly through unwounded surfaces, penetrating intact epidermal cells or between epidermal cells with infection pegs or slender infection hyphae (Endo and Colt 1974). Infection has been reported to occur anywhere on the root, however, the region of elongation and the young root hair region appear to be penetrated most frequently (Nemec 1972, Endo and Colt, 1974). Direct penetration is accomplished primarily by mechanical pressure, rather than by enzymatic action upon host cell walls. Ramification of hyphae within the host occurs both inter and intracellularly (Endo and Colt 1974).

Benard and Punja (1992) studied cavity spot and Pythium spp. isolated from cavity spot lesions. They demonstrated that several isolates secreted pectyolytic enzymes and also observed fungal hyphae and oospores among diseased carrot root cells.

OTHER PYTHIUM-INDUCED DISEASES OF CARROT

Pythium species cause two other diseases of carrot, damping-off (Howard et al. 1978, Huang et al. 1992) and pythium root dieback, which has also been called "rusty root" (Sutton 1975, Howard et al. 1978, Liddell et al. 1989). Numerous Pythium spp. have been reported to cause damping-off of carrot, including P. irregulare, P. paroecandrum Drechsler, P. spinosum Sawada, P. sulcatum, P. afertile Kanousa and Humphrey, P. sylvaticum, P. coloratum Vaartaja, P. periilum Dreschsler, P. ultimum and P. mammilatum Meurs. (Howard et al. 1978), Pythium sp."group G" (Huang et al. 1992) and P. ultimum, P. irregulare and P. aphanidermatum (Liddell et al. 1989).

Factors that influence the severity of damping-off, include seed quality, temperature, moisture, the prevalent Pythium spp. and cultivar (Hendrix and Campbell, 1983). The relationship can be summarized by the findings of Leach (1947) who concluded that, other factors being constant, the relative growth rate of the host and the pathogen determine the

severity of pre-emergence damping-off. This concept has been called the "relative competitive advantage".

Pythium root dieback is a disease complex brought about by one or more pathogenic species of Pythium acting singly or together (Howard et al. 1978). Affected carrots have numerous rusty-brown lateral roots and necrotic stunted or forked tap roots. Up to 80% reduction in marketable yield has been reported (Liddell et al. 1989). Infection of the primary carrot root takes place within the first weeks of growth and root tip necrosis can be observed once the carrots have two true leaves, about 21 days after seeding. The symptomatic root branching and the proliferation of lateral roots occurs when injury to the primary root destroys apical dominance (Howard 1975).

The Pythium spp. found to incite pythium root dieback in organic soils in North American were P. irregulare, P. sulcatum, P. sylvaticum, P. ultimum and P. coloratum (Howard et al. 1978, Pratt and Green 1971 and Wisbey et al. 1977). The two most pathogenic species in a survey conducted by Howard et al. (1978) were P. irregulare and P. sulcatum. On mineral soils in California, P. irregulare and P. ultimum were found to be most pathogenic (Liddell et al. 1989). All of the species that cause pythium root dieback can also cause pre-emergence damping-off. Pythium violae is the only species that has been associated with cavity spot but not damping-off or pythium root dieback, while P. coloratum has not been associated with cavity spot but has been shown to cause the other two diseases.

It is not unusual for several species of Pythium to affect the same host (Hendrix and Campbell 1983) or for a single species to cause different diseases on a single host (McElroy et al. 1971).

FACTORS AFFECTING CAVITY SPOT DEVELOPMENT

In the first report describing cavity spot on carrots, Guba et al. (1961) observed that high soil moisture and low soil fertility were

associated with severe cavity spot. Other factors such as aeration and temperature affect cavity spot development (Perry and Harrison 1979a, Jacobsohn et al. 1984). Little is known about the life cycles of Pythium violae or P. sulcatum and how the reproduction and survival of these fungi is affected by the environment. However, P. ultimum has been studied in more depth, and while it is less pathogenic than P. violae in cavity spot development, knowledge of the life cycle and host-pathogen relationships of P. ultimum on other hosts may provide some clues to the epidemiology of cavity spot. A summary of the factors reported to affect the Pythium spp. involved in cavity spot and disease development is provided in Tables 1 and 2.

Soil moisture

Soil moisture is one of the most important environmental factors known to favour seasonal activity of Pythium spp. (Stanghellini 1974). In general, these fungi are capable of germination, vegetative growth and colonization of living or dead substrates from 0 to -15 bars. The activity of Pythium spp. is generally reduced at matric water potentials lower than -0.3 bars (Stanghellini 1974). Populations of P. ultimum did not increase significantly in water-saturated soils (Lifshitz and Hancock 1981).

Cavity spot was more common on carrots grown in flat, imperfectly drained fields with poor soil structure than on those grown in other fields. Records from a local canning factory also showed that there was a higher incidence of lesions in years with greater than average rainfall in July and August (Perry and Harrison 1979a). In replicated field trials, an increase in soil moisture content from 10% (wet weight) to 23.1% (equivalent to -0.1 bar) in combination with rolling, increased the percentage of roots with cavity spot from 1.7% to 29.9%. Carrots in rolled plots that were not irrigated had 2.4% cavity spot. Mean daily soil temperatures were 18.8° and 20°C in wet and dry plots, respectively

1. Factors affecting the development of Pythium spp. involved in cavity spot.

ium spp.	Stage	Environmental Variable	Principal Observation	Reference
plae	Mycelial growth in culture	Temperature	Maximum: below 35°C Optimum: 25°C Minimum: 5°C	Van der Plaats - Niterink 198
licatum	Mycelial growth in culture	Temperature	Maximum: 36°-37°C Optimum: 20°-28°C Minimum: 2°-3°C	Van der Plaats - Niterink 198
	Zoospore formation in culture	Temperature	20°C	Van der Plaats - Niterink 198
lvaticum	Mycelial growth in culture	Temperature	Maximum: 35°-40°C Optimum: 25°C Minimum: below 5°C	Van der Plaats - Niterink 198
regulare	Mycelial growth in culture	Temperature	Maximum: 35°C Optimum: 30°C Minimum: 1°C	Van der Plaats - Niterink 198
ermedium	Mycelial growth in culture	Temperature	Maximum: 30°C Optimum: 28°-25°C Minimum: 5°C	Van der Plaats - Niterink 198

.../ continued

1. - continued

um spp.	Stage	Environmental Variable	Principal Observation	Reference
dermatum	Mycelial growth in culture	Temperature	Maximum: over 40°C Optimum: 35°-40°C Minimum: 10°C	Van der Plaats - Niterink 198
	zoospore formation	Temperature	25°-30°C	Van der Plaats - Niterink 198
imum	Mycelial growth in culture	Temperature	Maximum: 35°C Optimum: 25°-30°C Minimum: 5°C	Van der Plaats - Niterink 198
imum	Mycelial growth in culture, isolates from San Joaquin Valley	Temperature	Maximum: 23°-30°C, no growth at 36°C or 5°C	Hancock 1977
		Water potential	Reduced below -15 bars	Hancock 1977
	Sporangial development and oospore formation in culture	Water potential	Reduced below -25 to -35 bars	Hancock 1977

.../ continued

1. - continued

um spp.	Stage	Environmental Variable	Principal Observation	Reference
.mum	Sporangial development and oospore formation in culture	Temperature	Optimum formation at 20-30°C, no formation at 36°C, formed slowly at 3°C	Hancock 1977
	Germination of sporangia in culture	Water potential	Germination reduced below -20 to -30 bars	Hancock 1977
		Temperature	Germination optimal at 20°-30°C and reduced above 33°C and below 18°C	Hancock 1977
	Population increase in field	Water potential	Population increases between -0.3 and -8 bars, no increase in saturated soil or below -9 bars	Hancock 1977
	Population increase on cotton leaves in soil	Temperature	Maximum: 31°-33°C Optimum: 15°-20°C Minimum: 2°-4°C	Hancock 1977

2. Factors affecting the development of cavity spot.

of disease ycle	Variable	Principal Observation	References
position of	Host age	More lesions developed on 5 month old vs. 3 month old plants.	Vivoda et al. 1991
	Host age, flooded and sealed soil	Carrots 7, 11 and 16 weeks old developed 0,6, and 30% cavity spot after 5 days in flooded, sealed pots.	Perry and Harrison 1979b
	Flooded and sealed soil, temperature, time	5 days in flooded, sealed soil at 20°C was optimum for symptom development.	Perry and Harrison 1979b
	Flooded soil, temperature	Flooding for over 6 hours at 28°C or above stimulated lesion development.	Soroker et al. 1984
		Flooding for 24 or 48 hours at 20°C caused an increase in lesions/carrot.	Vivoda et al. 1991
m pment in eld	Soil moisture	High levels of soil moisture were associated with high incidence of cavity spot.	Guba et al. 1961

.../ continued

2. - continued

of disease ycle	Variable	Principal Observation	References
m pment in eld	Soil moisture	Irrigation to increase soil moisture from 10%-23% increased cavity spot from 3% to 14%.	Perry and Harrison 1979b
development irect ation	Temperature	Optimum temperature of 15°C, range of 5°-25°C. At 5,10 and 15°C lesions increased in size from 3 to 9 days after inoculation.	Montfort and Rouxel 1988
development nsplanted s	Temperature	More lesions developed at 15°C than at 20 or 25°C.	Vivoda et al. 1991

In a second experiment, irrigation increased the percentage of roots with cavity spot from 3.0% to 14.4% when irrigation water was applied in July or August, but not in October (4.4% cavity spot). In October, the soil moisture content of the irrigated plot was similar to plots irrigated in July or August but soil temperatures were lower, 8.6°C compared to 15.5° and 15.0°C, respectively.

The percentage of roots with cavity spot lesions also increased when carrots growing in pots were watered frequently (twice daily) or waterlogged as compared to carrots that were watered infrequently (at wilting point). High soil water levels appeared to predispose carrots to cavity spot (Perry and Harrison, 1979a).

Low Pythium populations in field soils in California during the fall months were associated with low soil moisture levels. Populations increased in most field sites following rain in November when soil temperatures were 2°-10°C. Populations of P. ultimum in soil did not increase at water potentials lower than -9 to -11 bars yet, in culture, the development and growth of most stages was not reduced until the water potential was -20 bars or lower. Possibly the sensitivity of hyphal growth to moisture stress negatively affected the competitive ability of P. ultimum in nature. The optimal environmental conditions for P. ultimum were different in nature than in culture (Hancock 1977).

Cavity spot-like symptoms on carrots were induced by flooding the soil in which the carrots were growing (Perry and Harrison 1979b, Soroker et al. 1984, Vivoda et al. 1991), and also by flooding and sealing the soil surface with wax (Perry and Harrison 1979b, Soroker et al. 1984). In one experiment, carrots in pots of compost subjected to this treatment had significantly more lesions than untreated carrots or carrots in pots standing in water but not sealed. However, in other experiments, watering pots of carrots twice a day also increased cavity spot. Even carrots watered infrequently developed some cavity spot symptoms (Perry and Harrison 1979b).

In one trial, standing sealed pots in water for a period of five days at 20°C was optimum for symptom development (Perry and Harrison 1979b). It was suggested that two days of growth under these conditions was required for the roots and soil microflora to utilize the available oxygen in the pots, and lesions developed after three days of anoxia. When lesions were observed immediately after treatment they were not depressed nor discoloured and were not typical of cavity spot. However, if the roots were kept in the pots for three more weeks without watering, the lesions resembled natural lesions. It was concluded that anaerobic conditions in the soil could be caused by heavy rainfall in areas with poor soil drainage and by the increased oxygen demand resulting when carrots were densely planted and high soil temperatures favoured a high soil respiration rate. These conditions would favour infection and reproduction by anaerobic bacteria.

In another group of experiments, carrots grown in pots of sandy loam soil were sealed with wax and flooded, flooded without sealing, or subjected to three cycles of flooding and drying (Soroker et al. 1984). Applications of stresses to plants at temperatures higher than 35°C or by sealing the soil surface with wax resulted in death of the carrots after 36 hours. The disease index was higher for carrots that had been flooded as compared to non-flooded checks at all of the temperatures tested. The disease index increased with increasing temperature from 20 to 35°C, and with increasing incubation time of one to seven weeks following the stress.

It was concluded that a combination of physiological and microbial factors were responsible for the formation of cavity spots on carrots. Two major environmental factors that caused cavity formation were short periods (six hours or more) of flooding and temperatures above 28°C. After carrots were exposed to this combined stress, a sizeable leakage of cell contents was observed and the leaked material was high in sugars. Non-

the plant's defense mechanisms. The plant responded and large amounts of oxidized polyphenol compounds accumulated, resulting in the brown-black cavity spots.

Flooding in relation to cavity spot development was also studied in California (Vivoda et al. 1991). Carrots transplanted into a growing medium artificially infested with P. violae or P. ultimum and flooded for 24 or 48 hours at 20°C had increased numbers of lesions but not disease incidence. Increasing the flooding period from 24 to 48 hours did not affect the number of lesions per carrot that developed. P. violae was more pathogenic than P. ultimum in all treatments.

High matric water potentials in soil and accompanying poor aeration indirectly favour Pythium spp. by decreasing host vigour, increasing host exudation, and by providing a suitable environment for the rapid diffusion of these exudates (Stanghellini 1974). The increased availability of host exudates stimulates the germination of dormant propagules and/or vegetative growth. Vegetative growth of Pythium spp. is apparently tolerant of, but not necessarily favoured by, saturated soil conditions. Water-saturated soils did not support the development of Pythium ultimum on cotton leaves in controlled environment studies (Hancock 1977). This was consistent with studies of flooding and cavity spot. For typical cavity spot symptoms to develop after flooding, the carrots had to be grown under normal moisture regimes (Soroker et al. 1984, Perry and Harrison 1979a, Vivoda et al. 1991). Subjecting carrot roots to flooded conditions at 30°C for more than five days killed the carrots (Soroker et al. 1984).

Leakage of electrolytes was enhanced in flooded carrots at temperatures of 30°C and above (Soroker et al. 1984). Analysis of leaked materials revealed that sugars composed 70% of the leaking substances which also contained proteins, amino acids, lipids, and minerals. An increase in nutrient availability would be expected to increase germination and infection by Pythium propagules present in the growing medium.

Soil temperature

Temperature does not appear to play as important a role as soil moisture in cavity spot development but undoubtably it can be a limiting factor. Only one study examined soil temperature in relation to infection of carrots in the field, and this was an indirect relationship. White (1988) sampled carrots in commercial carrot fields and found that the frequency of Pythium isolation from asymptomatic periderm was low when soil temperature at a 10 cm depth was high (15-20°C). A slight increase in the frequency of Pythium isolations occurred when temperatures were 10°C or below. Frequent rainfall was associated with increased frequency of Pythium isolations. It is not known whether the frequency of isolation from asymptomatic periderm has any relationship to the development of cavity spot symptoms. Carrots that were transplanted into growing media artificially infested with P. violae or P. ultimum developed more lesions when incubated at 15°C than at 20° or 25°C (Vivoda et al. 1991). The number of lesions per carrot decreased as the temperature increased. Pythium violae caused more lesions than P. ultimum at all temperatures tested, but there were no differences in the percentage of carrots infected by the two fungi.

The optimum temperature for lesion expansion on mature carrots inoculated with mycelial plugs of P. violae was 15°C (Montfort and Rouxel 1988). At 5, 10 and 15°C, lesions increased in size from three days to nine days after inoculation. At temperatures of 20 and 25°C, lesions reached their maximum size by three days after inoculation.

Observations of cavity spot development in the field have also provided indications about the temperatures that limit or enhance cavity spot development. In the San Joaquin Valley of California, average soil temperatures were 15°C or below at 15 cm depth from November to March, the period of time when cavity spot is most often observed (Vivoda et al. 1991). In Britain, cavity spot developed on carrots grown in pots where the average monthly temperatures varied from a high of 21.8°C in July to

a low of 6.0°C in December (White 1988). In Israel, temperatures above 28°C in conjunction with short periods of flooding were associated with cavity spot. These findings supported observations where severe cavity spot was observed in flooded areas of irrigated fields during the hot season (Soroker et al. 1984).

Mineral nutrition, pH and other factors

The first description of cavity spot (Guba et al. 1961) suggested a link between the disease and low fertilizer levels in soil. Maynard et al. (1961) reported a relationship between cavity spot and low levels of calcium in carrot roots and petioles, and suggested that the disease was the result of potassium-induced calcium deficiency (Maynard et al. 1963). Roots and leaves of carrots with cavity spot had elevated K/Ca ratios (DeKock et al. 1980).

Other reports on an association between cavity spot, nutrients and various soil factors have been mostly negative (Perry and Harrison 1979a, Scaife et al. 1980, 1981, 1983, Jacobsohn et al. 1984, Soroker et al. 1984, Vivoda et al. 1991). No relationship was found between the concentration of Ca, K or the Ca/K ratio in field soils or in pot culture and cavity spot (Perry and Harrison 1979a, White 1986) or between the K/Ca ratio in the leaves, peel or core of the carrot and any cavity spot measurement (Scaife et al. 1983). However, it is possible that a temporary lack of calcium may occur as a result of flooding and contribute to cavity spot development (Soroker et al. 1984). Concentrations of nitrogen, magnesium, copper, manganese, sodium, and boron in field soils were not correlated with cavity spot incidence (Perry and Harrison 1979a, White 1986). Similarly, the application of nutrient solutions containing different levels of nitrogen, phosphorous, potassium, calcium, magnesium, and sodium did not affect the incidence of cavity spot, nor were differences found in the nutrient element content of affected or symptomless carrot roots or foliage (Jacobsohn et al. 1984).

Analysis of carrots from four fields revealed a significant positive correlation between cavity spot and soil ammonia (Scaife et al. 1980). However, further research with carrots grown in pots led to the conclusion that it was unlikely that ammonium levels were responsible for cavity spot development in the field (Scaife et al. 1981). In contrast, high levels of ammonium nitrogen were reported to be conducive to cavity spot development (Goh and Ali 1983).

The effect of soil pH on cavity spot was investigated with varying results. One report indicated that cavity spot was reduced when soil pH was lowered below 6.6 (Perry and Harrison 1979a) but later studies found that low levels of cavity spot were associated with pH's above 7.0 (Scaife et al. 1983) and 8.0 (White 1988). This led to the suggestion that if carrots were grown in fields with a mean pH of 8.0 or above, fungicide applications could be reduced or eliminated. In a survey of commercial carrot fields on mineral soil in the San Joaquin Valley of California, cavity spot incidence was not correlated with soil pH (range 5.7-7.9), electrical conductivity, (0.79-2.82 millimhos/cm) total calcium, (12.6-71.0 meq/100 g) exchangeable calcium, (3.6-24.6 meq/100g) moisture content at -10 kPa, (7.5-32.3%) moisture content at -1500 kPa, (3.1-10.1%), sand, (53-78%) silt, (9-24%) clay, (8-26%) or organic matter, (0.41-1.10%) (Vivoda et al. 1991).

While the incidence of cavity spot may be reduced when carrots are grown in soil with a pH of 8.0 or higher, this pH is above the range recommended for carrot production on organic or mineral soils (5.0-6.0 and 6.0-7.5, respectively), (Ontario Ministry of Agriculture and Food 1992b). Other problems with nutrient imbalances may develop in carrots grown in soil with a pH over 8.0.

Plant density has also been examined as a factor which may predispose carrots to cavity spot. A high plant density can increase the incidence of pythium root dieback (Coffin 1978) and precision seeding of carrots to reduce crowding is recommended to reduce disease incidence

(Ontario Ministry of Agriculture and Food, 1992b). A high plant density might increase cavity spot by causing a localized depletion of oxygen in the soil (Perry and Harrison 1979b), but no significant differences were found in cavity spot on carrots seeded at the standard density (115 seeds/m) or at 0.5x or 2x this density (Vivoda et al. 1991).

Cultivar susceptibility

Varying levels of cultivar susceptibility to cavity spot were first reported by Guba et al. (1961) who noted that cv. Hutchinson developed less cavity spot than cv. Waltham Hicolor, in some years. However, the greatest differences in susceptibility were observed among different lots of Waltham Hicolor. They also found that parsnip cv. Model was more susceptible to cavity spot than were cv.'s Hollow Crown and All American.

The NIAB (National Institute of Agricultural Botany 1991) began assessing carrot cultivars for levels of cavity spot in 1981. The resistance ratings ranged from one, (low resistance) to nine (highly resistant). Screening tests demonstrated that susceptibility can vary within groups of carrots, including Chantenay cultivars Redca (resistance rating of (five) and Supreme (resistance rating of one), and Nantes cultivars Nandor (five) and Tino (two) (Sweet et al. 1989). Susceptibility also varied with harvest date. Increased cavity spot severity was observed on later types or when cultivars are harvested in late fall (National Institute of Agricultural Botany 1991). The Autumn King type Vita Long scored five when lifted early but only had a score of two when late harvested (Grower 1986).

The five major carrot cultivars grown in California were assessed for susceptibility to *Pythium violae* and *P. ultimum* in artificially-infested soil (Vivoda et al. 1991). *Pythium violae* produced more lesions on cv. Topak than on cv.'s Sierra and Dominator and *P. ultimum* produced more lesions on Topak than on any other cultivars. No resistance to cavity spot was found among the commercial cultivars grown in California, but low

ulevels of tolerance to cavity spot did exist.

The frequency of recovery of Pythium spp. from asymptomatic periderm of carrots was examined and no differences were found among three cultivars, Chantenay New Supreme, Fingor and Sweetheart, indicating no differences in susceptibility to infection (White 1988). Similarly, no useful genetic resistance was found when mature roots of 19 carrot cultivars representing five main groups of carrots were inoculated with mycelial plugs of P. violae, P. sulcatum and P. intermedium. However, Vivoda et al. (1991) conducted a similar trial and concluded that inoculation of carrots with mycelial plugs may not be an accurate technique for determining cultivar resistance. Recently Benard and Punja (1992) reported that laboratory inoculations of 36 carrot varieties with P. violae indicated differences in varietal susceptibility that corresponded to field results.

Several workers have reported that infected tissues react in a hypersensitive manner to abort Pythium infections. (Endo and Colt 1974, Klisiewicz 1968). However, others maintain that resistance to Pythium spp. is generally quantitative and may be evident as relatively small differences in disease severity or symptoms (Johnston and Palmer 1985). Initially, researchers believed cavity formation to be the result of a hypersensitive reaction to Pythium attack and that this hypersensitive reaction varied in severity according to the maturity of the carrot, the environment in which it was grown, and the variety (Grower 1986, 1988). The occurrence of a hypersensitive reaction in response to a pathogen suggests vertical resistance (Vanderplank 1963). More recently, White (1991) proposed that carrots had horizontal resistance to cavity spot, since some varieties develop fewer or smaller cavities than others.

One component of plant resistance to Pythium may be the impedance of the internal spread of the fungus (Endo and Colt 1974). Resistance in sorghum to Pythium arrhenomanes Drechsler was associated with smaller lesions compared to susceptible varieties, and production of secondary

roots above the point of inoculation. Both of these responses may be related to a containment of fungal colonization of the root tissue (Forbes et al. 1987).

During the process of cavity spot formation, the plant's defense mechanisms are activated following cell collapse and arrest the infection (Perry and Harrison 1979a, Soroker et al. 1984). Protease activity was high in cavity tissue as compared to tissue from healthy carrots. Peroxidase and polyphenol oxidase activity in extracts from cavities was much higher than from healthy tissue and the phenol content of the tissue increased proportionately to the disease index (Soroker et al. 1984). Subarin and lignin were deposited in the cell walls of the wounded periderm surrounding the lesion (Perry and Harrison 1979a).

Subarin and lignin accumulated in the phloem parenchyma cells near wound surfaces of carrot root tissue. However, the development of structural barriers was less important than the accumulation of antifungal substances in the resistance of healing wounds to fungal invasion (Garrod et al. 1982).

The speed at which a carrot responds to infection with these defense mechanisms may determine its susceptibility or resistance to cavity spot. Fast growing Pythium species were easily recovered from asymptomatic periderm but not from cavities (White 1988). The view that Pythium spp. are colonizers of juvenile tissue was supported by the high frequency of Pythium recovery while the crop was young (eight weeks after seeding), with the frequency dropping as the plant matured. It is possible that carrot defense mechanisms prevent infection by fast-growing species or conversely, do not react at all to these species, while slow-growing species elicit the typical cavity reaction.

Carrot root tissues contain a number of metabolites which inhibit the development of fungi. Some have been detected in extracts of noninoculated tissues, i.e. falcarindiol (Garrod and Lewis et al. 1978) while others are induced in response to injury or challenge by pathogens

or non-pathogens. Production of the phytoalexin 6-methoxymellein can be elicited by Chaetomium globosum Kunze: Fr. or by pectinolytic or proteolytic enzymes (Kurosaki et al. 1985). The antifungal compound, falcarindiol, was found to be more concentrated in the periderm and in the pericyclic parenchyma than in the xylem parenchyma. The levels of falcarindiol in the periderm were well above the ED_{50} value for inhibition of the pathogen Mycocentrospora acerina (Hartig) Deighton and appeared to account for the high level of resistance of the periderm (Garrod and Lewis et al. 1978). The phytoalexin 6-methoxymellein was found in highest concentrations in tissues colonized by M. acarina and is likely involved in limiting wound colonization, (Davies and Lewis 1981). No tests have been conducted on carrots that are relatively resistant or susceptible to cavity spot to measure preformed levels of compounds such as falcarindiol, to determine the rate of accumulation of phytoalexins such as 6-methoxymellien, or to determine whether preformed levels or rates of accumulation vary with plant age.

Plant age

Pythium spp. are considered unspecialized parasites which attack the juvenile tissues of seedlings up to a certain critical age; beyond this stage all tissues (except the root tips and feeder roots) become resistant (Garrett 1970). A number of explanations have been proposed for this "mature plant resistance" including secondary wall thickening in mature or resistant hosts, the formation of a suberized layer of cells following infection, formation of lignin beneath and around the lesion and the conversion of pectin to calcium pectate in plant cell walls as they age (Endo and Colt 1974). Cavity spot does not fit this description of a typical Pythium-incited disease.

In general, severity of cavity spot on carrots in the field increases with time (Maynard et al. 1963, Montfort and Rouxel 1988, Vivoda et al. 1991). In one study, the number of lesions per carrot root increased from

1.19 to 9.95 on field grown carrots in the ten weeks from 29 August to 5 November (Maynard et al. 1963). In commercial carrot fields in France, lesions could be found on young carrots less than 5 mm in diameter, and the incidence of cavity spot increased progressively during the four month growing season (Montfort and Rouxel 1988).

In Britain, carrots are often seeded in May and harvested in the fall and winter. In one trial, cavity spot levels increased four fold in cv.'s Camden and Vita Long between the October and January harvest dates (Sweet et al. 1989). Cultivars were often rated as more susceptible when harvested late rather than early (Grower 1986). The percentage of roots with lesions increased in late harvested carrots in England (Perry 1983) and in commercial carrot fields in California (Vivoda et al. 1991). The increased level of disease could be the result of increased susceptibility as carrots mature, an accumulation of lesions over time or an expansion of lesions as the diameter of the carrots increases (Vivoda et al. 1991). Another possible explanation is that the chance of infection increases as the carrot root surface increases with growth (Wagenvoort et al. 1989).

Carrots grown in pots also demonstrated differing susceptibility with age. Plants that were seven, eleven or sixteen weeks old were subjected to flooded conditions in sealed pots for five days. Lesions developed on zero, six and 36% of the roots, respectively (Perry and Harrison 1979b). Transplanting carrots that were three, four or five months of age into artificially-infested soil demonstrated that older carrots were more susceptible to infection by P. violae and P. ultimum (Vivoda et al. 1991). The number of cavity spot lesions was positively correlated with plant age and five month-old carrots had approximately twice as many lesions as three or four month-old carrots. There were no significant differences among the numbers of carrots with lesions.

EPIDEMIOLOGY

The Pythium species that cause cavity spot have been documented in a

number of different countries (Groom and Perry 1985, White 1986, Montfort and Rouxel 1988 and Vivoda et al. 1991) however the nature of the association of the pathogen with the host plant during crop growth and with the development of cavity spot lesions has not been established (Phelps et al. 1991).

Studies on the epidemiology of a disease often begin with quantification of the initial inoculum. However, this has not been possible with Pythium violae. There is only one report of isolation of P. violae from soil (Dick and Ali-Shtayeh 1986) and the frequency of isolation was low. Isolations on soil dilution plates have typically been dominated by fast-growing species which precludes the isolation and quantification of slow-growing species (Phelps et al. 1991).

Studies of the frequency distribution of cavity spot suggested that there were low levels of randomly-distributed inoculum in the fields tested (Phelps et al. 1991), which would also reduce the probability of successfully isolating P. violae on dilution plates.

The time period required for infection and symptom development to occur in the field has not been determined. Zoospores of Pythium spp. could infect cotton roots within two hours, while infection by mycelial fragments required 12 hours (Spencer and Cooper 1967). Penetration of peach roots by P. ultimum occurs five to eight hours after inoculation (Miller et al. 1966). In trials where carrot roots were inoculated with mycelial plugs of P. violae, sunken areas appeared within two to three days (Groom and Perry 1985, White 1986, Montfort and Rouxel 1988) and the tissue turned black within ten days (White 1986). However, when carrots were grown in the field or in pots, symptom expression apparently took much longer. Observations on carrots growing in commercial fields indicated that symptoms normally seen at harvest were initiated early in the growing season (Perry and Harrison 1979b). Soroker et al. (1984) subjected carrots in pots to high temperatures and flooding, and cavities appeared five weeks after the flooding. Similarly, Vivoda et al. (1991)

transplanted carrots into infested soil and waited four weeks before assessing lesions.

There are no reports of disease progress curves for cavity spot of carrot. Pythium spp. were recovered from asymptomatic periderm of field-grown carrots and the frequency of recovery was plotted against rainfall and soil temperature (White 1988). This does not constitute disease progress since there is no reason to believe that isolations from asymptomatic periderm would correspond to successful infections resulting in lesion development.

P. violae appears to be involved in a reproductive process on carrots, possibly involving mycelial growth (Phelps et al. 1991). During the growing season, increasing numbers of carrots were infected and these initial infections resulted in subsequent reinfection of the same root. The distribution of lesions implied that each primary cavity produced a maximum of one secondary cavity, possibly through mycelial growth, which itself produced a maximum of one tertiary cavity. The data also suggested that the mean number of cavity clusters per carrot seemed to be affected by external effects such as fungicide, while the reproduction rate was affected by cultivar (Phelps et al. 1991). A cultivar effect on rate of reproduction of lesions implies different levels of cultivar resistance, specifically horizontal resistance sensu Vanderplank (1963).

The relationship between the percentage of roots with cavities, and the size and number of cavities is difficult to determine from the literature. Some researchers evaluated cavity spot solely on incidence, (Lyshol et al. 1984), while others also counted the number of cavities per carrot (White 1986, 1988, Vivoda et al. 1991) or developed a rating system based on size and number of cavities (Perry 1983, Scaife et al. 1980). The relationship between the percentage of carrots with lesions, lesion number, and size varied. Jacobsohn et al. (1984) observed that a high incidence of cavity spot generally indicated severe crop damage, namely, many and relatively large lesions on affected roots. Perry (1983)

reported that cultivation reduced the size of the lesions but not the proportion of carrots affected. Similarly, Vivoda et al. (1991) found that the number of cavities per carrot increased with increasing plant age, but not the number of symptomatic carrots. Application of metalaxyl reduced the percentage of carrots with cavity spot and the number of cavities per carrot (White 1988, Walker 1991). Metalaxyl treatment did not affect the size distribution of the cavities in one trial in Britain (White 1988), but reduced cavity size in another (Phelps et al. 1991).

There is still much to be learned about the epidemiology of cavity spot of carrot. The life cycle of Pythium violae has not been described. The role of the environment in infection, symptom development and disease increase has not been elucidated beyond some observations and isolated experiments.

MANAGEMENT AND CONTROL OF CAVITY SPOT

Resistant cultivars

In 1984, the Muck Research Station added a cavity spot rating to the quality assessment of carrot cultivars (Valk et al. 1984). Assessment was based on percent and severity (very light, light, medium, heavy and very heavy) of cavity spots on the carrots. Severity was assessed on number and size of the lesions. The British Columbia Ministry of Agriculture and Fisheries used a similar method to report the susceptibility of cultivars to cavity spot (called horizontal lesions), (Odermatt and Snow 1991). Vivoda et al. (1991) concluded that low levels of tolerance to cavity spot existed among commercial carrot cultivars grown in California.

The resistance to cavity spot identified in commercial cultivars is partial resistance. In Britain, the NIAB warns growers that no carrot variety is completely immune to cavity spot, and advises growers to use a fungicide in conjunction with varieties showing high resistance (National Institute of Agricultural Botany 1991). There are no fungicides registered for cavity spot control on carrots in Canada; growers are

advised to select cultivars that are least susceptible to cavity spot (Ontario Ministry of Agriculture and Food 1992). However, the use of partially resistant cultivars does not always provide adequate control and submissions have been made for the registration of metalaxyl for cavity spot control (C. Hunter, Minor Use Coordinator for O.M.A.F., personal communication).

Horizontal and vertical resistance

Identifying whether resistance is horizontal or vertical is important in both breeding for resistance and resistance management (Vanderplank 1984). The terms horizontal and vertical resistance were used by Vanderplank (1963) to describe the two types of resistance a host may have to a pathogen. "The main effect of variation of the host, using the term "main effect" in a strictly biometric sense, determines horizontal resistance, while interaction, i.e. the differential effect, determines vertical resistance" (Vanderplank 1984). Vertical resistance delays the onset of an epidemic by reducing the amount of effective initial inoculum, while horizontal resistance slows the progress of the epidemic (Vanderplank 1982). However, there are exceptions. Slow-rusting of wheat infected by Puccinia recondita Rob. ex Desm. f. sp. tritici is incomplete vertical resistance which slows the rate of the rust development. Horizontal resistance can delay the start of an epidemic.

Partial resistance, regardless of whether it is horizontal or vertical, reduces the infection rate (Vanderplank 1984). Several components of the horizontal resistance of potatoes to late blight may be useful in interpreting the resistance reaction of carrots to cavity spot. The components of horizontal resistance were: 1) when plants were inoculated with the same number of spores, fewer lesions were formed on the resistant plants, 2) sporulation was less abundant 3) the latent period (time from inoculation to sporulation) was longer, and 4) the infectious period was shorter (Vanderplank 1984).

Fungicides

Selective fungicides played a unique role in the search for the causal agent of cavity spot. The report by Lyshol et al. (1984) that metalaxyl controlled the disease led to the discovery that P. violae was a causal agent of cavity spot (Groom and Perry 1985). Selective fungicides are used in several countries to manage cavity spot (Grower 1985, Walker 1991) but no fungicides are registered in Canada for this use (Ontario Ministry of Agriculture and Food 1992b).

The fungicides metalaxyl (Ciba-Geigy A.G., Switzerland), fosetyl-Al (Rhone Poulenc S.A., France) and propamocarb (Schering A.G., Germany) all significantly reduced cavity spot (Lyshol et al. 1984). These fungicides selectively control fungi of the Class Oomycetes. In a field experiment with carrots growing on sandy soil, metalaxyl at a rate of 202.5 mg ai/m^2 (2.0 kg ai/ha) reduced cavity spot from 46% on the check to 4.4%. Carrot root dieback was also reduced. Seed dressing with metalaxyl or fosetyl-Al at 1.4 and 9.6 g ai/kg seed had no effect on cavity spot, but there was some indication that the fosetyl-Al seed dressing was phytotoxic. None of the fungicides had an effect on seedling emergence. Metalaxyl also reduced cavity spot incidence when applied as a spray, drench or granular formulation (Sweet et al. 1989, Walker 1991, Davis et al. 1991). Early season application was generally found to be most effective, with one exception (Davis et al. 1991).

Metalaxyl seed dressings at rates of 1.4, 1.5, 3 or 6 g ai/kg seed had no effect on cavity spot (Lyshol et al. 1984, Walker 1991). Walker (1991) observed an increase in seedling survival with seed treated with these rates of metalaxyl, while Lyshol et al. (1984) observed no increase in seedling emergence with the use of a metalaxyl seed dressing at 1.4 g ai/kg seed.

In England, field trials were carried out on mineral and organic soils with metalaxyl plus mancozeb (Fubol 58WP) at rates of 0.6 and 1.2 kg ai/ha metalaxyl (Gladders and McPherson 1986, White 1988, Sweet et al.

1989). Cavity spot incidence on the untreated checks at harvest ranged from 9.2-73% on mineral soils and from 3.2-87% on the organic soil. Early application (zero to four weeks after seeding) was essential for control (Gladders and McPherson 1986). A small but significant reduction in cavity spot incidence was achieved with a metalaxyl application ten weeks after seeding but an application 14 weeks after seeding was not effective. A split application of 0.6 kg ai/ha of metalaxyl applied four and 14 weeks after seeding did not improve control.

Metalaxyl was tested on carrots grown on sandy loam soils in California at rates of 1, 2 and 4 lbs ai/acre, (equivalent to 1.12, 2.24 and 4.48 kg ai/ha, respectively) (Davis et al. 1991). The incidence of cavity spot in the untreated checks at harvest ranged from 29.6% to 59.5%. There was a significant linear correlation between cavity spot incidence and the rate of preplant metalaxyl. Soil drenches of metalaxyl (2.0 lbs ai/acre) applied 40-60 days after planting, or multiple dilute applications throughout the season were more efficacious than a single preplant application at comparable rates.

Trials with carrots grown on sandy loam in Australia showed that a single early treatment with metalaxyl reduced the incidence of cavity spot; rates of 0.43-2.14 kg ai/ha applied from four to 14 weeks after sowing were effective (Walker 1991). In British trials, metalaxyl application later than four weeks after seeding was much less effective than earlier applications (Gladders and McPherson 1986).

Early-season application of metalaxyl provided the most effective control of cavity spot but the efficacy of metalaxyl applications at the time of seeding and split applications throughout the growing season varied from area to area. The differences in effective fungicide rates may be the result of different inoculum levels in the soil or Pythium spp. that have different sensitivities to metalaxyl. White et al. (1988) found that P. sulcatum was less sensitive to metalaxyl than was P. violae. Different levels of resistance in the cultivars used in the trials could

also have an effect on the apparent efficacy of metalaxyl. Because the effective rates of metalaxyl differ among growing areas, it would be prudent to test different rates in each growing area.

Differences in the half-life of metalaxyl in organic and mineral soils may also contribute to differences in efficacy. The half-life of metalaxyl in Fox Sandy Loam was three weeks, while the half-life in Bradford Muck was eight weeks (Sharom and Edgington 1982). Metalaxyl also leached more rapidly in sandy loam than in muck soils. After 10 cm of simulated rainfall was applied to Bradford Muck, all of the metalaxyl remained in the top 5 cm of the soil column, while in Fox Sandy Loam, the metalaxyl residues could be found throughout the 25 cm core, with the greatest proportion concentrated around the 15 cm region. Split applications of metalaxyl may be more effective on sandy soils because the shorter half-life and leaching or irrigation combine to reduce the length of time that metalaxyl remains effective in the root zone. In California and Australia metalaxyl applications were followed by irrigation the same day (Davis et al. 1991, Walker 1991).

In addition to metalaxyl, Walker (1991) tested the efficacy of phosphonate (phosphoric acid) for the control of cavity spot at rates of 8, 10, 12, 16.5 and 25 kg ai/ha in the form of Foli-R-Fos 200 (200 g ai/L buffered phosphorous acid, UIM Agrochemicals, Australia). Only the 25 kg ai/ha rate, applied 12 weeks after seeding, was effective. Some phytotoxicity in the form of transient tip burn was observed when Foli-R-Fos was applied to carrots at a rate of 40 kg ai/ha. Fosetyl-Al reduced cavity spot incidence when applied to carrots growing in pots of naturally-infested sandy soil but the effective rate of fosetyl-Al (1.2 g ai/L) was almost seven times that of the effective rate of metalaxyl (0.18 g ai/L) (Lyshol et al. 1984).

It is not usual for metalaxyl to effectively control disease at lower rates than phosphorous acid, whether formulated as fosetyl-Al or phosphonate. The rate of phosphorous acid needed to control downy mildew

on grapes was 1.2 g/L as compared to the effective rate of 0.112 mg/L for metalaxyl (Wicks et al. 1991). In another study where the fungicides were applied to the soil to control Phythophthora root rot of citrus, metalaxyl applied at a rate of 10 ug/ml and fosetyl-Al at a rate of 3000 ug/ml prevented infection of pear fruits incubated with citrus orchard soil containing Phytophthora citrophora R.E. Smith and E.H. Smith and P. parasitica Dastur (Matherson and Matejka).

Mode of action of metalaxyl and fosetyl-Al

Metalaxyl is transported predominantly in an acropetal direction in the transpiration stream. Radio labelling has also identified limited basipetal movement (Zaki et al. 1981). Analysis of plants grown on metalaxyl-drenched soil indicates that the fungicide is readily taken up from the soil solution (Stone et al. 1987).

The biochemical mode of action in Pythium involves the inhibition of RNA synthesis which results in an inhibition of fungal growth and sporulation (Fisher and Hayes 1982). Metalaxyl does not affect the mobility or germination of zoospores, nor the formation of appressoria, host penetration or initiation of the first haustoria, but further fungal development is completely inhibited (Staub et al. 1978). Metalaxyl is fungistatic rather than fungicidal (Bruin and Edgington 1983).

Acylalanine fungicides, such as metalaxyl, are effective eradicants if applied during the first one-half to two-thirds of the incubation period after infection. Later applications do not inhibit lesion production but may reduce spore viability (Bruin and Edgington 1983). Metalaxyl resistant strains of Pythium and Phythophthora are also cross-resistant to other acylalanine fungicides (Bower and Coffey 1985).

Fosetyl-aluminum (fosetyl-Al) is an alkyl phosphonate fungicide. Fosetyl-Al breaks down rapidly in soils and plant tissue to carbon dioxide and phosphorous acid, the active metabolite of fosetyl-Al (Cohen and Coffey 1986). Phosphorous acid is extremely water soluble and has the

unique characteristic of being transported via the phloem. Thus, application to the leaves can provide control of soilborne diseases (Davis 1982). Generally, the fungicidal activity of phosphorous acid persists in soil for several months (Vegh et al. 1977) and remains active in plants for at least five weeks (Smillie et al. 1989). Fosetyl-Al has a narrower spectrum of biological activity than metalaxyl (Cohen and Coffey 1986).

The biochemical mode of action of phosphorous acid has not been determined. Phosphorous acid inhibited mycelial growth and sporangium production and zoospore release in Phytophthora cinnamomi Rands and P. citricola Sawada. Oospore formation by P. citricola was also inhibited, but oospore production by P. cinnamomi was less sensitive (Coffey and Joseph 1985).

Both metalaxyl and fosetyl-Al are reported to have an effect on host defense mechanisms against pathogens (Cohen and Coffey 1986). Metalaxyl application to soybean seedlings increased the concentration of the phytoalexin glyceollin in the early stages of the soybean - Phytophthora megasperma Drechs. interaction (Ward et al. 1980). Glyphosate, an inhibitor of the shikimic acid pathway, suppressed the accumulation of glyceollin and reduced the efficacy of metalaxyl (Ward 1984). Cohen and Coffey (1986) speculated that the fungistatic effect of metalaxyl may lead to a shift in the expression of host resistance, perhaps through the release of non-specific inhibitors by the damaged fungal cells.

Ward (1984) suggested that metalaxyl suppressed the RNA and protein syntheses in the pathogen that were essential for compatibility or the suppression of the resistance mechanisms in the host. Thus, the host developed a resistance response when challenged with a metalaxyl-treated pathogen.

The effect of metalaxyl on host resistance to pathogens has also been demonstrated on potatoes (Barak et al. 1984). Metalaxyl treatment increased the resistance of potato tubers to Fusarium sambucinum Fuckel, F. culmorum (Smith) Sacc. and Alternaria solani Sorauer, even though

these fungi are not Oomycetes and metalaxyl has no effect on them in vitro. Metalaxyl application resulted in a marked increase in the concentration of polyphenol oxidase in the tubers which may be the cause of the increased resistance to infection.

Fosetyl-Al may also stimulate host defenses to infection. Bompeix et al. (1981) found that treatment with glyphosate and α-aminooxyacetic acid reversed the antifungal effects of fosetyl-Al against Phytophthora capsici Leonian. Guest (1984) presented the hypothesis that fosetyl-Al increased phytoalexin production in tobacco. However, these findings are under dispute. Other researchers speculate that sufficient concentrations of phosphorous acid were present to account for the antifungal activity (Cohen and Coffey 1986).

In general, fungi develop resistance more rapidly to selective, site-specific, systemic fungicides than they do to broad-spectrum, protectant fungicides (Bruin and Edgington 1983). Resistance to metalaxyl has been documented in both Pythium and Phytophthora species (Bruin and Edgington 1983) and to fosetyl-Al in Phytophthora (Sanders et al. 1990).

Bruin and Edgington (1983) stated that "The introduction of systemic Oomycete fungicides was a significant step towards better directed, more subtle, cleaner and more efficient control of plant diseases caused by zoosporic fungi". They strongly supported the use of disease forecasting and resistant cultivars to improve the efficiency of fungicide use and reduce the development of resistance in pathogens.

The problem of resistance increases with increased fungicide use. Therefore, disease forecasting programs that reduce the amount of fungicide applied also reduce the rate at which resistance may develop. Improved application techniques, such as seed dressings, soil drenches, and granules, deliver the fungicide precisely to the site where it is needed, again helping to reduce the buildup of resistance.

Another method to slow the development of fungicide resistance is breeding for host resistance to the pathogen, and especially breeding for

horizontal resistance. Horizontal resistance tends to be long lasting resistance but always results in cultivars with less than complete disease resistance (Bruin and Edgington 1983). Low rates of fungicides can complement this resistance and keep disease at acceptable levels. Partial resistance, therefore, can be considered as a partial substitute for fungicides. This premise has been demonstrated with late blight on potatoes (Fry 1975).

The use of selective fungicides was pivotal in the discovery of the causal agent of cavity spot (Lyshol et al. 1984, Groom and Perry 1985) and these fungicides may have a further role to play in determining the epidemiology. Applications of metalaxyl, within eight weeks of seeding, provided the most effective control of cavity spot (Gladders and McPherson 1986, Sweet el al. 1989 and Davis et al. 1991) yet most of the cavities developed late in the growing season (Montfort and Rouxel 1988, Sweet et al. 1989, Vivoda et al. 1991). White (1991) reported that sequential harvest experiments indicated that cavities formed rapidly following prolonged rain and that it was possible to identify lesions of different ages on carrots.

There are a number of hypotheses to explain the success of early season applications of metalaxyl. The first is that metalaxyl persists in the soil and provides season-long protection. The short half-life of metalaxyl on mineral soil (Sharom and Edgington 1982) does not support this hypothesis. Also, applications of metalaxyl applied ten or 14 weeks after seeding were not as effective (Gladders and McPherson 1986).

A second hypothesis is that Pythium spp. infect the carrot root at an early stage of growth, within four to eight weeks after seeding, but the infections remain asymptomatic until the plant becomes more mature, or until environmental conditions favour active infectious growth and lesion development. These infections may be true latent infections, as discussed by Verhoeff (1974), where the fungal hyphae penetrate epidermal cells and then remain dormant for some time before establishing active parasitic

relationships. Alternatively, the infections may be asymptomatic, such as the symptomless growth of Botrytis allii Pers. in young onion leaves (Tichelaar 1967). There are no reports of latent infections by Pythium, although asymptomatic infections have been documented (Kalu et al. 1976, Wisbey et al. 1977). Vivoda et al. (1991) found that more cavities developed on five month-old than on three month-old carrots. This demonstrates that infection of older plants can take place. However, the frequency of infection or rate of disease development may be different on undisturbed carrots in the field.

A third hypothesis is that the metalaxyl stimulates the plants defense system, inducing resistance. The plant remains more resistant to cavity spot until it is harvested, possibly even in storage. Induced resistance could explain the season-long effects of a single metalaxyl application. Sweet et al. (1989) found that metalaxyl provided a greater reduction of cavity spot when applied to susceptible rather than partially resistant cultivars, which may indicate that the metalaxyl was increasing the host defenses of the susceptible cultivars, making them similar to the more resistant carrots. More research is necessary to support or refute these hypotheses, but one segment of the epidemiology of cavity spot remains clear. A significant number of Pythium infections must occur early in the growth of the carrot root, generally, within the first four and sometimes eight weeks after seeding. Fungicides applied after this time do not achieve the same level of control of cavity spot as do earlier applications.

Plant growth-promoting rhizobacteria

Selective fungicides effectively control cavity spot, however, there are problems associated with fungicide use, including pathogen resistance, enhanced degradation in the soil, and public pressure to reduce the amount of pesticides released into the environment.

One alternative to fungicide application is biological control. Much

of the research on the biological control of diseases caused by Pythium spp. has focused on the inoculation of seed with bacteria, especially the fluorescent pseudomonads, Pseudomonas fluorescens and P. putida (Paulitz 1991, Osburn et al. 1989) However, other genera of bacteria can also provide biological control. For instance, Enterobacter cloacae (Jordan) Hormaeche and Edwards, has been shown to be an effective biological control agent of pre-emergence damping-off of pea, beet, cotton and cucumber seedlings (Hadar et al. 1983, Howell et al. 1988). Seed rots and damping-off are well suited to biocontrol with bacteria applied to the seed because the period of host susceptibility is very short and the bacteria are placed directly on the infection court. Seeds also release exudates including sugars and amino acids which are potentially a rich source of nutrients for biocontrol agents in the spermosphere (Parke 1990). The application of fluorescent pseudomonads to seed has also been effective in reducing Pythium root rot of wheat. The control was equivalent to or better than a seed treatment with metalaxyl (Weller and Cook 1986). This implies that the bacteria colonize the root. Certain strains of fluorescent pseudomonads are adapted to aggressively colonize plant roots and can significantly promote plant growth. They are described as plant growth-promoting rhizobacteria (PGPR) (Kloepper et al. 1988). Many PGPR's provide biocontrol of Pythium-induced diseases as well as other diseases such as take all of wheat (Weller et al. 1988) and Fusarium wilt of flax (Sher and Baker 1982). In some instances the growth response can be directly related to control of the root disease, (Weller and Cook 1986), but this is not always the case.

A number of theories have been proposed to explain the bacteria-induced increase in growth. These include 1) production of siderophores (high affinity ferric iron chelators), 2) production of antibiotics which are toxic to soilborne plant pathogens, 3) production of plant growth regulators which stimulate plant growth, and 4) enhancement of phosphate uptake in the plant (Kloepper et al. 1988). Another theory is that the

PGPR colonize the root system and exclude deleterious rhizosphere microorganisms (DRMO). The DRMO do not parasitize plant roots but may reduce plant growth by producing harmful compounds such as cyanide (Weller et al. 1988). The role of bacteria in controlling diseases caused by Pythium spp. has been attributed to siderophore production (Becker and Cook 1988), competition for nutrients (Paulitz 1991, Tedla and Stanghellini 1992) and the production of antibiotics (Maurhofer et al. 1992).

It is generally assumed that root colonization by introduced bacteria is essential for biocontrol of root pathogens and that increasing the population of an introduced bacterium on the root should enhance disease control (Weller 1988). Root colonizing bacteria can be defined as introduced bacteria which become distributed along the root in natural soil, propagate, and survive for several weeks in the presence of competition from the indigenous rhizosphere microflora (Weller 1988). Sher et al. (1984) defined root colonizers as bacteria which attain a population level greater than $5X10^3$/g root.

Root colonization is affected by a number of factors. Howie et al. (1987) found that the population of P. fluorescens was greatest at soil matric potentials between -0.3 and -0.7 bars, however the bacteria spread from seed to roots in soil at -4.0 bars matric potential. Transport of bacteria along the elongating root did not require percolating water, but water movement through the soil did increase bacterial movement (Bahme and Schroth 1987). The optimal temperature for root colonization by P. fluorescens and P. putida is generally below 20°C (Loper et al. 1984).

There are no reports of trials involving bacterization of seed for the control of soilborne diseases of carrots. However, a number of bacterial strains have been identified that provide biocontrol of Pythium spp. on vegetable crops. The observations that early season infection of carrot roots plays an important role in cavity spot, and possibly other Pythium diseases of carrot, suggest that cavity spot can be managed with

seed-applied bacteria.

Models for analyzing disease progress

Quantitative epidemiology of diseases induced by soilborne plant pathogens remains largely unreported in the phytopathological literature due to the complexity of the host-pathogen environment and the lack of available quantitative biological data for such diseases. However, analysis of disease progression dynamics is very important in the characterization of disease cycles and eventual disease management systems (Campbell et al. 1980).

Several mathematical models have been developed to describe epidemics of plant diseases. The most common of these are the exponential (or logarithmic), monomolecular, logistic and Gompertz models. The Weibull model has also been used by plant pathologists to determine the shape of different disease progress curves (Campbell and Madden 1990). However, the Weibull shape parameter does not always provide a strong indication of shape or appropriate growth model (Campbell et al. 1980, Campbell and Powell 1980). None of the models was developed specifically for applications in plant pathology and thus care should be exercised in attaching strict biological interpretations to the variables and parameters of the models (Campbell and Madden 1990).

There have been several examples in the literature where soilborne diseases were found not to increase according to the monocyclic model (Campbell et al. 1980, Campbell and Powell 1980, Larsson and Gerhardson 1992). Gilligan (1983) asserted that the myth that all soilborne diseases are monocyclic has been dispelled. For some root diseases, the disease progress curves represent a composite of infection rates and pathogen growth rates that vary over time and do not necessarily indicate whether the disease is of the simple or compound interest type (Campbell 1982). Thus, disease progress curves of soilborne diseases such as cavity spot may provide an indication of the growth and reproduction cycle of the

pathogen but may be more difficult to interpret than similar curves for foliar diseases. For instance, the importance of the latent period and infectious period has not been documented in the epidemiology of root diseases (Gilligan 1983). More information on the epidemiology of cavity spot is needed to interpret the disease progress curves for cavity spot, while at the same time, the disease progress curves can provide some information on the epidemiology of the disease.

CONCLUSIONS

Cavity spot affects carrots in most carrot producing areas of the world. The disease is caused by a number of soil-borne Pythium spp. but the species most often involved in disease development vary in different areas of the world. Slow-growing species such as P. violae and P. sulcatum play a major role (White 1986, Nagai et al. 1986, Vivoda et al. 1991). Virtually nothing is known about the population dynamics of these fungi in soil.

The effects of environmental factors such as soil moisture and temperature on cavity spot development have been described (Perry and Harrison 1979b, White 1988) but no true epidemiological studies have been conducted on disease development over time. There is no information on the effects of the environment on cultivar resistance or other control measures. This information could be used to develop disease forecasting models to improve the timing of fungicide application or recommend a harvest date to avoid a disease increase. No one has investigated cavity spot development on harvested carrots in cold storage.

The selective fungicide, metalaxyl, provides an effective means of controlling cavity spot, but the optimal rates and timing of applications vary in different areas (Gladders and McPherson 1986, Davis et al. 1991, Walker 1991). Carrot cultivars with partial resistance to cavity spot have been identified but there have been no attempts to characterize the resistance. Only one report (Sweet et al. 1989) noted a possible

interaction between cultivar resistance and fungicide application. No one has investigated the potential for biological control of Pythium diseases of carrots.

A disease management system, incorporating disease forecasting, is required to suppress cavity spot while making the most efficient use of fungicides, cultivar resistance, and other management techniques. To achieve this, more information is required about life cycles of the major Pythium spp. that cause cavity spot, about the epidemiology of the disease, and about the relative effectiveness of the available control measures.

To address these areas of investigation, specific research objectives were outlined as follows: to investigate the association of Pythium spp. with cavity spot and carry out Koch's postulates; to investigate the relationship between plant age, rainfall, and soil temperature, and disease development; to determine the optimal rates, methods and timing of fungicide applications; to evaluate alternative methods of control; to identify and characterize cavity spot resistance; and to determine if cavity spot levels change while carrots are in storage.

Chapter 3

ASSOCIATION OF PYTHIUM SPECIES WITH CAVITY SPOT OF CARROT

INTRODUCTION

The cause of cavity spot of carrot was attributed to numerous physiological and biological agents prior to 1984 when Lyshol et al. (1984) reported that selective fungicides, which controlled fungi in the Class Oomycetes, reduced cavity spot and pythium root dieback on carrots. Subsequently, a number of Pythium species were reported to cause cavity spot. In Britain, the slow-growing species P. violae and P. sulcatum were identified as the main causal agents (White 1988), while in California P. violae and P. ultimum were reported to cause the disease (Vivoda et al. 1991). The reports agreed that P. violae was the species most pathogenic to carrots. Pythium irregulare was the species responsible for cavity spot symptoms on carrots in Israel (Shelvin et al. 1987). In Japan, a disease of carrot called brown blot, which closely resembles cavity spot, is caused by P. sulcatum (Nagai et al. 1986).

White (1986, 1988) isolated mostly slow-growing Pythium species from cavities and fast-growing species from asymptomatic periderm of carrots. Species recovered from the periderm included Pythium sylvaticum, P. ultimum, P. intermedium and P. irregulare. Pythium intermedium was the only fast-growing species recovered from cavities in significant numbers.

In the first study, Pythium spp. could not be isolated from cavities but several species were obtained from the fibrous roots of carrots with cavity spot symptoms (White 1988). These roots may be a primary site of Pythium infection since the growing root tips are sites frequently infected by Pythium species (Hendrix and Campbell 1973) and because the emergence of lateral roots from the tap root breaks the defensive barrier of the periderm (Esau 1940). The lateral root scars on the tap root are thus probable sites of Pythium infection.

White (1988) reported that Pythium spp. were recovered more frequently from asymptomatic periderm of young (six to ten week-old) than

from older carrots. Fewer Pythium ... temperatures were around 15°C and rainfall sporadic, whereas recovery was higher when soil temperatures were below 10°C and there had been rainfall in each of the preceding four weeks. The frequency of isolation from metalaxyl-treated carrots was always lower than from untreated carrots. The relationship between these factors and Pythium isolation from cavities was not investigated.

The present study was conducted to determine whether Pythium species were associated with cavity spot of carrot in organic soils in Ontario and to fulfill Koch's postulates to show that Pythium spp. caused the disease. The second objective was to determine whether cultivar resistance, fungicide treatment, plant age, rainfall and soil temperature affected the frequency of Pythium recovery from asymptomatic periderm, root scars and cavities. If a relationship was found between one or more of these factors and recovery frequency, this information could help to determine the nature of the resistance, the site of action of the fungicides, or the environmental conditions that influence infection of carrots by Pythium.

The association between Pythium species and cavity spot was investigated by:

a) determining the frequency of recovery of Pythium spp. from cavity spot lesions, asymptomatic periderm and lateral root scars of carrots,

b) carrying out Koch's postulates by identifying the Pythium spp. recovered from carrots, growing carrots in a soilless growing medium artificially infested with the Pythium isolates, determining the severity of cavity spot in comparison to carrots grown in non-inoculated medium, and reisolating Pythium from the lesions,

c) determining whether slow-growing Pythium species were associated with cavities and fast-growing species associated with the periderm of carrot roots in Ontario,

as was the case in Britain,

d) exploring the effects of cultivar resistance and treatment of carrots with metalaxyl or fosetyl-Al on the frequency of Pythium isolation and,

e) studying the effects of plant age, the amount or frequency of rainfall or irrigation, and soil temperature on the frequency of Pythium recovery.

Portions of this research were reported previously (McDonald 1991).

MATERIALS AND METHODS

Cultivars

Carrot cultivars that had previously been assessed as susceptible or resistant (tolerant) to cavity spot were evaluated. In this report, carrot cultivars that consistently exhibited less than 50% "light" lesions in Muck Research Station cultivar evaluations (Valk et al. 1986, Valk et al. 1988, McDonald et al. 1989) were referred to as "resistant" to cavity spot.

Resistant cultivar Six Pak (Harris Moran, Kettleby, ON) was used each year and the susceptible cultivars Red Core Chantenay (Asgrow Seed Co., Newmarket, ON) and Chanton (Arco Seed Co., El Centro, CA) were included in 1988, SR-481 (Sunseeds, Brooks, OR) in 1991, and Red Core Chantenay in 1992.

Seeding rate of the processing carrots, Red Core Chantenay and Chanton, was 40-50 seeds/m and of packaging carrots Six Pak and SR-481 was 82-122 seeds/m. All were seeded with a hand-operated V-belt seeder.

Field plots

All trials were conducted in organic soil (73% organic matter) at the Muck Research Station, Ontario, at 44° 10'N latitude and 79° 35'W longitude. Fertilizer was applied each spring and incorporated prior to seeding in accordance with soil analyses (Ontario Ministry of Agriculture

and Food 1992b). Nitrogen, [illegible] ammonium nitrate, superphosphate and muriate of potash, respectively. Borax was also applied at 1 kg boron/ha. Registered insecticides and herbicides were applied as needed (Ontario Ministry of Agriculture and Food 1992b). Fungicides were not applied, except those used as treatments. Plots in all trials were arranged in a randomized complete block design with four replications per treatment. Each replicate plot consisted of a single 6 m row (1988), or a single bed, 1.7 by 6 m, (1991-1992) with three or four rows of carrots per bed.

Fungicides

Fungicides were applied as drench and furrow treatments at the time of seeding. Metalaxyl plus mancozeb (Ridomil MZ 72 WP, 8% metalaxyl plus 64% mancozeb, Ciba-Geigy Canada Inc.) and fosetyl-Al (Aliette, 80% fosetyl-Al, Rhone Poulenc Inc.) (2.0 plus 16.0 and 4.0 kg ai/ha, respectively), were applied as a drench in 2,000 L water/ha in an 8 cm band over the seed row. The granular formulation of metalaxyl (Subdue 5G, 5% metalaxyl, Ciba-Geigy, Canada Inc.) was applied at a rate of 0.5 kg ai/ha in the seed furrow with the seed.

Plant growth-promoting rhizobacteria

The isolates of plant-growth promoting rhizobacteria (PGPR) used in the studies in 1988 were Sp-102, isolate 1-102 of *Serratia proteamaculans*, Pf-12, isolate 31-12 of *Pseudomonas fluorescens* and Pp-2, isolate GR12-2 of *Pseudomonas putida* (Allelix Inc., now Esso Ag Biologicals, Saskatoon, Saskatchewan). The origin of these isolates was not released. *Pseudomonas fluorescens* and *P. putida* are both gram negative rods which produce fluorescent pigments but can be distinguished because in contrast to *P. putida*, *P. fluorescens* liquifies gelatin at 22°C, has the ability to reduce nitrate and can utilize citrate as the sole carbon source (MacFadden 1976) as well as trehalose and sorbitol (Fahy and Persley

1983). Serratia proteamaculans belongs to the family Enterobacteriaceae. These bacteria are small gram negative rods which produce acid from the fermentation of glucose, other carbohydrates and alcohols (MacFadden 1976).

The isolates were received from the supplier as cell suspensions (10^8 cfu/ml) on each day of treatment. One half ml of suspension was added to a plastic bag with a 10 g aliquot of seed of Six Pak, Chanton or Red Core Chantenay, mixed for ten minutes, air-dried for one hour, then seeded.

Seeding date

Seeding date was examined in relation to cavity spot development and frequency of Pythium recovery in 1991. Six Pak and SR-481 were seeded on 9 May, 30 May, 21 June and 12 July in 1991. Pythium spp. were recovered from these carrots harvested 13 November and 8 December, 1991.

Rainfall, soil temperature and host age in relation to frequency of Pythium recovery from carrot roots

Environmental factors were measured approximately 200 m from the plots. Rainfall was recorded using a standard funnel-type rain gauge (issued by the Atmospheric Environment Services) and checked twice daily at 8:30 a.m. and 4:30 p.m. Soil temperature was measured using a thermistor in a water-resistant probe buried horizontally 5 cm below the soil surface. In 1988, the thermistor was located in a carrot plot which was within 110 m of the plots. Soil temperature was recorded every five minutes on a Honeywell Recorder and the readings for each day were averaged. In 1992, soil temperature was measured using a Model 107 temperature probe (Fenwal Electronics VVT51J1 thermistor in a water-resistant probe) positioned 5 cm below the grass-covered surface of the soil and connected to a 21X micrologger (Campbell Scientific Canada Inc.). Temperature readings were taken at intervals of 16.67 milliseconds and integrated. The mean soil temperature for each calendar day was averaged

from one sample date to the next to obtain the mean soil temperature value for each sample date. Temperatures at 10, 15 and 20 cm depths were recorded but previous trials had shown that soil temperature at 5 cm was most highly correlated to cavity spot development and was thus chosen for this study.

Rainfall was expressed as cumulative rainfall (mm) from day of seeding, total rainfall in the one, two, or three weeks prior to harvesting the carrots and incidence of rainfall greater than 5 mm/day in the four weeks prior to harvest. The number of days from seeding to each harvest date was used as an estimate of the physiological age of the carrots in each sample.

Irrigation

To evaluate the effect of irrigation on the frequency of Pythium recovery, two plots were established 100 m apart in 1992. The irrigated plot received 2.54 cm of water once a week from 11 June to 2 July and again on 16 July and 17 September. During the other weeks, the natural rainfall was high and the soil was near saturation.

Sampling and cavity spot assessment

Carrots were harvested at two to three week intervals throughout the growing season. Ten carrots were harvested from each replication, except on 28 June and 13 July, 1988 when five carrots were harvested at random from each treatment. Following harvest, roots of seedling carrots (< 5 mm in diameter at the crown) and enlarged tap roots (≥ 5 mm) were washed in running tap water. Washed carrots were air-dried for five to ten minutes, weighed and assessed for cavity spot. Incidence of cavity spot was calculated as the percent of carrots in the sample with one or more cavity spot lesions.

A cavity spot index was calculated as an estimate of disease severity. Carrots were placed into the following severity classes based

on the vertical width of the largest lesion on each carrot: 1, < 1 mm; 2, 1-2 mm; 3, 2-5 mm; 4, 5-10 mm; and 5, > 10 mm. The severity values were transformed to an index with a 0-100 scale using a modified formula of Kobriger and Hagedorn (1983). Using the modified formula, the number of carrots in each severity class was multiplied by the severity class value (1-5) and the results from each severity class were summed. This value was divided by the total number of carrots examined, multiplied by the number of severity classes (five). This figure was multiplied by 100.

$$\text{Disease index} = \frac{\text{Sum of (severity class} \times \text{Number of roots in that class)}}{\text{Total number of roots} \times 5} \times 100$$

If carrots could not be assessed immediately they were placed in plastic bags which were sealed and placed in a temperature controlled Filacell storage at 1.0°C ± 1.0°C and 90% ± 5% relative humidity for two to sixty days. Assessments were done on a block by block basis so any variability due to length of time in storage could be accounted for by differences between blocks in the statistical analysis.

Recovery of Pythium species

Pythium spp. were recovered from roots of seedling carrots in 1988 and 1991 and from enlarged tap roots in 1988, 1991 and 1992. The root systems of seedling carrots were washed, air-dried and placed on the surface of a semi-selective medium for Pythium isolation (MPVP) in petri plates. This selective medium contained 20 g sucrose, 10 mg CaCl, 10 mg $MgSO_4 \cdot 7H_2O$, 1 mg $ZnCl_2$, 0.02 mg each of $CuSO_4 \cdot 5H_2O$, MoO_3, $MnCl_2$, and $FeSO_4 \cdot 7H_2O$, 100 μg thiamine hydrochloride, 17 g cornmeal agar, 23 g agar, and the antibiotics pimaricin (100 ppm) rifampicin (30 ppm, as a replacement for vancomycin), penicillin (50 ppm), pentachloronitrobenzene (100 ppm) and rose bengal (5 ppm) in one litre of demineralized water (Mircetich 1971, Mircetich and Kraft 1973). The medium retained its selective properties for 15 to 20 days after inoculation if the plates were incubated in the dark.

The length (cm) of the tap root and major secondary roots was measured from the underside of the petri plate. Plates were stored in the dark (18-23°C) and numbers of colonies per root were recorded daily for a minimum of nine days.

Pythium species were also recovered from the surface of enlarged tap roots. The roots were washed and thin surface pieces (approximately 0.5 cm^2) were cut using a sharp scalpel, from the edge of cavity spot lesions, from asymptomatic periderm, and from lateral root scars.

In 1988 and 1991, five pieces each of periderm, root scars or lesions were taken per replication. In 1992, 15 pieces of asymptomatic periderm and when possible, pieces of lesions, were taken from carrots of each treatment replication. Pieces were not taken from the root scars because previous trials showed there were few differences in the frequency of isolation from periderm and root scars. Because Pythium spp. were isolated infrequently from the periderm the number of periderm pieces that were plated was increased to obtain more isolates. When isolations could not be done immediately after harvest, carrots were placed in sealed plastic bags in a temperature controlled storage at 1°C until the isolations could be made (two to sixty days). Isolations were made from all four replications per treatment except on 8 September and 19 October, 1988 when only three replications were used. To determine the frequency of Pythium recovery, pieces were placed, interior-side down, on MPVP and stored in the dark as described above. Mycelial plugs from the edge of each colony were placed on the bottom of a petri plate under water agar. Fungi growing through the water agar were examined microscopically for the presence of coenocytic mycelium and oogonia or sporangia characteristic of Pythium species. Features were recorded that could aid in identification to species.

Pythium identification

For identification to species, mycelial plugs from cultures that

appeared to have different growth habits on water agar were transferred to rolled-oat agar (Hancock, 1977) which had been poured to form a slant in each petri plate. The plates were incubated at room temperature for two days, then the bottom of each plate was covered with sterile tap water. The plates were incubated again and the mycelium grew over the surface of the water. These cultures were examined for diagnostic features of Pythium spp.

Mycelial plugs from the edge of pure cultures on water agar were transferred to test tubes containing autoclaved tap water and hemp seeds or popcorn, for long-term storage. Plugs of mycelium were also transferred to corn-meal agar, and growth rates were measured.

Pythium isolates were identified according to the keys of Vander Plaats-Niterink (1981) and Dick (1990). Representative isolates were also sent to the Biosystematics Laboratory, Ottawa, for identification by Dr. D.J.S. Barr. The source of each isolate was recorded but the frequency of isolation of each species compared to the total number of sections was not calculated.

Pathogenicity tests on greenhouse-grown carrots

Three isolates of P. violae, two of P. irregulare, and one of P. ultimum and Pythium group G were tested for pathogenicity on carrots. Isolates recovered from cavity spot lesions were cultured on rolled-oat agar (Hancock 1977) for three weeks. The mycelial mats were harvested, homogenized in a blender and the volume was increased to one litre with sterile tap water. The resulting suspension was mixed with approximately eight litres of soilless growth medium (Pro-Mix BX, Plant Products, Brampton, ON) and placed in one litre plastic pots. Twenty seeds/pot of carrot cv. Huron (Sunseeds, Brooks, OR) were seeded into the growth medium with or without inoculum on 18 January, 1993. Six replicate pots per isolate and non-infested checks were placed in a greenhouse maintained at

15-25°C. Pots were watered as needed to prevent wilting. Plants were fertilized twice with 20-20-20.

To determine the inoculum concentration, 10 g aliquots of growth medium with and without inoculum were removed after mixing and before the medium was divided into pots. The growth medium was added to 100 ml of sterile tap water in 250 ml flasks and placed on a rotary shaker at 130 rpm for one hour. One hundred μL aliquots of the supernatant were spread on plants of MPVP (ten plates per isolate) which were incubated in the dark at 20°C. Plates were checked daily and the number of Pythium colonies per plate were counted.

The carrots were harvested on 16 June, 1993, washed, and examined for characteristic cavity spot lesions. Pieces of root tissue from the edge of the lesions were removed and plated on MPVP for reisolation.

A second trial to evaluate the pathogenicity of more isolates failed because carrots grown in the non-infested growth medium had similar numbers of lesions/carrot as those grown in medium infested with Pythium propagules.

Statistical analysis

All field trials were arranged in a randomized complete block design with four replications per treatment. Isolations were made from samples of three to ten carrots randomly chosen from each replication. N-way analysis of variance (ANOVA) was performed using the general linear models procedure of SAS, version 6.03.

Means separation was performed using Duncan's New Multiple Range Tests (Duncan's NMR). Least significant difference (LSD) values were calculated to allow comparison of adjacent means. If analysis of variance indicated there was a significant ($P<0.05$) interaction between factors, simple effects of the treatments were examined. If the interaction was not significant, main effects of the treatments were examined.

Simple linear regression analysis was performed for each of the nine independent variables (days after seeding, rainfall at different time periods, incidence of rainfall and soil temperature at 5 cm) in relation to the frequency of isolation from each replicate of each type of root piece (periderm, root scar or cavity) for the 1988 and 1992 data. The recovery data from the seedling roots was not included because the units of assessment were different (cfu/cm root vs. cfu/piece) and could not be converted to a single unit of measurement. The 1991 isolation data was not included because there were only three sample dates, which would not provide sufficient data points for regression analyses. Analyses were performed separately for each cultivar, untreated or treated with metalaxyl + mancozeb. Graphs of the data were examined, and where there appeared to be a quadratic relationship between the independent and dependent variables, second-order polynomial regression was also performed. Linear and polynomial regression analyses were run using Statview 4.0 (Abacus Inc., Berkeley, CA) on a MacIntosh LC.

RESULTS

Recovery of Pythium species

Several species of Pythium were recovered from seedling carrot roots and from sections of asymptomatic periderm, lateral root scars and cavities of enlarged tap roots (Table 3). The fast-growing species Pythium irregulare and P. ultimum were recovered from all portions of the carrot root examined, as was the slow-growing P. sulcatum. The most species (six) were obtained from cavity pieces and the fewest species (three) were obtained from pieces of asymptomatic periderm. Pythium violae and Pythium group G were obtained from cavity sections but not from asymptomatic portions of carrot root, while P. paroecandrum and P. aphanidermatum were not found on cavity sections but were obtained from seedling roots and root scars.

Table 3. *Pythium* species isolated from seedling roots, asymptomatic periderm, lateral root scars and cavities in 1988 and 1991, and asymptomatic periderm and cavities in 1992.

Pythium species and number of isolates identified[1]			
Seedling roots	Asymptomatic periderm	Root scars	Cavities
P. intermedium (1)	*P. irregulare* (3)	*P. aphanidermatum* (1)	*P. intermedium* (1)
P. irregulare (13)	*P. ultimum* (1)	*P. irregulare* (1)	*P. irregulare* (7)
P. paroecandrum (1)	*P. sulcatum* (1)	*P. paroecandrum* (1)	*P. sulcatum* (7)
P. sulcatum (10)		*P. ultimum* (2)	*P. ultimum* (5)
P. ultimum (8)		*P. sulcatum* (1)	*P. violae* (6)
			Pythium group G (3

1 Numbers in brackets indicate the number of isolates recovered and positively identified.

Pathogenicity Studies

All the isolates tested caused characteristic cavity spot lesions on carrots grown in infested growth medium (Table 4). Pythium violae isolates 93-09, 93-03 and 93-06 and P. ultimum isolate 93-10 were most pathogenic. The isolates of P. irregulare and Pythium group G did not cause significantly more lesions than developed on carrots grown in the non-infested check but isolates of P. irregulare did cause an increase in disease incidence. A small number of lesions (0.1/carrot) were found on carrots from non-infested growth medium. All of the isolates, except that of Pythium group G, resulted in a higher incidence of cavity spot than was found on those carrots from the non-infested check (Table 4).

Frequency of Pythium recovery from seedling roots, and pieces of asymptomatic periderm, lateral root scars and cavities from tap roots

The frequency of Pythium recovery from seedling carrot roots was analyzed as a factorial experiment with two factors, cultivar and treatment, in 1988; in 1991, cultivar was the only factor. The frequency of Pythium recovery was 3-8 colony-forming units (cfu)/10 cm of root (Table 5a). Significant differences were found for the main effect of cultivar of roots sampled on 28 June, 1988. Analysis of variance indicated that the cultivar effects were significant (P=0.0012) but the cultivar by fungicide interaction was not (P=0.8343 Appendix II Table 5). Therefore, main effects of cultivar were examined (Table 5b). More Pythium colonies were recovered from seedling roots of Six Pak carrots than from those of Chanton or Red Core Chantenay.

The frequency of Pythium recovery from pieces (periderm, lateral root scars, and cavities) of enlarged tap roots was analyzed as one factor (piece) of three-factor factorial experiments in 1988, 1991 and 1992. Simple effects of the factors are presented in Tables 6a, 7, and 8a, respectively. There were no significant three-way interactions, except on the 3 December, 1988, sample date. If significant two-way interactions

Table 4. Pathogenicity of *Pythium* isolates on greenhouse-grown carrots.

Pythium species and isolate	Inoculum concentration[1] (cfu/g)	Cavity spot rating	
		Lesions/ carrot[2]	Incidence (%)
P. violae (93-09)	80	4.9 a[3]	78 a
P. ultimum (93-10)	820	3.6 ab	59 abc
P. violae (93-03)	780	2.5 bc	68 ab
P. violae (93-06)	20	2.4 bc	67 ab
P. irregulare (93-05)	170	1.1 cd	39 bcd
P. irregulare (93-04)	40	0.5 cd	36 cd
Pythium group G (93-01)	270	0.3 cd	13 de
Check	0	0.1 d	6 e

1. Inoculum concentration in soilless growth medium on 18 January, 1993 when carrots were seeded.

2. Lesions were counted immediately after harvest on 16 and 17 June, 1993.

3. Values in a column followed by the same letter are not significantly different at P=0.05, Duncan's New Multiple Range Test.

5a. Carrot cultivar and metalaxyl plus mancozeb treatment in relation to frequency of recovery of Pythium from roots of carrot seedlings in 1988 and 1991.

Sample Date[1]	Number of colony forming units/10 cm root							
	Six Pak		Chanton		Red Core Chantenay		SR-481	LSD
	Check	Fungicide[2]	Check	Fungicide	Check	Fungicide	Check	(P=0.05)
28 June	7[3]	6	1	1	3	1		N.S.
13 July	2	5	7	7	8	3		N.S.
6 June	6						1	N.S.

arrots were seeded on 2 June, 1988 and 9 May, 1991.

domil MZ 72WP (8% metalaxyl plus 64% mancozeb), 2.0 kg ai metalaxyl/ha applied in an 8 cm band over th eed row.

reatments on any sample date are not significantly different at P=0.05, Duncan's New Multiple ange Test.

Table 5b. Main effects of cultivar in relation to frequency of *Pythium* isolation from young carrot roots on 28 June, 1988.

Cultivar	Samples/ mean	cfu/10 cm root
Six Pak	15	7 a*
Chanton	10	1 b
Red Core Chantenay	15	2 b

* Values in a column followed by the same letter are not significantly different at P=0.05, Duncan's New Multiple Range Test.

6a. Cultivar, metalaxyl plus mancozeb treatment, and plant growth-promoting rhizobacteria in relation to frequency of Pythium recovery from cavities, root scars and periderm, and to disease incidence in 1988.

Cultivar	Treatments: Fungicide[1] formulation and rate (kg ai/ha)	Treatments: PGPR[2] ($5x10^7$ cfu 10 g seed)	Colony forming units/10 pieces: Periderm	Colony forming units/10 pieces: Root scars	Colony forming units/10 pieces: Cavity	Cavity spot index (0-100)	Disease incidence (%)
Six Pak	Check		1	1		3	15
	Drench (2.0)		0	1		2	8
Chanton	Check		1	0		2	8
	Drench (2.0)		3	2		0	0
Red Core Chantenay	Check		3	0		0	0
	Drench (2.0)		2	1		0	0
LSD(P=0.05)			N.S.	N.S.		N.S.	N.S.
Six Pak	Check		0	0	0	2	11
	Drench (2.0)		0	0	0	0	0
		Pf-12	0	0	0	2	11
Chanton	Check		0	1	4	15	78
	Drench (2.0)		0	0	7	11	44
		Pf-12	0	1	4	17	67
Red Core Chantenay	Check		0	1	2	7	22
	Drench (2.0)		0	1	6	5	22
		Pf-12	0	2	8	2	11
LSD (P=0.05)			3	3	3	N.S.	48.6

.../ continued

6a - continued

e	Cultivar	Treatments: Fungicide[1] formulation and rate (kg ai/ha)	Treatments: PGPR[2] ($5x10^7$ cfu 10 g seed)	Colony forming units/10 pieces: Periderm	Colony forming units/10 pieces: Root scars	Colony forming units/10 pieces: Cavity	Cavity spot index (0-100)	Disease incidenc (%)
pt.	Six Pak	Check		1 gh*	1 gh	4 c-f	7	28
		Drench (2.0)		0 h	1 gh	0 h	4	15
			Pf-12	1 f-h	1 gh	1 f-h	7	28
			Pp-2	1 gh	1 gh	6 bc	7	33
	Chanton	Check		0 h	0 h	6 bc	23	60
		Drench (2.0)		1 gh	2 e-h	5 b-e	14	58
			Pf-12	0 gh	3 e-h	10 a	24	70
			Pp-2	1 gh	1 gh	6 bc	20	62
	Red Core Chantenay	Check		3 e-h	1 f-h	6 bcd	14	38
		Drench (2.0)		1 gh	1 f-h	0 h	4	18
			Pf-12	1 gh	0 h	7 ab	20	62
			Pp-2	0 gh	3 d-g	7 ab	13	44
	LSD (P=0.05)						10.5	26.3
t.	Six Pak	Check		0	1	8	10	30
		Drench (2.0)		1	0	6	5	23
			Sp-102	0	1	4	10	33
	Chanton	Check		1	1	7	32	81
		Drench (2.0)		1	1	5	18	50
			Sp-102	0	0	7	38	90

.../ continued

6a - continued

Cultivar	Treatments: Fungicide[1] formulation and rate (kg ai/ha)	Treatments: PGPR[2] ($5x10^7$ cfu 10 g seed)	Colony forming units/10 pieces: Periderm	Colony forming units/10 pieces: Root scars	Colony forming units/10 pieces: Cavity	Cavity spot index (0-100)	Disease incidence (%)
Red Core Chantenay	Check		1	2	6	11	33
	Drench (2.0)		0	1	3	17	48
		Sp-102	0	1	7	24	70
LSD (P=0.05)			2	2	2	12.8	29.7
Six Pak	Check		0	0	8	9	32
	Drench (2.0)		0	0	-	4	13
		Sp-102	0	1	3	12	48
		Pf-12	1	1	8	18	38
		Pp-2	1	0	5	12	43
Chanton	Check		0	1	5	28	73
	Drench (2.0)		0	1	7	24	73
		Sp-102	0	1	9	29	68
		Pf-12	0	3	7	27	73
		Pp-2	1	2	8	20	58
Red Core Chantenay	Check		0	1	5	14	40
	Drench (2.0)		0	1	7	11	30
		Sp-102	0	0	5	23	70
		Pf-12	1	0	5	24	68
		Pp-2	0	0	7	24	70
LSD (P=0.05)			2	2	2	14.4	28.8

.../ continued

6a - continued

Cultivar	Treatments: Fungicide[1] formulation and rate (kg ai/ha)	Treatments: PGPR[2] ($5x10^7$ cfu 10 g seed)	Colony forming units/10 pieces: Periderm	Colony forming units/10 pieces: Root scars	Colony forming units/10 pieces: Cavity	Cavity spot index (0-100)	Disease incidence (%)
Six Pak	Check		0	2	5	13	48
	Drench (2.0)		0	0	5	10	31
	Granular (0.5)		0	1	5	12	26
		Sp-102	0	2	5	20	60
		Pf-12	0	0	4	15	44
		Pp-2	1	0	8	13	39
Chanton	Check		0	1	8	31	80
	Drench (2.0)		1	1	6	20	71
	Granular (0.5)		1	1	10	18	55
		Sp-102	0	1	8	22	68
		Pf-12	0	2	6	38	87
		Pp-2	0	1	6	24	70
Red Core Chantenay	Check		1	1	4	30	72
	Drench (2.0)		0	1	5	17	52
	Granular (0.5)		0	1	2	17	32
		Sp-102	0	2	4	33	79
		Pf-12	1	2	7	29	66
		Pp-2	1	1	6	26	73
LSD (P=0.5)			2	2	2	11.8	19.7

... / continued

6a - continued

e	Cultivar	Treatments: Fungicide[1] formulation and rate (kg ai/ha)	Treatments: PGPR[2] ($5x10^7$ cfu 10 g seed)	Colony forming units/10 pieces: Periderm	Root scars	Cavity	Cavity spot index (0-100)	Disease incidenc (%)
c.	Six Pak	Check		0 c	1 c	5 b	18	56
		Drench (2.0)		0 c	0 c	4 b	6	22
			Sp-102	0 c	0 c	9 a	14	48
			Pf-12	0 c	0 c	5 b	11	43
			Pp-2	0 c	1 c	5 b	8	35
	Chanton	Check		0 c	1 c	9 a	33	83
		Drench (2.0)		0 c	1 c	6 b	23	64
			Sp-102	0 c	1 c	6 b	36	83
			Pf-12	0 c	1 c	5 b	34	85
			Pp-2	0.10 c	1 c	4 b	30	53
	Red Core Chantenay	Check		0 c	1 c	6 b	34	83
		Drench (2.0)		0 c	1 c	2 c	15	49
			Sp-102	0 c	2 c	4 b	34	83
			Pf-12	0 c	1 c	6 b	28	69
			Pp-2	0 c	1 c	6 b	34	85
	LSD (P=0.05)						16.1	25.8

ungicide drench was Ridomil MZ (8% metalaxyl and 64% mancozeb at a rate of 2.0 kg ai/ha metalaxyl and 6.0 kg ai/ha mancozeb), granular application was Subdue 5G. Both were applied at seeding.

lant growth promoting rhizobacteria Sp-102, Pf-12 and Pp-2 were isolate 1-102 of Serratia roteamaculans, isolate 31-12 of Pseudomonas fluorescens and isolate GR12-2 of Pseudomonas putida espectively.

alues in a column followed by the same letter are not significantly different at P=0.05, Duncan's New ultiple Range Test.

Table 6b. Main effects of source of root piece (asymptomatic periderm, root scar or cavity) in relation to frequency of Pythium recovery from carrot roots on different harvest dates in 1988.

Date	Colony-forming units/10 tissue pieces		
	Periderm	Root scars	Cavity
8 September	1 c[1](27)[2]	3 b (28)	7 a (10)
21 September*	1 b (47)	1 b (47)	6 a (37)
5 October	0 b (35)	1 b (36)	6 a (35)
19 October	0 b (45)	1 b (46)	6 a (42)
1 November	0 c (83)	1 b (83)	6 a (83)
3 December*	0 b (59)	1 b (59)	6 a (59)

1 Values in a row followed by the same letter are not significantly different at P=0.05, Duncan's New Multiple Range Test.

2 Values in brackets indicate the number of replications per mean.

* Significant interactions, refer to Table 6a for simple effects.

Table 6c. Main effects of cultivar in relation to frequency of Pythium recovery from carrot root pieces on different harvest dates in 1988.

Date	Colony-forming units/10 tissue pieces		
	Six Pak	Chanton	Red Core Chantenay
8 September	2 b[1] (18)	3 a (26)	2 ab (21)
19 October	2 b (43)	3 a (45)	2 b (45)
1 November	2 b (81)	2 a (84)	2 ab (84)

1 Values in a row followed by the same letter are not significantly different at P=0.05, Duncan's New Multiple Range Test.

2 Values in brackets indicate the number of replications per mean.

7. **Cultivar and seeding date in relation to frequency of *Pythium* recovery from asymptomatic periderm, root scars or cavities of carrot roots, and cavity spot index and disease incidence in 1991.**

	Cultivar	Date seeded	Colony forming units/10 pieces			Cavity spot index (0-100)	Disease incidence (%)
			Periderm	Root scars	Cavities		
y	Six Pak	9 May	0	1		0	0
		30 May	1	0		0	0
	SR-481	9 May	0	0		0	0
		30 May	2	0		0	0
=0.05)			N.S.	N.S.		N.S.	N.S.
.	Six Pak	9 May	0 g[1]	1 fg	3 cd	6.8	13
		30 May	0 g	0 g	1 fg	10.2	16
		21 June	0 g	0 g	3 bc	9.2	19
		12 July	0 g	1 fg	3 abc	9.2	21
	SR-481	9 May	0 g	0 g	2 cd	13	25
		30 May	0 g	0 g	2 df	15.8	25
		21 June	0 g	0 g	4 ab	20.0	30
		12 July	0 g	0 g	4 a	18.8	33
=0.05)						N.S.	N.S.

.../ continued

7. - continued

	Cultivar	Date seeded	Colony forming units/10 pieces Periderm	Root scars	Cavities	Cavity spot index (0-100)	Disease incidence (%)
.	Six Pak	9 May	1 df	0 f	2 cdf	7.8	14
		30 May	0 f	0 f	1 df	2.8	5
		21 June	0 f	0 f		4.5	8
		12 July				8.8	16
	SR-481	9 May	0 f	1 df	3 bc	13.8	25
		30 May	1	0 f	4 b	12.5	20
		21 June	0 f	1 df	2 cd	5.5	10
		12 July	0 f	0 f	8 a	4.5	10
P=0.05)						N.S.	N.S.

ues followed by the same letter are not significantly different at P=0.05, Duncan's New
tiple Range Test.

8a. Cultivar and fungicide treatment in relation to the frequency of Pythium recovery from asymptomatic periderm and cavities of carrots grown in non-irrigated and irrigated plots in 1992.

e	Cultivar	Fungicide treatment & rate (kg ai/ha)	Colony forming units/10 pieces			
			Non-irrigated plot		Irrigated plot	
			Periderm	Cavities	Periderm	Cavities
ly	Six Pak	Check	3	-	1	-
		Metalaxyl (2.0)[1]	0	-	1	-
		Fosetyl-Al (4.0)[2]	3	-	2	-
	Red Core Chantenay	Check	2	-	2	-
		Metalaxyl (2.0)	1	-	0	-
		Fosetyl-Al (4.0)	3	-	1	5
P=0.05)			2		N.S.	N.S.
ust	Six Pak	Check	0	10	1 cd[3]	4 bc
		Metalaxyl (2.0)	0	5	1 d	5 b
		Fosetyl-Al (4.0)	0	-	1 d	5 b
	Red Core Chantenay	Check	0	2	0 d	8 a
		Metalaxyl (2.0)	0	-	0 d	1 d
		Fosetyl-Al (4.0)	0	1	1 d	2 bcd
P=0.05)			N.S.	N.S.		

.../ continued

8a. - continued

	Cultivar	Fungicide treatment & rate (kg ai/ha)	Colony forming units/10 pieces			
			Non-irrigated plot		Irrigated plot	
			Periderm	Cavities	Periderm	Cavities
ust	Six Pak	Check	1	4	1 ef	2 de
		Metalaxyl (2.0)	1	3	1 f	1 ef
		Fosetyl-Al (4.0)	1	2	2 ef	4 cd
	Red Core Chantenay	Check	1	5	1 f	8 a
		Metalaxyl (2.0)	1	-	1 f	5 bc
		Fosetyl-Al (4.0)	1	4	1 ef	6 b
=0.05)			3	3		
tember	Six Pak	Check	0 b	-	0 c	0 c
		Metalaxyl (2.0)	0 b	-	0 c	0 c
		Fosetyl-Al (4.0)	0 b	-	0 c	-
	Red Core Chantenay	Check	1 b	2 a	0 c	2 b
		Metalaxyl (2.0)	0 b	-	0 c	-
		Fosetyl-Al (4.0)	1 b	1 b	1 c	6 a

... /continued

8a. - continued

	Cultivar	Fungicide treatment & rate (kg ai/ha)	Colony forming units/10 pieces			
			Non-irrigated plot		Irrigated plot	
			Periderm	Cavities	Periderm	Cavities
ober	Six Pak	Check	1	5	0	-
		Metalaxyl (2.0)	0	-	0	-
		Fosetyl-Al (4.0)	2	5	1	-
	Red Core Chantenay	Check	0	-	0	4
		Metalaxyl (2.0)	0	2	1	5
		Fosetyl-Al (4.0)	0	5	0	2
P=0.05)			1	1	3	3
tober	Six Pak	Check	1	8	0	12
		Metalaxyl (2.0)	0	1	0	1
		Fosetyl-Al (4.0)	0	4	1	25
	Red Core Chantenay	Check	0	5	1	6
		Metalaxyl (2.0)	0	0	1	12
		Fosetyl-Al (4.0)	0	7	0	4
P=0.05)			5	5	N.S.	N.S.

... /continued

8a. - continued

e	Cultivar	Fungicide treatment & rate (kg ai/ha)	Colony forming units/10 pieces			
			Non-irrigated plot		Irrigated plot	
			Periderm	Cavities	Periderm	Cavities
vember	Six Pak	Check	0	8	1 b	1 b
		Metalaxyl (2.0)	0	1	0 b	12 a
		Fosetyl-Al (4.0)	0	1	0 b	6 ab
	Red Core Chantenay	Check	0	2	0 b	3 b
		Metalaxyl (2.0)	0	4	1 b	12 a
		Fosetyl-Al (4.0)	0	2	0 b	3 b
P=0.05)			N.S.	N.S.		
ber	Six Pak	Check	0	5	0	0
		Metalaxyl (2.0)	1	6	0	1
		Fosetyl-Al (4.0)	1	2	0	5
	Red Core Chantenay	Check	1	6	0	5
		Metalaxyl (2.0)	1	-	1	4
		Fosetyl-Al (4.0)	0	4	0	5
P=0.05)			5	5	3	3

domil MZ 72 WP (8% metalaxyl plus 64% mancozeb, Ciba-Geigy Canada Inc.) 2.0 kg ai/ha metalaxyl
us 16.0 kg ai/ha mancozeb.
iette 80WP (80% fosetyl-Al, Rhone Poulenc Canada Inc.)
lues followed by the same letter are not significantly different at P=0.05, Duncan's New Multiple
nge Test.

Table 8b. Main effects of source of root piece (asymptomatic periderm or cavity) in relation to frequency of *Pythium* recovery from carrots grown in non-irrigated or irrigated plots in 1992.

	Colony-forming units/10 pieces			
	Non-irrigated plot		Irrigated plot	
Date	Periderm	Cavity	Periderm	Cavity
4 August			1 b[1] (24)[2]	8 a (12)
25 August	1 b (24)	6 a (6)	*1 b (24)	9 a (12)
15 September	0 b (20)	7 a (2)	0 b (24)	6 a (5)
6 October	0 b (12)	10 a (7)	1 b (16)	7 a (7)
27 October	0 b (12)	6 a (16)	1 a (12)	2 a (20)
17 November	0 b (8)	4 a (17)	*0 b (20)	7 a (21)
8 December	1 b (24)	6 a (16)	0 b (20)	5 a (17)

1 Values in a row for each plot type followed by the same letter are not significantly different at P=0.05, Duncan's New Multiple Range Test.

2 Values in brackets indicate the number of replications per mean.

* Some interactions significant, see simple effects Table 8a.

were found the simple effects were examined and treatments were compared using Duncan's New Multiple Range Test. When there were no interactions, main effects were examined (Tables 6b, 8b).

Pythium species were recovered from all types of pieces of the enlarged tap root. Numbers of cfu/section were consistently higher in cavities than in other pieces of the tap roots. Recovery frequency from asymptomatic periderm ranged from 0-3 cfu/10 pieces in 1988, and 1992, and from 0-2 in 1991 (Tables 6a, 8a, 7, respectively) while the frequency of recovery from lateral root scars ranged from 0-3 in 1988 and 0-1 in 1991 (Tables 6a and 7 respectively). Pythium spp. colonies were recovered more frequently from cavities than from asymptomatic periderm or lateral roots scars in 1988, 1991, and 1992 (Tables 6b, 7, 8b, respectively).

The number of Pythium cfu/tissue piece obtained from lateral root scars and from asymptomatic periderm was similar except on 8 September and 1 November 1988 (Table 6b) when the numbers were significantly higher for the root scars. In 1992, more cfu's were recovered from cavity spot sections as compared to periderm sections, (Table 8b) with the exception of samples collected on 17 November from the non-irrigated plot and on 27 October from the irrigated plot.

Cultivar resistance, fungicide and PGPR treatment and seeding date in relation to frequency of Pythium recovery from carrot roots

The effect of cultivar resistance, fungicide and PGPR treatment, and seeding date on frequency of Pythium recovery from carrot roots was examined as part of three-factor factorial experiments in 1988, 1991 and 1992. The frequency of Pythium recovery from portions of the tap root (factor piece) was discussed above. The other factors were cultivar and treatment in 1988 (Tables 6a, c), cultivar and days after seeding in 1991 (Table 7), and cultivar and fungicide in 1992 (Tables 8a, c, d).

Frequency of recovery of Pythium spp. from enlarged tap roots differed among carrot cultivars with differing resistance to cavity spot

Table 8c. Main effects of cultivar in relation to the frequency of *Pythium* isolation from root pieces of carrots grown in non-irrigated and irrigated plots in 1992.

Date	Cultivar	Non-irrigated plot N[1]	Non-irrigated plot Cfu/10 pieces	Irrigated plot N	Irrigated plot Cfu/10 pieces
4 August	Six Pak			17	4 a
	Red Core Chantenay			19	2 b
25 August	Six Pak	16	3 b[2]		
	Red Core Chantenay	20	4 a		
15 September	Six Pak			15	0 b
	Red Core Chantenay			17	2 a
8 December	Six Pak			19	2 b
	Red Core Chantenay			22	3 a

1 Number of replications per mean.

2 Values in a column followed by the same letter are not significantly different at P=0.05, Duncan's New Multiple Range Test.

Table 8d. Main effects of fungicide treatment in relation to *Pythium* recovery from pieces of carrot roots grown in non-irrigated and irrigated plots in 1992.

Date	Fungicide and rate (kg ai/ha)	Non-irrigated plot N[1]	Non-irrigated plot Cfu/10 pieces	Irrigated plot N	Irrigated plot Cfu/10 pieces
15 July	Check	8	3 a[2]		
	Metalaxyl+ mancozeb (2.0)[3]	8	0 b		
	Fosetyl-Al (4.0)[4]	8	3 a		
25 August	Check			12	4 a
	Metalaxyl+ mancozeb (2.0)			11	3 b
	Fosetyl-Al (4.0)			13	4 ab
15 September	Check	5	2 a	9	1 ab
	Metalaxyl+ mancozeb (2.0)	8	0 b	8	0 b
	Fosetyl-Al (4.0)	9	1 b	12	2 a
6 October	Check	6	4 b		
	Metalaxyl+ mancozeb (2.0)	5	2 c		
	Fosetyl-Al (4.0)	8	6 a		
17 November	Check			12	2 b
	Metalaxyl+ mancozeb (2.0)			13	8 a
	Fosetyl-Al (4.0)			16	2 b

1 Number of replications per mean.

2 Values in a column for each date followed by the same letter are not significantly different at P=0.05, Duncan's New Multiple Range Test.

3 Ridomil MZ 72WP (8% metalaxyl plus 64% mancozeb), 2.0 kg ai/ha metalaxyl plus 16 kg ai/ha mancozeb.

4 Aliette 80WP (80% fosetyl-Al).

in 1988 (Table 6c) and 1992 (Table 8c) but not in 1991 (Appendix II Table 7). In 1988, fewer cfu/10 root pieces were recovered from Six Pak than from Chanton on three of the seven sample dates, 8 September, 19 October and 1 November (Table 6c). Fewer cfu/10 cavity pieces were recovered from Six Pak than Chanton on 21 September and 3 December. Cultivar effects on the frequency of Pythium isolation were also found in 1991 and 1992 on one of six and seven of 13 sample dates respectively. In 1991, Six Pak carrots seeded 30 May and harvested 11 December had fewer cfu/10 cavity pieces than SR-481 (Table 7). In 1992 fewer cfu/10 pieces were recovered from Six Pak carrots harvested from the non-irrigated plot on 25 September and from the irrigated plot harvested on 4 August, 15 September and 8 December (Table 8c).

Differences were also found in the association between fungicide treatment and the frequency of Pythium recovery from tap roots. Pythium spp. were recovered less frequently from carrots treated with metalaxyl plus mancozeb on two of seven sample dates in 1988 (Table 6a) and on three of eight dates in 1992 from carrots grown in the non-irrigated plot, but on only one date in the irrigated plot (Table 8d). Treatment with metalaxyl plus mancozeb was also associated with a significant increase in Pythium recovery from carrots grown in the irrigated plot and sampled on 17 November. In carrots treated with fosetyl-Al in the non-irrigated plot, the frequency of Pythium recovery was significantly lower than from untreated carrots on 15 September 1992, but significantly higher on 6 October, 1992, (Table 8d).

No differences in frequency of Pythium recovery were found in carrots grown from seed treated with plant-growth promoting rhizobacteria, as compared to the untreated check. However, more Pythium cfu/10 pieces were recovered from PGPR-treated carrots than from fungicide-treated carrots on 21 September and 3 December 1988 (Table 6a).

Seeding date was related to differences in the frequency of Pythium recovery from cavities of both cultivars harvested on 21 November and from

SR-481 harvested 3 December, 1991 (Table 7a). Fewer cfu/10 cavity pieces were recovered from carrots seeded on 30 May and from SR-481 carrots seeded on 9 May and harvested on 21 November. When SR-481 carrots were harvested 11 December, carrots seeded 12 July had the highest cfu/10 cavity pieces and those seeded on 21 June, the least.

Frequency of Pythium recovery in relation to incidence and severity of cavity spot

Frequency of Pythium recovery from asymptomatic periderm, root scars or cavities was not clearly related to incidence (r^2=0.01-0.15) or severity (r^2=0.01-0.19) of cavity spot in Six Pak or Red Core Chantenay carrots treated with metalaxyl plus mancozeb or untreated in 1988 and 1992 (Appendix II Tables 6-2, 6-3, 8-2 and 8-3).

Cavity spot incidence was positively correlated (r^2=0.19) to the frequency of Pythium recovery from Six Pak treated with metalaxyl plus mancozeb in 1988 (Appendix II Table 6-3). In 1992, a significant negative correlation was found between cavity spot index and cfu/10 cavity pieces of Red Core Chantenay grown in the irrigated plot and treated with metalaxyl plus mancozeb (r^2=0.25) and untreated (r^2=0.19) (Appendix II Table 8-2).

Plant age, rainfall and soil temperature in relation to frequency of Pythium recovery from carrot roots

Low r^2 values indicated that only a small proportion of the variation in incidence of Pythium recovery from the tap roots was accounted for by variation in the amount and frequency of rainfall, mean daily soil temperature and age of carrots in both 1988 and 1992. In 1988, only 6 of 60 r^2 values were significant and all involved rainfall parameters. Total rainfall in the first, second and third weeks prior to sampling, and number of preceding four weeks with rainfall over 5 mm, were positively

(r^2=0.42, 0.42, 0.20 and 0.35, respectively). Rainfall in the preceding four weeks was also related to cfu/10 root scar pieces of fungicide-treated Six Pak (r^2=0.15) (Table 9a).

In 1992, r^2 values were significant for ten and seven of 56 regression analyses on Pythium recovery from carrots grown in the non-irrigated and irrigated plots, respectively. Most of the significant relationships involved rainfall and Pythium recovery from Six Pak carrots. When carrots were grown in the non-irrigated plot, total rainfall in the preceding one and three weeks was positively correlated with cfu/10 cavity pieces of untreated Six Pak (r^2=0.24 and 0.25, respectively) but negatively correlated with cfu/10 periderm pieces of fungicide-treated Six Pak (r^2=0.16 and 0.14, respectively) (Table 9b). The strongest relationship (r^2=0.49) was between the number of preceding four weeks with rain and cfu/10 cavity pieces from untreated Six Pak carrots. Both cumulative rainfall and days after seeding were negatively correlated to Pythium recovery from periderm pieces of untreated Six Pak (r^2=0.29 and 0.20) and Red Core Chantenay (r^2=0.22 and 0.17) (Table 9b). Cumulative rainfall and days after seeding were found to be highly correlated in these trials (r^2=0.97, Appendix III Table 10-2). For carrots grown in the irrigated plot, cumulative rainfall, days after seeding and rainfall in previous three weeks was negatively correlated to cfu/10 periderm pieces of Six Pak carrots treated with metalaxyl plus mancozeb. The strongest relationship (r^2 = 0.42) was between cfu/cavity piece of these carrots and rainfall in preceding four weeks.

DISCUSSION

This is the first study to establish that Pythium violae and P. ultimum cause cavity spot of carrots in Ontario. It is also the first to compare the frequency of Pythium isolation from asymptomatic periderm, lateral root scars and cavity spot lesions and to determine that the

9a. Coefficients of determination for regression of frequency of Pythium recovery from pieces of asymptomatic periderm, lateral root scars or cavities and days after seeding, cumulative rainfall, rainfall in preceding weeks, and soil temperature in relation to cultivar and treatment with metalaxyl plus mancozeb in 1988.

ar	Metalaxyl+ mancozeb (2.0 kg ai/ha)	Root piece	Co-efficient of determination (r^2) Days after seeding	Cumulative rainfall	Total rainfall in previous 1 wk	2 wk	3 wk	Preceding weeks with rain (1-4)	Soil temperature (5 cm depth)
k	Check	Periderm	.14	.15*	.01	.01	.06	.01	.14
		Root scar	.01	.01	.08	.09	.06	.06	.02
		Cavity	.01	.01	.12	.16	.01	.04	.01
	Drench[1]	Periderm	.05	.06	.01	.01	.01	.01	.06
		Root scar	.02	.01	.15	.11	.14	.16	.04
		Cavity	.11	.12	.05	.02	.17	.11	.12
re tenay	Check	Periderm	.05	.04	.01	.02	.10	.01	.05
		Root scar	.09	.03	.42**	.42**	.27**	.35**	.13
		Cavity	.04	.04	.02	.03	.01	.02	.02
	Drench	Periderm	.01	.01	.01	.04	.09	.02	.01
		Root scar	.13	.11	.09	.09	.15*	.09	.14
		Cavity	.12	.13	.02	.01	.11	.12	.07

Drench of Ridomil MZ 72WP (8% metalaxyl plus 64% mancozeb), 2.0 kg ai/ha metalaxyl plus 16.0 kg ai/ha mancozeb applied over seed row after seeding.

indicates r^2 significant at P=0.05 and P=0.01, respectively, simple linear regression analysis

9b. Coefficients of determination for regression of frequency of Pythium recovery from pieces of asymptomatic periderm, lateral root scars or cavities and days after seeding, cumulative rainfall, rainfall in preceding 4 weeks and soil temperature in relation to cultivar and treatment with metalaxyl plus mancozeb for carrots grown in non-irrigated or irrigated plots in 1992.

ar	Metalaxyl+ mancozeb (2.0 kg ai/ha)	Section	Co-efficient of Determination (r^2) Days after seeding	Cumulative rainfall	Total rainfall in previous 1 wk	2 wk	3 wk	Preceding weeks with rain (1-4)	Soil temperature (5 cm depth)
rigated Plot									
k	Check	Periderm	.20**	.29**	.01	.01	.01	.01	.06
		Cavity	.09	.07	.24*	.17	.25*	.14	.06
	Drench[1]	Periderm	.01	.01	.16*	.19*	.14*	.10	.01
		Cavity	.15	.15	.34	.01	.23	.49*	.12
re enay	Check	Periderm	.17*	.22**	.01	.01	.01	.01	.08
		Cavity	.02	.03	.03	.07	.01	.04	.05
	Drench	Periderm	.01	.01	.05	.05	.05	.01	.01
		Cavity	.11	.11	.11	.11	.11	.11	.11

.../ continued

9b. - continued

ar	Metalaxyl+ mancozeb (2.0 kg ai/ha)	Section	Co-efficient of Determination (r^2) Days after seeding	Cumulative rainfall	Total rainfall in previous 1 wk	2 wk	3 wk	Preceding weeks with rain (1-4)	Soil temperature (5 cm depth)
ted Plot									
k	Check	Periderm	.11	.10	.09	.03	.08	.09	.08
		Cavity	.04	.05	.01	.04	.01	.14	.04
	Drench[1]	Periderm	.19**	.20**	.11	.09	.13*	.15*	.05
		Cavity	.01	.01	.40	.36	.16	.42*	.03
re enay	Check	Periderm	.08	.10	.01	.05	.03	.03	.03
		Cavity	.16	.18*	.06	.12	.01	.04	.24*
	Drench	Periderm	.09	.08	.09	.06	.10	.11	.07
		Cavity	.10	.09	.01	.02	.06	.01	.10

dicates r^2 is significant at P=0.05

dicates signficance at P=0.01, simple linear regression analysis.

ench of Ridomil MZ 72WP (8% metalaxyl plus 64% mancozeb), 2.0 kg ai/ha metalaxyl plus 16.0 kg ai/ha ncozeb applied over seed row at seeding.

related to cumulative rainfall in the first, second or third weeks preceding sampling or mean daily soil temperature, under Ontario conditions. This is also the first study to examine the relationship between the frequency of Pythium recovery from carrot roots and cavity spot index or incidence, and to experimentally determine the effects of cultivar and fungicide treatment on the isolation of Pythium from carrots.

Pythium recovery from periderm, root scars and cavities

Pythium species were more frequently recovered from cavity spot lesions than from the asymptomatic periderm or secondary root scars of carrot roots. The low frequency of Pythium recovery from lateral root scars suggests that these were not important sites of infection by Pythium spp. Pathogenicity tests with Pythium isolates recovered from cavities of field-grown carrots indicated that P. violae and one isolate of P. ultimum were pathogenic on carrots while P. irregulare and one isolate of Pythium group G caused few lesions. Pythium irregulare did increase the incidence of cavity spot in comparison to the non-infested check. The pathogenicity of P. violae was also demonstrated by White (1988) in Britain and Vivoda et al. (1991) in California. While the frequency of Pythium recovery from asymptomatic periderm and roots scars was low in this study, several species of Pythium were recovered and identified. No strong association was found between slow-growing Pythium species and recovery from cavities or fast-growing species and asymptomatic portions of the root. Slow-growing P. sulcatum and fast-growing P. ultimum and P. irregulare were isolated from seedling carrot roots and all portions of the tap root that were examined. Pythium violae was identified only from cavity sections, but this may have reflected the greater number of isolates obtained from cavities as compared to the periderm, rather than the absence of this species. The pathogenicity trial indicates that cavity spot in Ontario is associated with both slow

the situation in California (Vivoda et al. 1991). Many of the species recovered from cavities produce asymptomatic infections of the carrot root.

Pathogenicity tests on more isolates and species, especially P. sulcatum, are needed to support or refute White's (1988) suggestion that slow-growing Pythium spp. cause cavity spot while fast-growing species produce asymptomatic infections of the carrot root.

The present study also demonstrated that there was no relationship between the frequency of Pythium recovery from asymptomatic portions of the carrot root and cavity spot incidence or severity on the same sample date. However, there remains a possibility that asymptomatic infections may develop into cavities under certain environmental conditions or in response to a change in host resistance, since the same species are capable of both types of infections. Asymptomatic Pythium infections of carrots and other vegetables have been reported by other researchers (Wisbey et al. 1977, Kalu et al. 1976), and while their role in cavity spot development is uncertain, they may represent a significant but previously unrecognized source of inoculum that could develop on crops grown in rotation with carrots. Wisbey et al. (1977) recovered Pythium sylvaticum, P. ultimum and P. sulcatum from both diseased and apparently healthy carrot rootlets and the roots of lettuce, while Kalu et al. (1976) isolated P. sulcatum and Pythium sp. NNK1 from symptomless onion roots. White (1988) isolated these and several other Pythium species from the asymptomatic periderm of carrot roots.

Pythium recovery in relation to cultivar resistance, fungicide and plant growth-promoting rhizobacteria treatment and planting date

Control measures that reduced the incidence or severity of cavity spot in field trials (Chapter 5) were associated with lower frequency of Pythium isolation from carrot roots on some sample dates, but the relationships were not consistent. The numbers of Pythium spp. recovered

from carrot roots were lower on resistant cv. Six Pak and on carrots treated with fungicides on some harvest dates but not on carrots treated with plant growth-promoting rhizobacteria (PGPR), even though some of the PGPR treatments effectively reduced cavity spot symptoms. Planting date was associated with a lower frequency of Pythium isolation on one harvest date, although planting date did not affect the cavity spot incidence or index in the trial.

These conflicting observations indicate that the frequency of Pythium recovery from a seedling carrot root or root sections as carried out in the present study will not provide a reliable indication of the resistance or susceptibility of the carrot to cavity spot. Repeating the trial with an increased sample size might reveal a stronger trend. However, the fact that recoveries of Pythium from pieces of Six Pak roots yielded fewer colonies on several dates suggests that some resistance mechanisms may be involved that reduced the number of successful Pythium infections of Six Pak. Six Pak may have higher levels of preformed antifungal compounds in the periderm, or the periderm may be physically more difficult for the infection peg to penetrate. For instance, the antifungal compound falcarindiol, has been found in the periderm of some carrot cultivars at sufficiently high levels to inhibit the germination of chlamydospores of Mycocentrospora acerina (Hartig) Deighton and conidia of Cladosporium cladosporoides (Fres.) de Vries (Garrod et al. 1978).

The lower number of Pythium colonies recovered from cavity sections of resistant Six Pak may indicate a build up of phytoalexins or other fungitoxic compounds in response to infection, which kill the mycelium or inhibit further infection. More susceptible cultivars may produce lower concentrations of phytoalexins, or produce them more slowly, allowing the pathogen to remain active. The phytoalexin, 6-methoxymellein, increased in cultured carrot cells in response to inoculation with Chaetomium globosum (Kurosaki et al. 1985). The concentrations of falcarindiol, 6-methoxymellein or other antifungal compounds in carrots have not been

examined in relation to cavity spot resistance.

Treatment of carrots with metalaxyl plus mancozeb reduced cavity spot (Chapter 5). Metalaxyl is fungistatic (Bruin and Edgington 1983) and has been reported to increase plants' resistance to infection by fungi (Ward et al. 1980). Thus, one would expect treatment with metalaxyl plus mancozeb to reduce the rate of infection of carrot roots by Pythium. Again the results are too variable to suggest a firm trend. The field trials conducted for this study were not adequate for determining the effect of metalaxyl plus mancozeb on the infection rate of Pythium spp. on carrot. A similar study with an increased number of samples from a smaller number of carrots might reveal a stronger trend. A large variability in inoculum density in the soil probably confounds the results. Other more direct methods of studying the modes of action of the fungicides or cultivar resistance, such as relationships of inoculum density to disease incidence, may be more efficient.

Observations on the frequency of Pythium recovery from carrot roots in relation to cultivar resistance and fungicide treatment suggested some trends, but were inconclusive. Perhaps the variability among replications was masking some stronger associations so they were not apparent in the statistical analysis. To account for this possibility, regression analyses were conducted on a replication by replication basis for each cultivar and treatment. No associations were found between the frequency of Pythium isolation from carrot root sections and cavity spot index or incidence. Treatment with metalaxyl plus mancozeb may reduce the cavity spot index and also the number of cfu/10 pieces recovered from cavities or the periderm, but these effects were not related on individual samples of carrots on single sample dates.

Pythium recovery in relation to rainfall, soil temperature and plant age

Regression analyses of data from two years, including both an irrigated and non-irrigated plot in 1992, showed few relationships between

the several rainfall parameters, soil temperature at 5 cm depth, or plant age and the frequency of Pythium recovery from carrot root sections. Small but significant positive relationships were found between cfu/10 pieces and the number of the preceding four weeks with rainfall. Cumulative rainfall was sometimes related to number of cfu/10 pieces. The negative slope (Appendix IV Table 8a) suggests that this may be related to plant age.

The 1988 growing season was relatively dry (376.8 mm of rainfall) compared to the 1992 season where carrot plots received 567 mm (non-irrigated plot) or 720 mm (irrigated plot) of rainfall or irrigation. If rainfall had a major influence on the infection of carrots by Pythium as estimated by frequency of Pythium isolation, that effect should have been apparent during one of these years.

There were no significant relationships between plant age and Pythium recovery in 1988 and only three with low r^2 values (0.17-0.20) in 1992. All of these involved recovery from periderm sections and had a negative slope, indicating that the frequency of Pythium recovery decreased with increasing plant age. White (1988) also recovered Pythium spp. more frequently from the asymptomatic periderm of carrots sampled six to eight weeks after seeding than from older carrots. However, he did not confirm this relationship with statistical analysis. In the present study, only a small portion of the variation in recovery frequency is accounted for by the increase in plant age. Isolations from the periderm were started on carrots harvested ten weeks after seeding in 1988 and seven weeks after seeding in 1992. Thus the 1988 study may have begun too late to detect the higher infection rates on young carrot roots.

This study found no strong association between rainfall parameters, soil temperature or plant age and the frequency of Pythium recovery from asymptomatic periderm or other pieces of tap roots of carrots grown in organic soil in Ontario. The data did not concur with White's (1988) observations that the frequency of Pythium recovery from asymptomatic

periderm increased when soil temperatures were below 10°C and there was rainfall in each of the preceding four weeks.

In 1988 only 10 percent (6/60) of the regression analyses showed a significant relationship between the frequency of Pythium recovery and the various parameters. In 1992 the percentages were slightly higher, 18 percent (10/56) and 12 percent (7/56) of the regressions for the non-irrigated and irrigated plots, respectively. These figures are close to the 5 percent confidence limits and thus some of the relationships that were identified may be spurious.

White (1988) grouped the data from different cultivars together to make observations on the association between rainfall, soil temperature and metalaxyl treatment on the frequency of Pythium recovery from asymptomatic periderm. He did not perform any statistical analyses on these data. If he had done so, the results may have shown little or no relationship among the variables as demonstrated here.

The number of periderm pieces examined per replication or treatment may not have been large enough for a definitive study of cultivar resistance, fungicide activity or the effects of the environment. In 1988 and 1992, there were 180-360 and 360 periderm pieces (0.5 cm^2) plated per harvest date, respectively, approximately 90-180 cm^2 of root surface tissue. This corresponds to 20 and 60 periderm pieces/treatment in 1988 and 1992. Considering the low frequency of Pythium recovery from these sections, usually in the range of 0-10%, there is a large chance of missing a portion of periderm that may be infected. White (1988) made recoveries from 210 and 710-1320 periderm pieces (0.1 cm^2 per harvest date in 1985 and 1986, respectively (21-132 cm^2 of surface tissue). Thus, more pieces were plated, but this represented a smaller area of the root surface.

The frequency of Pythium spp. recovery from these periderm pieces ranged from a high of 0.44 cfu/piece from cv Chantenay Red Core Supreme

cv. Chantenay Long harvested 12 weeks after seeding in 1986. These correspond closely to the frequency of Pythium recovery in the present study, ranging from 3 cfu/10 periderm pieces from Six Pak harvested eight weeks after seeding in 1992, to 0 cfu/10 periderm pieces from Six Pak 10 weeks after seeding and Red Core Chantenay harvested 19 weeks after seeding in 1992. However if the relative sizes of the periderm pieces used in the two trials are considered, (0.1 cm^2 vs. 0.5 cm^2) White (1988) recovered approximately 44 cfu/10 cm^2 while in this study, the maximum recovery rate was 2 cfu/10 cm^2 on 17 July 1992.

Isolating Pythium spp. from large numbers of periderm or cavity sections from field grown carrots requires considerable time and resources and may not be the best or most efficient method of determining the effects of plant age or environment factors on Pythium infection of carrot. Controlled environmental trials will be necessary to pursue these investigations further. Unfortunately, most of the controlled environment work conducted to study the effects of soil temperature and moisture on cavity spot was done before Pythium spp. had been identified as the causal agent. (Perry and Harrison 1979b, Soroker et al. 1984).

CONCLUSIONS

Several isolates of Pythium violae and one of P. ultimum were pathogenic on carrots and caused characteristic cavity spot lesions. Two isolates of P. irregulare also caused characteristic lesions and increased disease incidence. Several Pythium spp. were readily recovered from cavity spot lesions on carrot roots, while the frequency of Pythium recovery from asymptomatic periderm and lateral root scars was significantly lower. The Pythium spp. recovered from the lesions included P. violae, P. sulcatum, P. ultimum, P. irregulare, P. intermedium and Pythium group G. Pythium paroecandrum and P.aphanidermatum were also recovered from asymptomatic periderm and lateral root scars. No strong

spp. from cavities and fast-growing species from asymptomatic portions of the roots.

There were some indications that cultivar resistance and treatment with metalaxyl plus mancozeb at seeding reduced the frequency of infection of carrots by Pythium spp. Bacterization of carrot seed with plant growth-promoting rhizobacteria did not affect the frequency of Pythium recovery from carrot roots. The lower frequency of Pythium recovery from resistant than from susceptible cultivars warrants further inspection, since a reduction in successful or progressive infections may be one of the components of resistance to Pythium. However, this should not be the only test used to determine resistance to cavity spot, since the results were not always consistent.

Several environmental parameters and plant age were examined in relation to the frequency of Pythium recovery from carrot roots, but none appeared to have an important effect. There were no consistently strong associations between the frequency of Pythium recovery from cavities or asymptomatic portions of the root and days after seeding, cumulative rainfall, rainfall in the first, second, or third weeks preceding sampling, number of the four preceding weeks with rainfall events over 5 mm and soil temperature at 5 cm depth. White (1988) reported that the frequency of Pythium recovery from asymptomatic periderm increased when soil temperatures were below 10°C and when there was rainfall in the preceding four weeks. This was not the case for carrots grown in organic soils in Ontario. Determining the frequency of Pythium recovery in relation to these environmental parameters did not provide any information that could be incorporated into a disease forecasting system for cavity spot.

In conclusion, the present study confirmed that species of Pythium were associated with cavity spot development, as has been reported in Israel (Shlevin et al. 1987), Britain (White 1988), France (Montfort and

1993). Resistant cultivars and treatment with metalaxyl plus mancozeb, two control measures which reduced cavity spot incidence, reduced the frequency of Pythium recovery from carrots at several times during the growing season, but the effect was not consistent. The study failed to identify any environmental parameters that were strongly associated with the recovery of Pythium from carrot roots.

CHAPTER 4

EFFECT OF RAINFALL, SOIL TEMPERATURE AND PLANT AGE ON THE DEVELOPMENT OF CAVITY SPOT

INTRODUCTION

The disease, cavity spot of carrot, causes significant crop losses in many parts of the world (Perry 1983, Lyshol et al. 1984, Jacobsohn et al. 1984, Walker 1991). Several researchers have noted that an increase of cavity spot was associated with environmental factors such as high soil moisture and various soil temperatures (Guba et al. 1961, Perry and Harrison 1979b, Jacobsohn et al. 1984, Sorokor et al. 1984 and White 1988). The severity of cavity spot was also observed to increase with increasing plant age (Jacobsohn et al. 1984, Sweet et al. 1989, Vivoda et al. 1991). White (1988) suggested that Pythium infection of carrot roots was higher on carrots sampled after a four week period where there was rainfall each week, than on those sampled after a dry period. There have been no studies on the epidemiology of cavity spot, and no attempts to correlate these factors with cavity spot development throughout the growing season.

Since the first description of cavity spot, researchers have observed that high levels of disease were associated with wet growing conditions, poorly drained soils or flooding (Guba et al. 1961, Perry and Harrison 1979b). Jacobsohn et al. (1984) and Perry (1983) both found that the incidence of cavity spot was reduced when carrots were grown in well-drained soil on raised beds.

Reports on the range of soil temperatures associated with increased cavity spot are varied. Perry and Harrison (1979b) found that cavity spot was induced on carrots grown in soils maintained at field capacity for two weeks during July and August when mean soil temperatures were 15.3°C, but not when similar conditions were maintained in October, when mean soil temperatures were 8.6°C. Sorokor et al. (1984) reported that cavity spot formation depended upon exposure to environmental stress consisting of at

least six hours of flooding at temperatures above 28°C. After exposure to the stress conditions, carrots were grown in a glasshouse for five to seven weeks. The optimum temperature for lesion development was found to be 15°C when carrots were inoculated with mycelial plugs of Pythium violae (Montfort and Rouxel 1988) and also when carrots were transplanted into artificially-infested soil (Vivoda et al. 1991).

Fungicide trials (Chapter 5) indicated that Pythium infection of carrot roots occurs by the fourth or sixth week after seeding, even though lesions usually develop later in the season. Thus, environmental conditions immediately after seeding may influence the incidence or severity of cavity spot that develops later in the season.

Plant age may also be a factor in disease development. The incidence and severity of cavity spot increases as the crop matures (Perry 1967, Montfort and Rouxel 1988, Vivoda et al. 1991) In England, carrot cultivars were found to have a higher incidence of cavity spot when harvested in January than in October (Sweet et al. 1989). In greenhouse trials susceptibility to cavity spot increased with age (Perry and Harrison 1979b). Vivoda et al. (1991) found more cavities per carrot on five month-old carrots than on three month-old carrots, when these were transplanted into artificially-infested soil.

No epidemiological studies of cavity spot have been conducted although several researchers have harvested carrots at various intervals from commercial fields (Montfort and Rouxel 1988, White 1988, Vivoda et al. 1991). Pythium violae has been identified as the most pathogenic of the Pythium spp. that cause cavity spot (White 1986, Vivoda et al. 1991) but it has not been possible to isolate this species from cavity spot conducive soils using quantitative techniques that are available (Phelps et al. 1991). Thus, there have been no studies to determine the effect of inoculum density on disease development, nor to evaluate the effects of rainfall, soil temperature or other factors on the populations of P. violae in soil.

The goal of the present study was to determine whether plant age, rainfall or soil temperature were related to changes in cavity spot incidence, and to quantify the relationship, where possible, to develop a prototype predictive system for cavity spot of carrots grown in organic soils in Ontario as part of an integrated disease management strategy.

The objectives were to examine plant age, rainfall and soil temperature in relation to cavity spot development:

a) to study the relationships between plant age, estimated as weeks after seeding, several rainfall parameters and average soil temperature, and cavity spot incidence, or increments in the area under the disease progress curve (AUDPC). The rainfall parameters examined were: cumulative rainfall, total rainfall in the one, two, three, five and seven weeks prior to sampling and number of weeks with rainfall over 5 mm in the four weeks prior to sampling. Also, to investigate whether cultivar susceptibility or treatment with metalaxyl plus mancozeb affected these relationships.

b) to determine if the rainfall or average daily soil temperature within the first four, six or eight weeks after seeding was related to the maximum disease incidence or AUDPC.

c) to assess the potential of total rainfall as an indicator of the maximum incidence or AUDPC developed during the season.

d) to use time domain reflectometry to measure the moisture content of muck soil and determine the relationship between soil moisture content and rainfall.

Field trials were conducted over a period of six years to address these objectives. Portions of this work have been presented (McDonald and Sutton 1993).

MATERIALS AND METHODS

Field plots

Trials were conducted yearly from 1986-1992, except 1989, with carrots seeded in naturally-infested organic soil at the Muck Research Station. The field plot arrangement and drench application of fungicides were previously described in Chapter 3.

Cavity spot assessment

Sampling of the carrots and assessment of disease incidence were previously described in Chapter 3. Area under the disease progress curve (AUDPC) was calculated using the midpoint rule for area estimation (Campbell et al. 1980). The sum of the average disease rating between two consecutive sample dates was divided by two and multiplied by the number of days that lapsed between the two sample dates. The AUDPC values for each sample period were summed to obtain the total AUDPC. The first sample date in the calculation was the date with a disease rating of zero which was just prior to a disease rating greater than zero.

Cultivars

Carrot cultivars used in the trials were Chanton (Arco Seed Co., El Centro, CA), Red Core Chantenay, Chancellor, Cellobunch and XPH-3507 (Asgrow Seed Co., Newmarket, ON), SR-481 and Huron (Sun Seeds, Brooks, OR, and Six Pak (Harris Moran, Kettleby, ON). Unless otherwise indicated, seed of all cultivars in a trial received the same treatments and were seeded on the same day. Seeding rate of packaging carrots (Six Pak, Chancellor, Cellobunch, Huron, Eagle, XPH-3507 and SR-481), was 82-112 seed/m and that of precessing carrots (Red Core Chantenay, Chantenay Comet and Chanton) was 40-50 seed/m. Six Pak was evaluated every year except 1987. Red Core Chantenay was included in the trials in 1987, 1988 and 1992. Chanton and SR-481 were each evaluated over two years, 1986 and 1988, and 1991 and 1992, respectively. Cellobunch and Chancellor were

compared to Six Pak in 1990 and Eagle and Huron were included in the 1992 trial.

Monitoring of rainfall, soil temperature and soil moisture

Rainfall and soil temperature were measured throughout the growing season, as described in Chapter 3. Soil moisture readings were taken in the field plots in 1991 and 1992 using time domain reflectometry (TDR). In 1991, eight pairs of TDR probes were placed in the plot. A pair of each of 10 cm-long probes and of 15 cm probes were placed 10 cm apart in each replication seeded on 9 May, 1991. The 10 cm probes were placed in the ground at a 45° angle, to take readings 5 cm below the soil surface. The 15 cm probes were placed vertically in the ground with the top of the probes flush with the soil surface. In 1992, a pair of 10 cm and 15 cm probes were placed in each block of the irrigated and non-irrigated plots. The 10 and 15 cm probes were placed horizontally in the soil 5 and 15 cm below the soil surface, respectively. Readings were taken approximately twice weekly from early June to the end of August with a portable Time Domain Reflectometer (Tektronix Inc. Barrie, ON) by Rodger Tshanz, Department of Horticultural Science, University of Guelph, who also determined the equations for calculating the moisture content. Soil water content (percent by weight) was equal to $13.87 + 8.12\ (K) - 0.072\ (K)^2$ where K = dielectric constant of the soil and was calculated as $K=[\text{TDR reading/probe length (m) mc/Vp}]^2$. MC, the machine constant was 1.0293 in 1991 and 1.053 in 1992. The propagation velocity (Vp) was set at 0.99.

Statistical analysis

Simple linear regression and second order polynomial regression were used to determine the association between cavity spot and the environmental factors measured in these trials. The dependent variables were disease incidence and the incremental area under the disease progress curve between consecutive harvest dates. The independent variables were:

days after seeding, cumulative rainfall, average rainfall over the one, two, three, five and seven week period preceding the sample date and average soil temperature for the assessment period at 5 cm depth. The association between soil temperature, rainfall in the first four, six and eight weeks after seeding and the maximum disease incidence and AUDPC was also examined. Maximum incidence during the epidemic was chosen because incidence on the final harvest date was often lower than the peak incidence.

Simple linear regression and second order polynomial regression analyses were performed using Statview (Abacus Concepts Inc., Berkeley, CA) or SAS version 6.03. Standard errors were calculated for each point on a disease progress curve to determine if points were significantly different from each other.

RESULTS

Plant age, rainfall and soil temperature in relation to disease progress

Linear and second order polynomial regression analysis of days after seeding, several rainfall parameters and soil temperature at 5 cm depth, on disease incidence and increments of AUDPC demonstrated that plant age, estimated as days after seeding, was correlated to cavity spot development throughout the epidemic (Table 10). The relationship was usually linear with a positive slope, but occasionally a quadratic equation provided the best fit (i.e. days after seeding vs. AUDPC for Red Core Chantenay in 1987, Table 10). Cumulative rainfall was more closely related to cavity spot development than any of the other rainfall parameters (rainfall in the one, two, three, five or seven weeks prior to assessment and number of the preceding four weeks with rainfall over 5 mm). However days after seeding and cumulative rainfall were highly correlated (r^2=.0.74-0.94, Appendix III Table 10-2). Soil temperature was also associated with changes in cavity spot level but, in general, the coefficients of determination were not as high as for days after seeding or cumulative

Table 10. Coefficients of determination for regression of plant age, rainfall parameters and soil temperature on cavity spot index, incidence, area under cavity spot index curve (AUCSIC) and area under disease progress curve (AUDPC) on several cultivars, untreated or treated with metalaxyl plus mancozeb in 1987, 1988 and 1992.

			Coefficient of Determination								
Year	Cultivar + treatment	Cavity spot rating	Days after seeding	Cumulative rainfall	Total rainfall in previous weeks 1wk	2wk	3wk	5wk	7wk	Preceding weeks with rain (1-4)	Soil temp. 5 cm
1986	Six Pak	Incidence	N.S.[1]	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	(0.91)
	Check	AUDPC	0.82**[2]	0.73	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	0.76
1986	Chanton	Incidence	0.76	0.64	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
	Check	AUDPC	0.59	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
1987	Red Core Chantenay	Incidence	0.28	0.30	N.S.	(0.18)	(0.28)	0.16	N.S.	N.S.	0.15
	Check	AUDPC	(0.80**)	(0.76**)	N.S.	0.17	N.S.	N.S.	N.S.	N.S.	N.S.
1988	Six Pak	Incidence	0.52	0.47	0.13	0.24	0.30	N.S.	N.S.	N.S.	0.49
	Check	AUDPC	0.56	0.50	(0.27)	0.15	(0.37)	N.S.	N.S.	N.S.	0.47
	Six Pak	Incidence	0.29**	0.26**	N.S.	N.S.	N.S.	N.S.	(0.27)	N.S.	0.28**
	Drench[4]	AUDPC	0.59**	0.52**	(0.27)	0.14	0.22**	(0.29**)	(0.23)	N.S.	0.50**
	Chanton	Incidence	0.63	0.78	N.S.	(0.28)	(0.27)	N.S.	(0.53**)	0.15	0.47
	Check	AUDPC	0.79	0.76	(0.25)	0.17	(0.37)	N.S.	N.S.	N.S.	0.57
	Chanton	Incidence	0.60**	0.63**	N.S.	(0.29**)	N.S.	N.S.	(0.49**)	N.S.	0.56
	Drench	AUDPC	0.58**	0.64**	N.S.	0.17	(0.18)	N.S.	(0.35**)	N.S.	0.51

.../ continued

Table 10. - continued

Year	Cultivar + treatment	Cavity spot rating	Coefficient of Determination: Days after seeding	Cumulative rainfall	Total rainfall in previous weeks: 1wk	2wk	3wk	5wk	7wk	Preceding weeks with rain (1-4)	Soil temp. 5 cm
1988	Red Core Chantenay	Incidence	0.70**	0.66**	(0.32)	(0.29)	(0.48**)	N.S.	(0.33**)	N.S.	0.66
	Check	AUDPC	0.72**	0.67**	(0.36**)	(0.21**)	(0.52**)	(0.43**)	(0.23)	N.S.	0.58
	Red Core Chantenay	Incidence	0.50**	0.51**	N.S.	N.S.	(0.22)	N.S.	(0.27)	N.S.	0.45**
	Drench	AUDPC	0.64**	(0.77**)	(0.27**)	0.13	(0.42**)	(0.32**)	(0.24)	N.S.	0.56**
1990	Six Pak 7 June	Incidence	0.36**	0.33**	N.S.	N.S.	N.S.	(0.20**)	(0.26**)	0.12	0.34**
		AUDPC	0.35**	0.33**	(0.18**)	N.S.	N.S.	(0.14)	0.15**	N.S.	0.30**
	Chancellor 7 June	Incidence	0.50**	0.50**	(0.15)	N.S.	(0.14)	(0.22**)	(0.40**)	(0.12)	0.49**
		AUDPC	0.45**	0.44**	(0.29**)	N.S.	(0.14)	(0.14)	(0.24**)	N.S.	0.37**
	Chancellor 9 July	Incidence	0.76**	0.78**	N.S.	N.S.	N.S.	N.S.	(0.31**)	0.24**	0.76**
		AUDPC	0.63	0.69**	N.S.	N.S.	N.S.	N.S.	(0.36**)	0.11	0.59
	Cellobunch 7 June	Incidence	0.30**	0.30**	N.S.	(0.12)	N.S.	N.S.	(0.19**)	N.S.	0.27**
		AUDPC	0.24**	0.25**	N.S.	N.S.	N.S.	(0.12)	(0.12)	N.S.	0.19**
	Cellobunch 9 July	Incidence	0.74**	0.71**	0.14	N.S.	N.S.	N.S.	(0.26**)	0.24**	0.72**
		AUDPC	0.45**	0.46**	(0.25)	N.S.	N.S.	N.S.	N.S.	0.23	0.40

.../ continued

Table 10. - continued

Year	Cultivar + treatment	Cavity spot rating	Coefficient of Determination: Days after seeding	Cumulative rainfall	Total rainfall in previous weeks: 1wk	2wk	3wk	5wk	7wk	Preceding weeks with rain (1-4)	Soil temp. 5 cm
1991	Six Pak 9 May	Incidence	0.58**	0.48**	N.S.	N.S.	N.S.	0.39**	0.42**	N.S.	0.56**
		AUDPC	0.63**	0.54**	0.23	(0.28)	N.S.	0.37**	0.51**	N.S.	0.61**
	Six Pak 30 May	Incidence	0.28**	0.25**	N.S.	N.S.	N.S.	0.28**	0.28**	N.S.	0.34**
		AUDPC	0.51**	0.43**	0.19**	N.S.	N.S.	0.32**	0.36**	N.S.	0.57**
	Six Pak 21 June	Incidence	0.22	0.17	N.S.	N.S.	N.S.	(0.44**)	(0.49**)	N.S.	0.26**
		AUDPC	0.47**	0.39**	N.S.	N.S.	N.S.	0.36**	0.45**	N.S.	0.48**
	Six Pak 12 July	Incidence	0.17	0.17	N.S.	N.S.	N.S.	(0.27)	0.22	N.S.	0.22
		AUDPC	0.38	0.37**	0.16	N.S.	N.S.	N.S.	0.23	N.S.	0.39**
	SR-481 9 May	Incidence	0.17	0.16	(0.23)	N.S.	N.S.	0.22**	0.16	(0.20)	N.S.
		AUDPC	0.30**	0.30	0.23**	N.S.	N.S.	0.19	0.20	(0.36**)	0.21**
	SR-481 30 May	Incidence	0.34**	0.32**	0.13	N.S.	N.S.	0.30**	0.32**	N.S	.29**
		AUDPC	0.51**	0.43**	N.S.	N.S.	N.S.	0.32**	0.36**	N.S	0.57**
	SR-481 21 June	Incidence	0.14	0.14	N.S.	N.S.	N.S.	0.19	0.22**	N.S.	0.14
		AUDPC	0.40**	0.38**	N.S.	N.S.	N.S.	0.26**	0.29**	N.S.	0.40**
	SR-481 12 July	Incidence	0.25**	0.24**	N.S.	N.S.	N.S.	0.16	0.18	N.S.	0.28**
		AUDPC	0.39**	0.37**	N.S.	N.S.	N.S.	N.S.	0.21	N.S.	0.39**

.../ continued

Table 10. - continued

Year	Cultivar + treatment	Cavity spot rating	Coefficient of Determination: Days after seeding	Cumulative rainfall	Total rainfall in previous weeks: 1wk	2wk	3wk	5wk	7wk	Preceding weeks with rain (1-4)	Soil temp. 5 cm
	Non-irrigated										
1992	Six Pak	Incidence	0.15	0.16	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	.16
	Check	AUDPC	0.25**	0.26**	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	.22**
	Six Pak	Incidence	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
	Drench	AUDPC	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
	Red Core Chantenay	Incidence	0.18	0.19	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	0.22**
	Check	AUDPC	0.40**	0.42**	N.S.	N.S.	N.S.	N.S.	N.S.	(0.19)	0.44**
	Red Core Chantenay	Incidence	0.14	0.16	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	0.18
	Drench	AUDPC	0.51**	0.49**	N.S.	N.S.	N.S.	N.S.	(0.21)	N.S.	0.63**
	Eagle	Incidence	0.27**	0.28**	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	0.30**
	Check	AUDPC	0.51**	0.51**	N.S.	N.S.	N.S.	N.S.	(0.25)	(0.20)	0.54**
	Eagle	Incidence	0.17	0.19	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	0.21**
	Drench	AUDPC	0.43**	0.41**	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	0.49**
	Huron	Incidence	0.38**	0.41**	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	0.38**
	Check	AUDPC	0.56**	0.56**	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	0.55**
	Huron	Incidence	N.S.	N.S.	0.14	0.14	N.S.	N.S.	N.S.	N.S.	N.S.
	Drench	AUDPC	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	(0.21)

.../ continued

Table 10. - continued

Year	Cultivar + treatment	Cavity spot rating	Coefficient of Determination: Days after seeding	Cumulative rainfall	Total rainfall in previous weeks: 1wk	2wk	3wk	5wk	7wk	Preceding weeks with rain (1-4)	Soil temp. 5 cm
1992	Irrigated Six Pak	Incidence	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	(0.19)	N.S.	N.S.
	Check	AUDPC	0.17	0.19**	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	0.14
	Six Pak Drench	Incidence	0.18	0.17	N.S.	N.S.	N.S.	N.S.	0.14	N.S.	0.16
		AUDPC	0.37**	0.36**	(0.25**)	(0.18)	0.17	0.14	0.22**	N.S.	0.33**
	Red Core Chantenay	Incidence	0.43**	0.43**	N.S.	(0.33)	N.S.	N.S.	(0.49**)	N.S.	0.43**
	Check	AUDPC	0.65**	0.63**	(0.30)	(0.31)	0.28	0.14	0.26**	(0.19)	0.63**
	Red Core Chantenay	Incidence	0.21**	0.22**	0.16	(0.17)	0.17	N.S.	(0.18)	N.S.	0.14
	Drench	AUDPC	0.48**	0.48**	(0.41**)	(0.30**)	0.24	0.23**	0.36**	(0.28**)	0.40**
	Eagle	Incidence	0.45**	0.43**	N.S.	N.S.	N.S.	N.S.	(0.33**)	N.S.	0.51**
	Check	AUDPC	0.56**	0.52**	N.S.	N.S.	N.S.	N.S.	0.18	N.S.	0.59**
	Eagle	Incidence	0.41**	0.39**	(0.19)	(0.18)	0.11	N.S.	(0.27**)	N.S.	0.42**
	Drench	AUDPC	0.56**	0.51**	0.13	N.S.	0.23**	0.15	0.28	N.S.	0.59**
	SR-481	Incidence	0.26**	0.27**	0.13	(0.24)	0.15	N.S.	N.S.	N.S.	0.17
	Check	AUDPC	0.40**	0.41**	0.26**	0.24**	0.29**	0.16	0.13	(0.23)	0.23**
	SR-481	Incidence	N.S.	N.S.	N.S.	(0.25)	N.S.	N.S.	N.S.	N.S.	N.S.
	Drench	AUDPC	0.22**	0.24**	N.S.	(0.20)	N.S.	N.S.	N.S.	N.S.	0.14

.../ continued

Table 10. - continued

1 C.S. index = cavity spot index based on a severity rating of 1-100; AUCSIC=area under the cavity spot index curve; AUDPC=area under the disease progress curve.

2 N.S.= not significant at P=0.05, values shown are significant at P=0.05, ** indicates significance at P=0.01, linear or second order polynomial regressions.

3 r^2 values in brackets indicate second order polynomial regression.

4 Drench application of metalaxyl + mancozeb (Ridomil MZ 72WP) at 2.0 kg ai/ha metalaxyl plus 16.0 kg ai/ha mancozeb applied in an 8 cm band over the seed row immediately after seeding.

rainfall. Soil temperatures at 5 cm depth were negatively associated with days after seeding (r^2=0.83 -0.95 Appendix III Table 10-2). Other rainfall parameters (total rainfall in the one, two, three, five or seven weeks prior to assessment and the number of preceding four weeks with incidents of rainfall over 5 mm) were more associated with cavity spot in some years than others but the r^2 values tended to be low ($\leq$ 0.53, Table 10).

In each year, cavity spot was assessed as incidence at the time of sampling and the AUDPC for each assessment period was calculated. In 1986, AUDPC of Six Pak for each sample period was correlated with plant age, as were the incidence and AUDPC of Chanton (r^2=0.86, 0.76 and 0.59, respectively, Table 10). Cumulative rainfall was correlated with increasing AUDPC on Six Pak and incidence on Chanton. None of the other parameters was associated with changes in cavity spot, except soil temperature.

During the 1987 season, plant age and cumulative rainfall were closely related to the change in AUDPC of Red Core Chantenay (r^2=0.80 and 0.76). Cavity spot incidence was also positively associated with these parameters (r^2=0.28 and 0.30) as was soil temperature at 5 cm (r^2=0.15). Rainfall in the five and seven weeks prior to assessment was negatively associated with incidence. The association between rain in the previous two and three weeks and AUDPC was described by a concave line with the lowest level at 55 mm rainfall (Appendix III Table 10-1). The r^2 values were low for all these rainfall parameters (r^2=0.16-0.28).

In 1988, cavity spot increased with increasing days after seeding and cumulative rainfall, and with decreasing soil temperature. These independent variables were highly related (r^2=0.97 and 0.87 for days after seeding vs. cumulative rainfall and soil temperature at 5 cm depth, respectively, Appendix III Table 10-2). There were relationships between the amount of rainfall preceding assessment and cavity spot although the r^2 values were often low (0.15-0.53, Table 10). Often the relationships were best described by quadratic equations (Table 10, Appendix III Table 10-1).

Application of metalaxyl plus mancozeb at seeding had inconsistent effects on the degree of association with the independent variables. Regressions involving fungicide-treated Six Pak carrots had similar r^2 values for days after seeding vs. AUDPC as the check, but lower values for the regressions involving cavity spot incidence. The r^2 values for regressions of days after seeding and cavity spot ratings were lower on fungicide-treated Chanton and Red Core Chantenay than on the untreated checks.

Most of the relationships between the amount of rainfall preceding assessment and cavity spot were best described by quadratic equations (Table 10). In 1990, there were higher r^2 values for regressions involving carrots seeded 9 July, than for the same cultivars seeded on 7 June. Significant regressions were identified for days after seeding, cumulative rainfall and soil temperature. Where there were significant relationships between preceding rainfall and the cavity spot ratings, the r^2 values were low (0.13-0.40) and the relationships were best described by quadratic equations resulting in concave curves (Appendix III Table 10-1). Cavity spot increased with decreasing number of weeks (one to four) with rainfall events exceeding 5 mm, but the r^2 values were low (0.11-0.24, Table 10).

In the 1991 trial, low ($r^2<0.51$) but significant r^2 values were obtained for regressions of the cavity spot ratings for all cultivars and seeding dates (Table 10). Cavity spot consistently increased with decreasing total rainfall in the weeks preceding assessment (Appendix III Table 11.1).

In 1992, the r^2 values for the regressions of cavity spot on the various parameters were often low (Table 10). Soil temperature was most closely related to cavity spot development on carrots in the non-irrigated plot ($r^2=0.16-0.63$), while days after seeding remained the parameter most associated with cavity spot on carrots in the irrigated plot ($r^2=0.15-0.65$, Table 10).

Few of the rainfall parameters were correlated with cavity spot

development on carrots in the non-irrigated plot. Where there were significant r^2 values, the regression lines were best described by quadratic equations (Appendix III Table 10-1). Cavity spot on carrots grown in the irrigated plot increased with decreasing total rainfall in the preceding five and seven weeks, except on Six Pak and untreated Red Core Chantenay where cavity spot was lowest at median levels of rainfall (Appendix III Table 10-1).

Examination of the cavity spot progress curves in relation to rainfall and soil temperature confirmed some of the relationships identified by the regression of cavity spot on these parameters (Figures 2a-g and Table 10). Cavity spot incidence increased with increasing days after seeding on Chanton in 1986, and on Chancellor seeded 7 June and Cellobunch seeded 9 July in 1990 (Figures 2a, d). In other years and on other cultivars, the incidence of cavity spot reached a maximum and remained constant or decreased before the final harvest (Figures 2a-g).

In 1986, there appeared to be four increases in cavity spot incidence on Chanton; these occurred on 24 August, 8 and 29 September and 8 October (Figure 2a). Disease incidence was not recorded for each replication in 1986, therefore standard errors were not calculated. There were three events of heavy rainfall (>30 mm) during the cavity spot epidemic; these occurred on 8 and 26 August and 10-11 September, 14 to 19 days prior to the first three increases. Frequent rainfall totalling 89.8 mm also occurred from 15 to 25 September, 12 to 22 days prior to the increase on 6 October. Cavity spot incidence on Six Pak was very low until 22 September, 27 and 10 days following the rainfall on 26 August and 10 September, respectively, and increased again on 8 October, 28 days after the 10 September rainfall (Figure 2a). Soil temperatures gradually decreased during the 1986 season, although there was an increase in late August and again in the last half of September. Average daily soil temperature in the periods between rainfall and the increase in incidence were 19.6, 18.1, 15.6 and 14.5°C for the increases on 25 August, 8

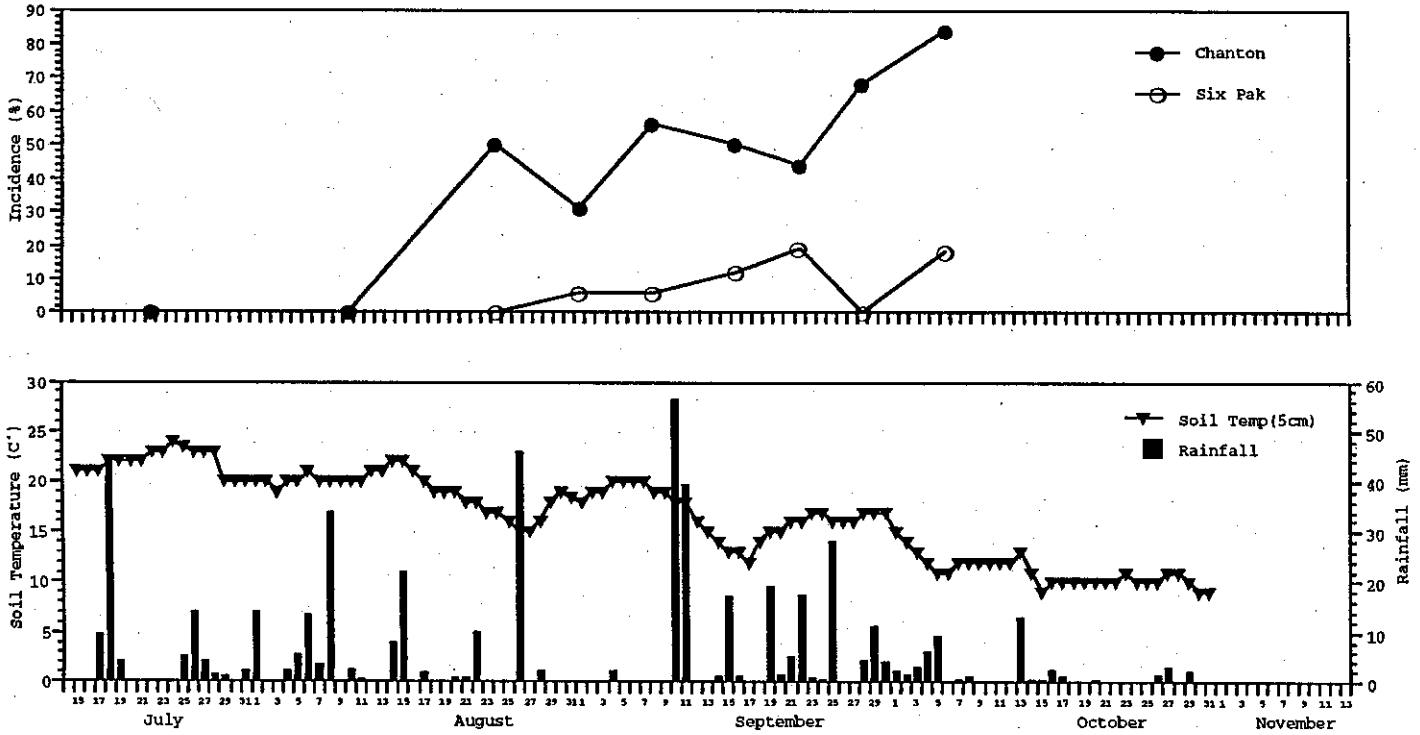

Figure 2a. Rainfall and soil temperature in relation to cavity spot incidence on Six Pak and Chanton in 1986.

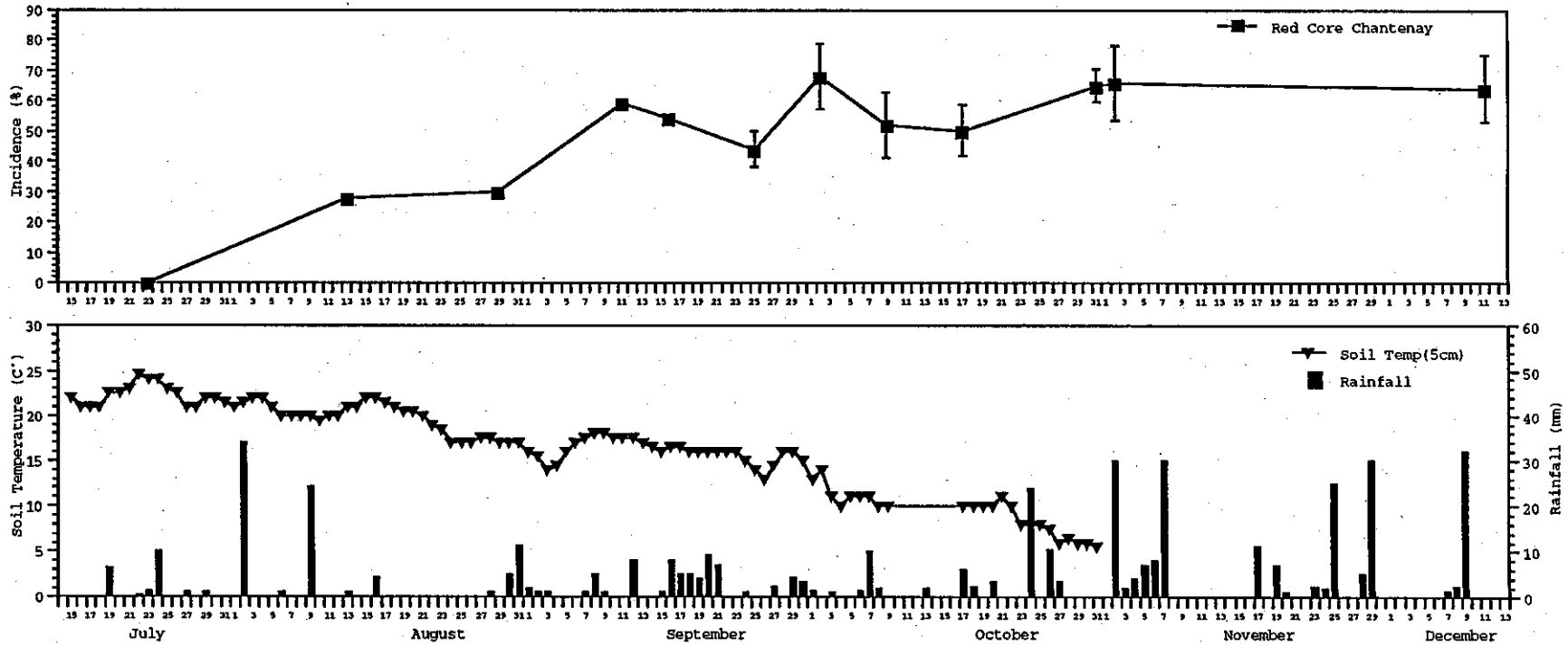

Figure 2b. Rainfall and soil temperature in relation to cavity spot incidence on Red Core Chantenay in 1987.

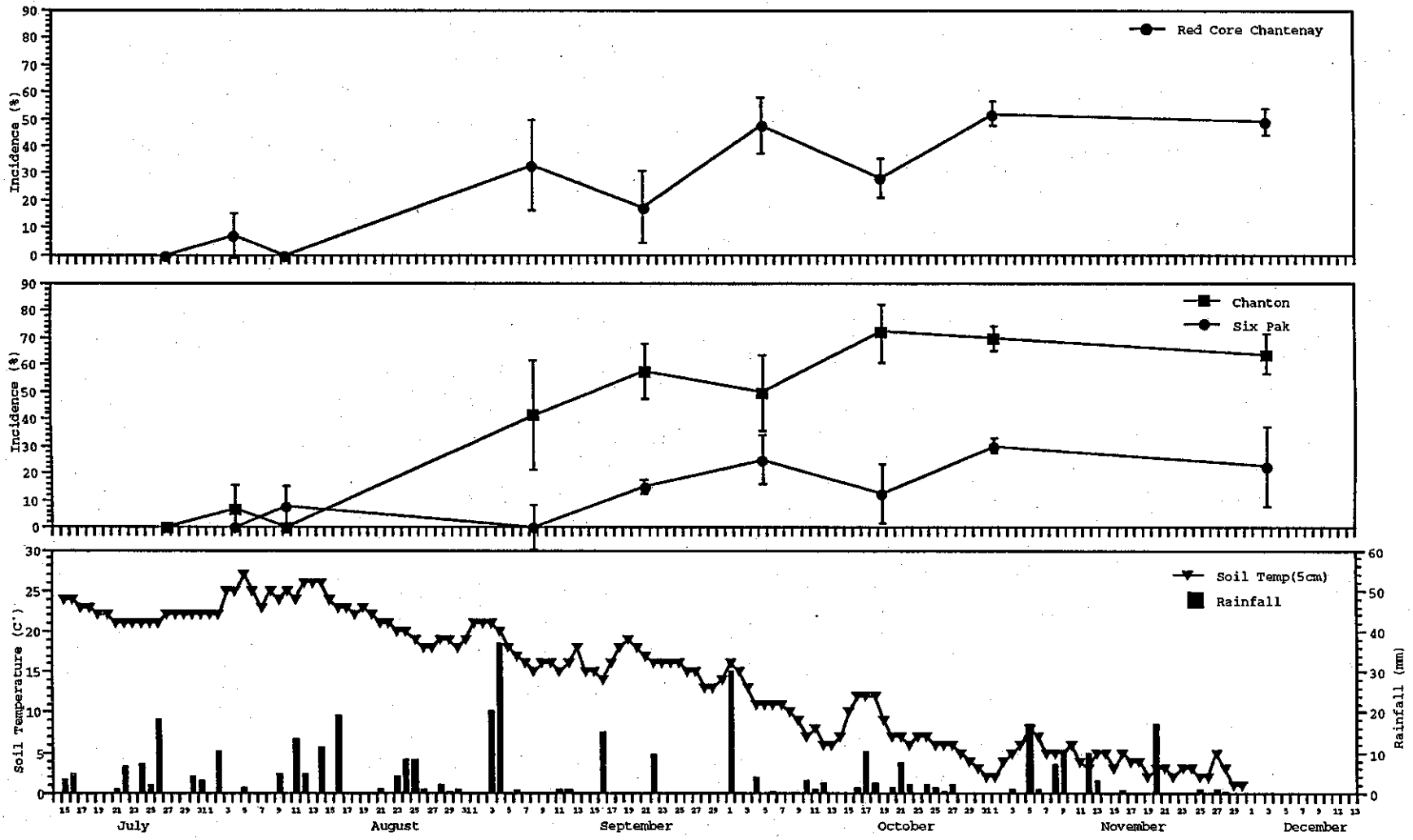

Figure 2c. Rainfall and soil temperature in relation to cavity spot incidence on Six Pak, Chanton and Red Core Chantenay in 1988.

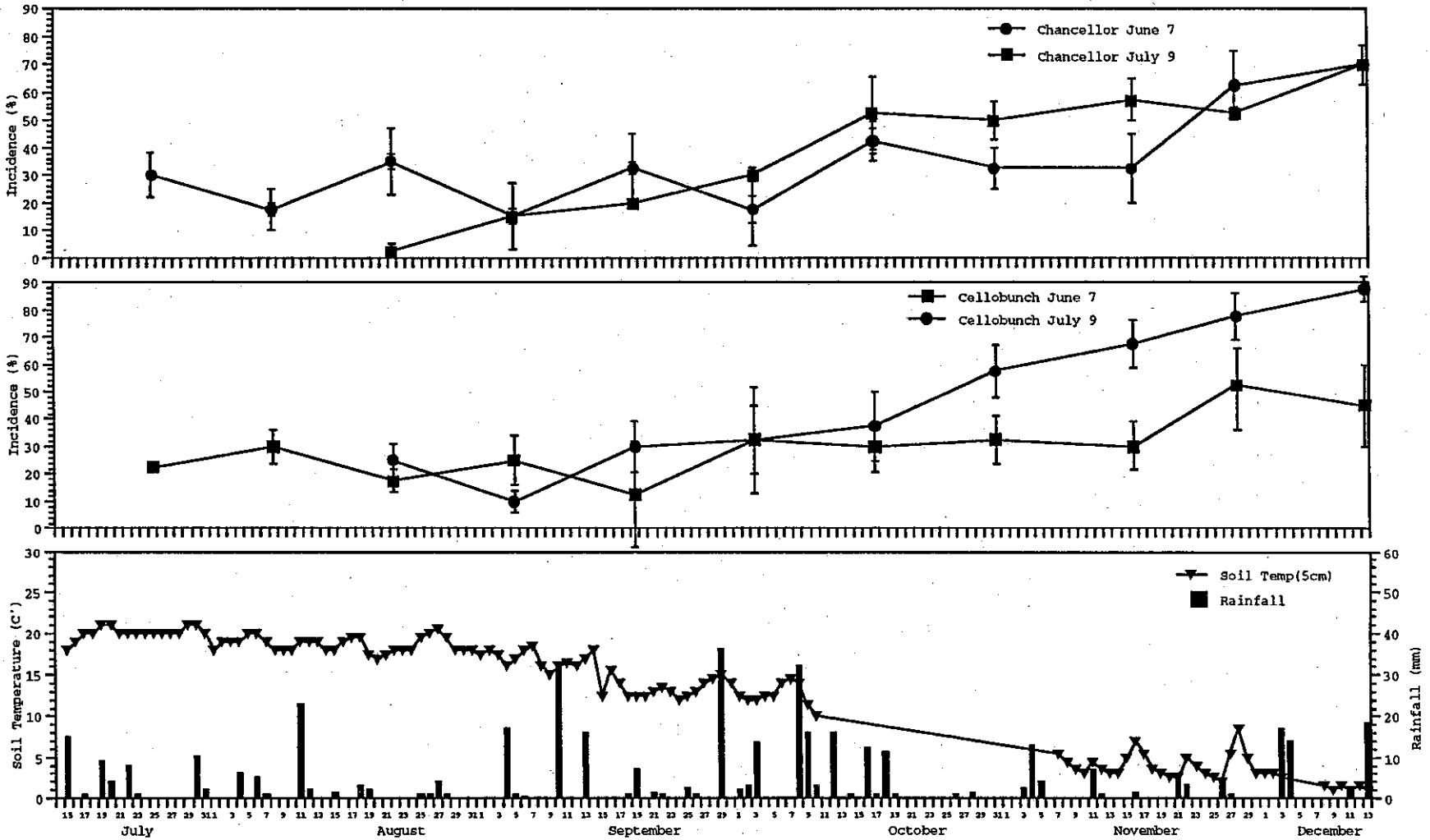

Figure 2d. Rainfall and soil temperature in relation to cavity spot incidence on Six Pak, seeded 7 June and on Cellobunch seeded 7 June and 9 July in 1990.

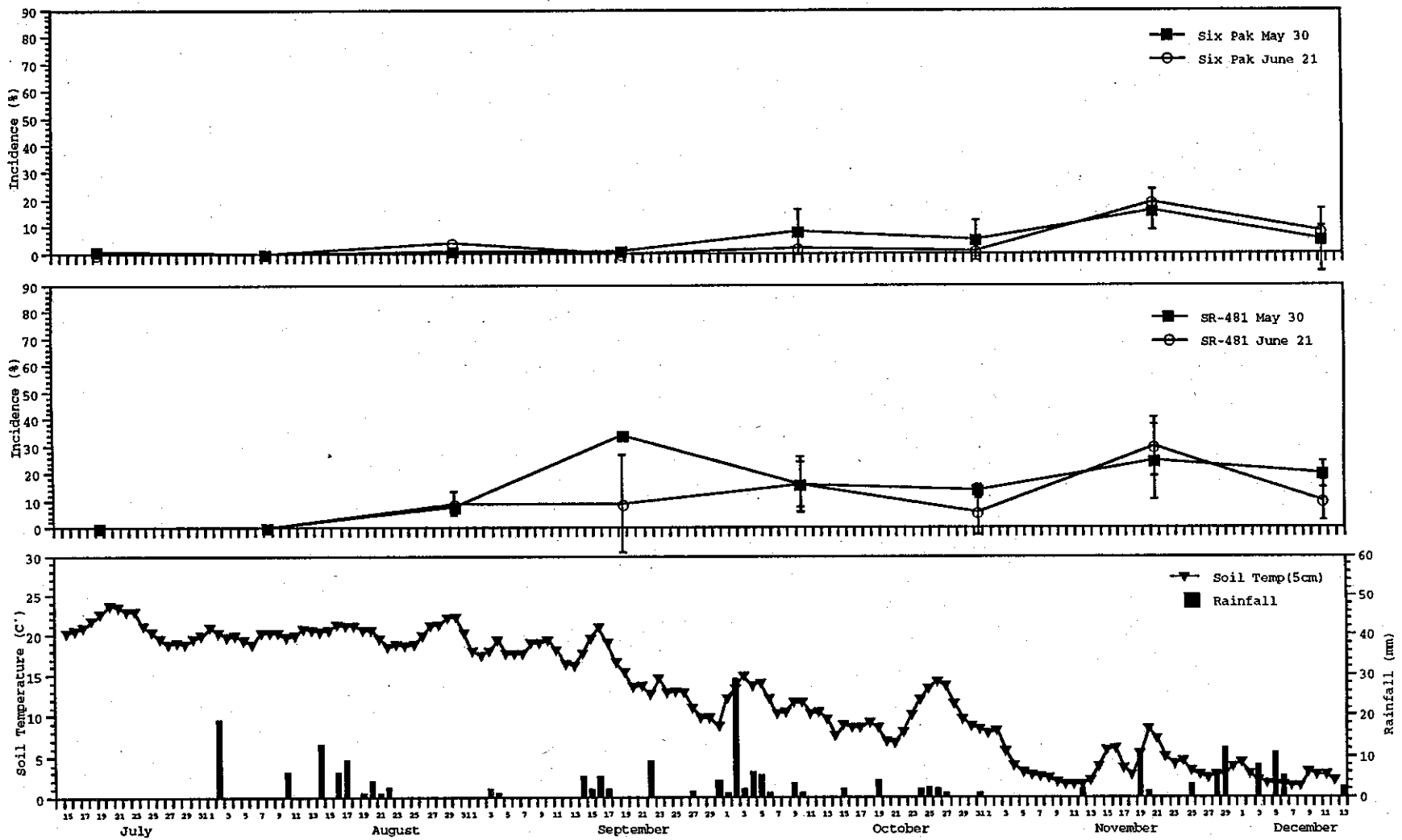

Figure 2e. Rainfall and soil temperature in relation to cavity spot incidence on Six Pak and SR-481 seeded 30 May and 21 June, 1991.

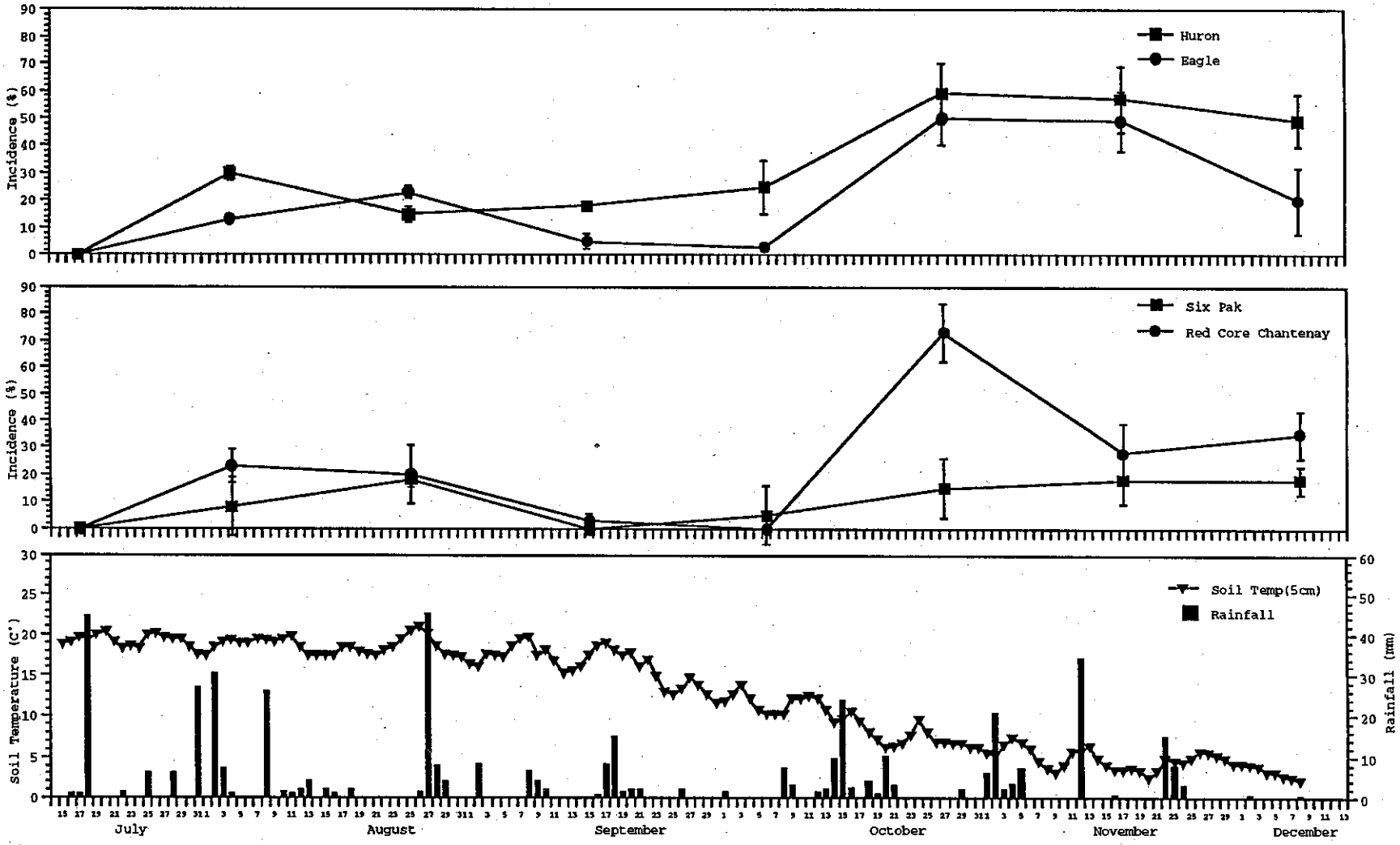

Figure 2f. Rainfall and soil temperature in relation to cavity spot incidence of Six Pak, Red Core Chantenay, Eagle and Huron in the non-irrigated plot 1992.

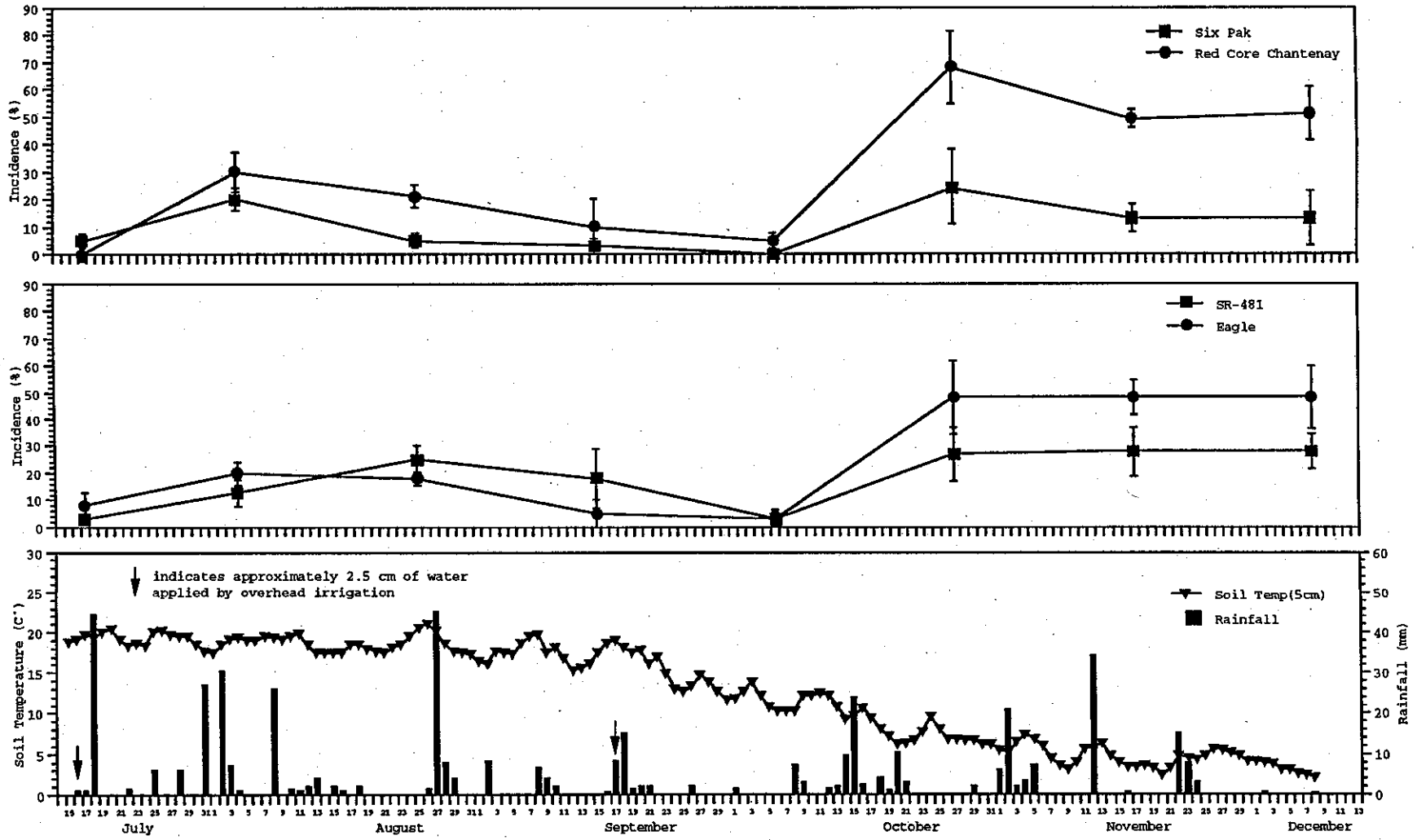

Figure 2g. Rainfall, irrigation and soil temperature in relation to cavity spot incidence on Six Pak, Red Core Chantenay, Eagle and SR-481 in the irrigated plot in 1992.

September, 29 September and 6 October, respectively.

In 1987, cavity spot incidence on Red Core Chantenay increased by 13 August, 11 September and 2 October, then remained constant until the final harvest on 11 December (Figure 2b). Incidence ratings were not recorded for each replication prior to the 25 September sample date, so standard errors were not calculated for earlier dates. Rainfall events occurred on 13 July (not shown), 5 and 9 August and 12-21 September, 31, 33 and 20-11 days prior to the increases, respectively. Rainfall from 12-21 September totalled 47.2 mm but was less than 10 mm per day. The average soil temperature for each of these periods was 21.9, 19.7, 18.4 and 15°C. There were several other days with rainfall less than 5 mm between 13 August and 1 October but none totalled 20 mm or more over a 10 day period. The cavity spot incidence remained constant from 2 October to 11 December although rain fell on several days during this period. No soil temperature data were available for November and December.

During the 1988 growing season, cavity spot incidence remained low on Six Pak until 8 September, increased by 21 September and 5 October, then remained constant until 3 December (Figure 2c). Rainfall from 11 to 16 August and 3 to 4 September, totalling 53.6 and 57.0 mm, occurred 37 and 32 days prior to the increases in incidence. The average soil temperature during these periods was 18.9, and 15.9°C for assessments on 21 September and 5 October, respectively.

Cavity spot incidence on Chanton and Red Core Chantenay increased to 8 September, 30 to 23 days after the rain on 9 to 16 August, and did not increase further for the duration of the season. There was a significant increase on Red Core Chantenay and Six Pak from 19 October to 1 November, but incidence did not exceed levels reached on 5 October. These increases occurred 32 days after 30 mm of rain on 1 October. There were several other days with rainfall prior to 1 October but most were less than 5 mm and none exceeded 20 mm over five days. (Figure 2c).

The pattern of cavity spot development on Chancellor and Cellobunch

was different for the 7 June and 9 July seeding dates (Figure 2d). Incidence on Chancellor seeded 7 June increased from 8 to 22 August, decreased by 5 September and increased from 5 September to 17 October. A further increase occurred between 17 October and 28 November. When Chancellor was seeded on 9 July, incidence increased from 5 September to 17 October then remained constant for the rest of the season. Rainfall occurred on 12 August, 10 days prior to the increase on 22 August. Several days of rain occurred during the period from 5 September to 17 October and there were three days with over 20 mm of rainfall, 10 and 29 September and 8 October (33, 36.2 and 32.3 mm rain, respectively). These rainfall events occurred 27, 19 and 9 days prior to the 17 October sample date, but it cannot be determined if the rain on 8 October was associated with the 17 October increase. There were no days with rainfall over 20 mm from October to the end of the season.

Incidence on Cellobunch seeded 7 June did not increase after 8 August but there was a small difference between 19 September to 28 November (Figure 2d). In contrast, incidence on Cellobunch seeded on 9 July decreased from 22 August to 5 September then increased by 19 September to 31 October, 17 October to 16 November and 16 November to 13 December. The increase on 31 October followed rainfall events on 29 September and 8 October, 19 and 9 days prior to the sampling date, respectively. Rainfall also occurred on 4, 10 and 13 September (66.1 mm total) 15-6 days prior to the 19 September increase, but only the 10 September rainfall was over 20 mm.

Cavity spot incidence was very low on Six Pak carrots seeded 30 May and 21 June (Figure 2e). Disease progress curves of carrots of the same cultivar seeded 9 May and 30 May were roughly parallel, as were those of carrots seeded 21 June and 12 July (Table 26a Chapter 5) so data from carrots seeded 30 May and 21 June are presented.

Cavity spot incidence on Six Pak seeded 30 May and 21 June and SR-481 seeded 21 June was extremely low (maximum 16%) throughout 1991 and was

significantly higher than zero only on 21 November. Incidence increased from 19 September to 21 November on Six Pak. The only day with rainfall over 20 mm was 5 October (29.1 mm rain), 47 days prior to 21 November. Rainfall was very low (<6.3 mm per day) 47 days prior to the 21 November increase. Some rainfall (11.4 mm) did occur two days before the increase, on 19 November, but could not have been associated with the increase. Average soil temperature from 5 October to 21 November was 8.6°C.

Cavity spot incidence increased from 8 August to 19 September on SR-481 carrots seeded 30 May and did not change throughout the rest of the season (Figure 2e). Increases on 30 August and 19 September were preceded by rainfall on 2 August (19 mm) and 15-22 August, (20.2 mm) 28 and 35-28 days prior to the increases. Average soil temperatures during these periods were 20.1 and 19.3°C. The rainfall on 5 October did not appear to be associated with an increase in incidence.

In 1992, disease progress on all cultivars in both the non-irrigated and irrigated plots followed a similar pattern (Figures 2f,g). Cavity spot incidence increased to a peak on 4 or 25 August, then decreased considerably before increasing again on 27 October.

On Six Pak carrots in the non-irrigated plot, cavity spot increased from 17 July to 4 August (Figure 2f). Several rainfall events preceded these increases, but there was heavy (>20 mm) rainfall on 18 and 31 July and 3 and 8 August, 17 days before the 4 August increase. Average soil temperatures were 19.1 and 18.5°C for periods from the rainfall to the 4 and 25 August sampling dates, respectively. Incidence decreased by 15 September, even though 45 mm of rain fell on 27 August, then increased gradually on 6 and 27 October and remained constant for the rest of the season. Rainfall on 17-18 September and 14-15 October occurred 18 and 13 days prior to increases of incidence on 6 and 27 October. Alternatively, the increases on 27 October may have been related to the rainfall on 17-18 September, 39 days prior to the increase. Average soil temperatures in the 14 and 39 days preceding 27 October were 8.2 and 11.6°C, respectively.

Cavity spot incidence on Red Core Chantenay increased from 17 July to 4 August, decreased from 25 August to 15 September and increased from 6 to 27 October (Figure 2f). A marked decrease occurred from 27 October to 17 November. The increases on 4 August and 27 October may have been associated with the rainfall events described for these increases on Six Pak. Heavy rainfall (>20 mm) occurred on 27 August and was followed by a decrease in cavity spot incidence.

Disease progress was similar on Eagle and Huron grown in the non-irrigated plot and resembled that of Six Pak, except that the first peak in disease incidence occurred on 4 August on Huron and incidence on 27 October and 17 November was higher. Disease incidence on Eagle decreased from 17 November to 8 December.

Cavity spot incidence on Six Pak grown in the irrigated plot increased to 4 August, then decreased to 6 October prior to an increase by 27 October. Incidence remained constant for the rest of the season (Figure 2g). This pattern of disease progress was similar to that of Red Core Chantenay and Eagle grown in the irrigated plot, and Eagle, grown in the irrigated plot, although incidence on Red Core Chantenay decreased from 27 October to 17 November. Average soil temperatures from 25 October to 17 November and 17 November to 8 December was 5.4 and 3.8°C, respectively.

Cavity spot incidence in November and December continued to increase in 1990 on Chancellor seeded 7 June and Cellobunch seeded 9 July but remained constant or decreased in 1987, 1988, 1991, and 1992. Soil temperatures during this period did not vary much from year to year. Soil temperatures in 1990 averaged 8.5, 5.5, 4.0 and 3.0°C from 17 to 31 October, 31 October to 16 November, 16 November to 28 November and 28 November to 13 December, respectively. Soil temperatures for November and December were not available in 1987, but temperatures for the similar period in 1991 were 9.8, 4.4 and 3.0°C from 10-31 October, 31 October to 21 November and from 21 November to 11 December, respectively. In 1992,

soil temperatures were 5.4 and 3.8°C from 27 October to 17 November and 17 November to 8 December.

Decreases in cavity spot incidence from one sample date to the next were identified by comparing standard errors. These occurred in 1990 and 1992 (Figure 2d,2f,2g). In 1990, disease incidence decreased from 22 August to 5 September during a period where rainfall was less than 5 mm each day from 12 August to 4 September (Figure 2d). In 1992, disease incidence decreased from 4 August to 25 August on Huron in the non-irrigated plot (Figure 2f) and Six Pak in the irrigated plot (Figure 2g). There were 17 days during this period (8 August to 25 August) when rainfall was less than 5 mm each day. However, decreases in disease incidence also occurred between 4 August and 5 September on Six Pak, Red Core Chantenay and Eagle in the non-irrigated plot and Eagle in the irrigated plot, even though 45 mm of rain fell on 27 August. Disease incidence also decreased from 27 October to 17 November on Red Core Chantenay in the non-irrigated and irrigated plot and from 17 November to 8 December on Eagle in the irrigated plot, despite rainfall of over 20 mm on 2 and 13 November and rain totalling 27 mm from 22 to 24 November.

Early season rainfall and soil temperature in relation to maximum and final levels of cavity spot

Early season rainfall and soil temperature were not closely associated with either the maximum cavity spot incidence, nor AUDPC, on either susceptible or resistant cultivars (Table 11). The maximum incidence that occurred during the season was examined, rather than incidence on the final sample date because incidence often decreased by the end of the season. Rainfall within the first four, six, eight, or four to eight weeks after seeding was not strongly related to the maximum incidence of cavity spot or the AUDPC on the susceptible cultivars ($r^2 \leq 0.12$). However, 40% of the variation in maximum disease incidence on Six Pak was associated with the rainfall in the four weeks after seeding, when this relationship was described by second order polynomial regression

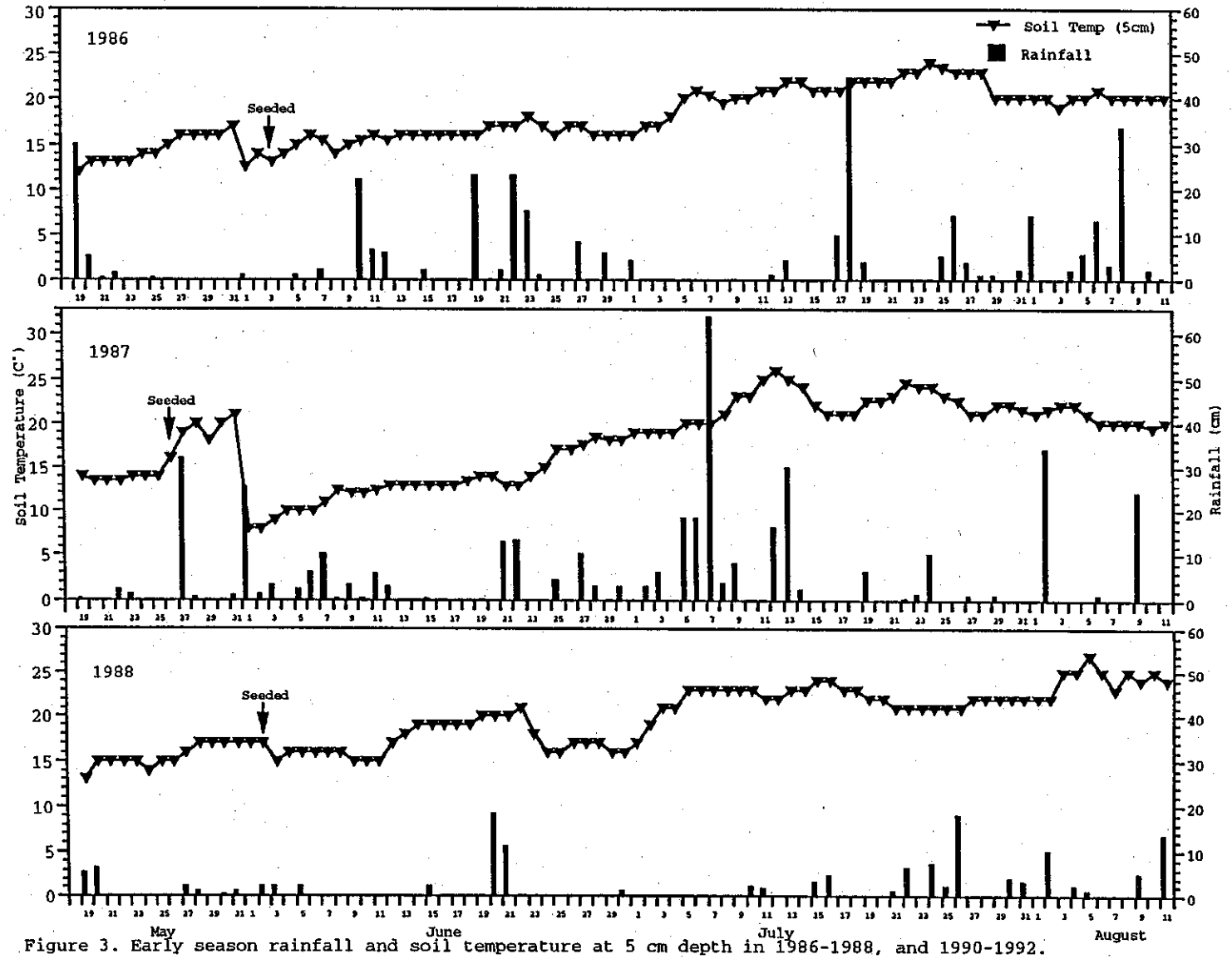

Figure 3. Early season rainfall and soil temperature at 5 cm depth in 1986-1988, and 1990-1992.

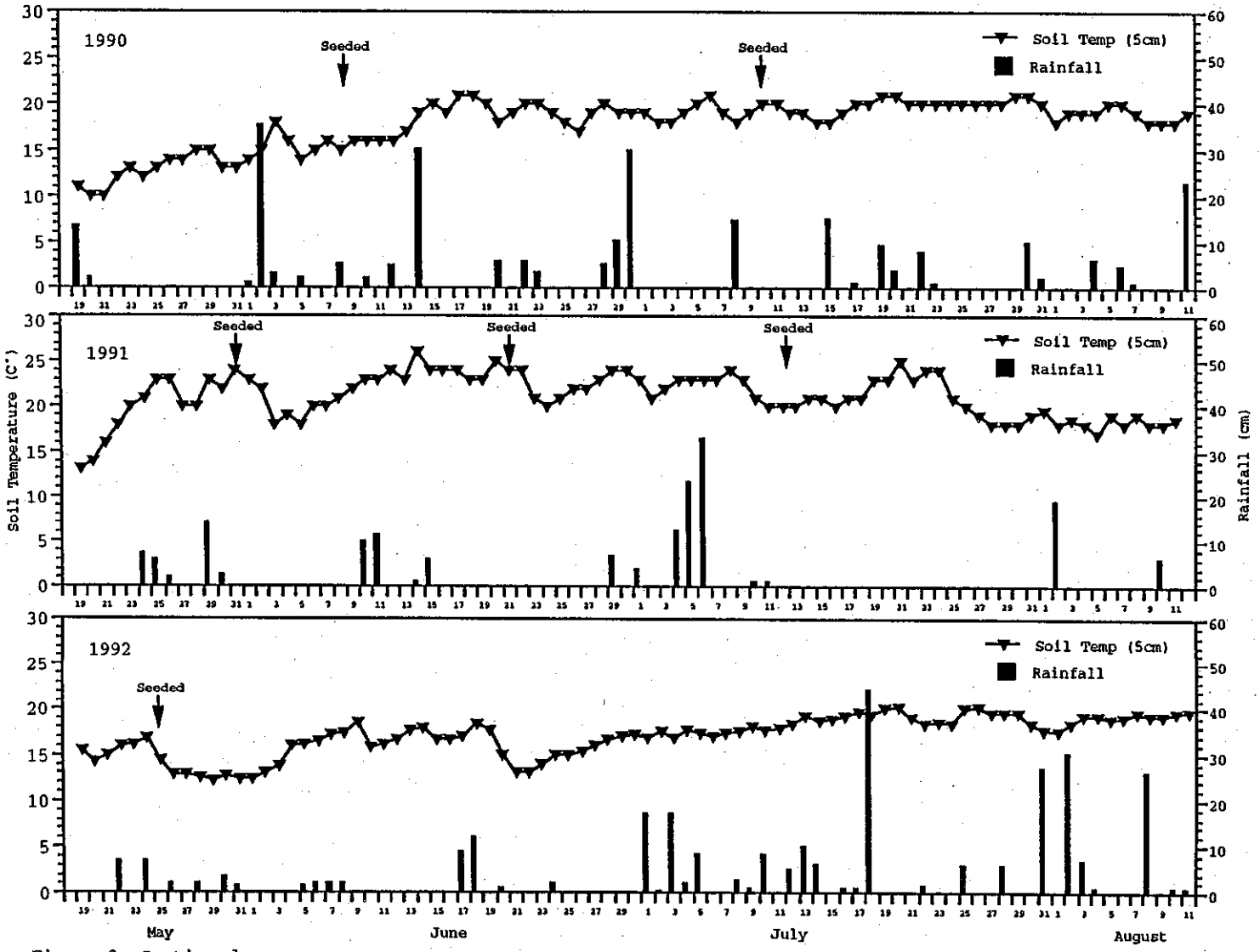

Figure 3. Continued

Table 11. Coefficients of determination for regression of total rainfall and early-season rainfall and soil temperature on maximum and final levels of cavity spot during 1986-1992, for susceptible and resistant cultivars.

Cultivar resistance	Cavity spot rating	Total rainfall	Coefficients of determination: Early-season rainfall, weeks after seeding 0-4	0-6	0-8	4-8	Mean soil temperature (5 cm), Weeks after seeding 0-4	0-6	0-8	4-8
Susceptible[1]	Maximum incidence	(0.12)[3]	0.06	0.12**	N.S.	N.S.	(0.20**)	(0.19**)	(0.13**)	N.S.
	Final AUDPC	(0.28**)	0.06	N.S.	N.S.	N.S.	(0.22**)	(0.43**)	(0.21**)	0.12
Resistant[2]	Maximum incidence	N.S.	(0.40**)	(0.28**)	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
	Final AUDPC	N.S.	N.S.	N.S.	N.S.	N.S.	0.19	0.14	0.27**	0.22**

1 Susceptible cultivars were Chanton, 1986, Chanton and Red Core Chantenay, 1988, Chancellor and Cellobunch seeded 7 June and 9 July, 1990, SR-481 seeded 9 May, 30 May, 21 June and 12 July 1991 and Red Core Chantenay and Eagle, non-irrigated and irrigated, Huron non-irrigated and SR-481 irrigated, 1992.

2 Resistant cultivar was Six Pak in 1986, 1988, 1990, 1991 seeded 9 May, 30 May, 21 June and 12 July and 1992 non-irrigated and irrigated.

3 r^2 values in brackets indicate 2nd order polynomial regression.

4 Values shown are significant at P=0.05; ** indicates significance at P=0.01.

(Table 11, Appendix III Table 11). Maximum levels of cavity spot incidence were found on Six Pak carrots that received either low (0-20 mm) or high (100 mm) amounts of rainfall during the four weeks after seeding (as in 1988 and 1990, respectively, Figure 3, Appendix III Table 11). The lowest value for maximum incidence was associated with approximately 65 mm of rainfall in the four weeks after seeding (i.e. carrots seeded on 9 May 1991, Figure 3, Appendix III Table 11).

More significant regressions were found between soil temperatures early in the season and cavity spot, especially the AUDPC (Table 11). Mean soil temperatures zero to four, zero to six and zero to eight weeks after seeding were related to maximum cavity spot incidence and AUDPC of the susceptible cultivars. Relationships between soil temperatures and maximum disease incidence and AUDPC were described by quadratic equations but, in all cases maximum cavity spot was achieved when early-season soil temperatures were 16-17.5°C and lowest when temperatures were 20-22°C. (Appendix III Table 11). For Six Pak, there were significant regressions between the soil temperatures and AUDPC (r^2=0.19, 0.14, 0.27 and 0.22 for zero to four, zero to six, zero to eight and four to eight weeks, respectively Table 11). The time period that was most closely associated with the final AUDPC was zero to six weeks after seeding for the susceptible cultivars and zero to eight weeks after seeding for Six Pak. In all cases the highest levels of cavity spot were associated with low soil temperatures (16.0-17.5°C) and the lowest levels were associated with high soil temperatures (20-22°C) during the weeks after seeding (Appendix III Table 11).

<u>Total rainfall as an indicator of maximum or final levels of cavity spot</u>

Total rainfall during the growing season was not a reliable indicator of maximum or final levels of cavity spot that developed in any year. Regression analysis of total rainfall for the years 1986-1992 in relation to the maximum cavity spot incidence resulted in no significant

regressions except for the maximum incidence of susceptible cultivars, but the coefficient of determination was very low (r^2=0.12, Table 11). A significant relationship was found between total rainfall and final AUDPC for the susceptible cultivars (r^2=0.28 Table 11). The highest AUDPC occurred in years where 500 to 600 mm of rain occurred during the growing season.

Soil moisture in relation to rainfall

The moisture content (percent by weight) of organic soil in the carrot plots usually increased following rainfall and irrigation and decreased during periods of little or no rainfall in both 1991 and 1992 (Figures 4 and 5). Moisture content of the soil 5 cm below the surface was consistently lower than at the 15 cm depth.

In 1991, the maximum moisture content of soil during the monitoring period was 173% (Figure 4). This value was recorded on 11 July, after a total of 68.8 mm of rain fell 4 to 6 July. Soil moisture levels decreased from 11 July to 27 July. Mean soil moisture content at 5 cm depth was roughly parallel to that measured at 15 cm. Two other increases in soil moisture were observed, on 11 June, following rainfall totalling 21.4 cm on 10 and 11 June and on 2 August, following 18 mm of rainfall that day. The increase on 11 June was significant at the 5 cm depth but not the 15 cm depth (Figure 4).

Mean soil moisture content decreased markedly during two periods when no rainfall was received. Low levels of soil moisture were recorded on 27 June following 11 days with no rain, and also on 25 July after a period of 18 days where daily rainfall was 1.2 mm or less. Moisture content at 5 cm depth remained constant from 2 to 20 August over a period where there were seven consecutive days without rain and rainfall events of 6.2 and 13.0 mm on 10 and 14 August and 6, 9.2, 1 and 4.2 mm rain received on 16, 17, 19 and 20 August.

Rainfall was more frequent in 1992 than in 1991 and the soil moisture

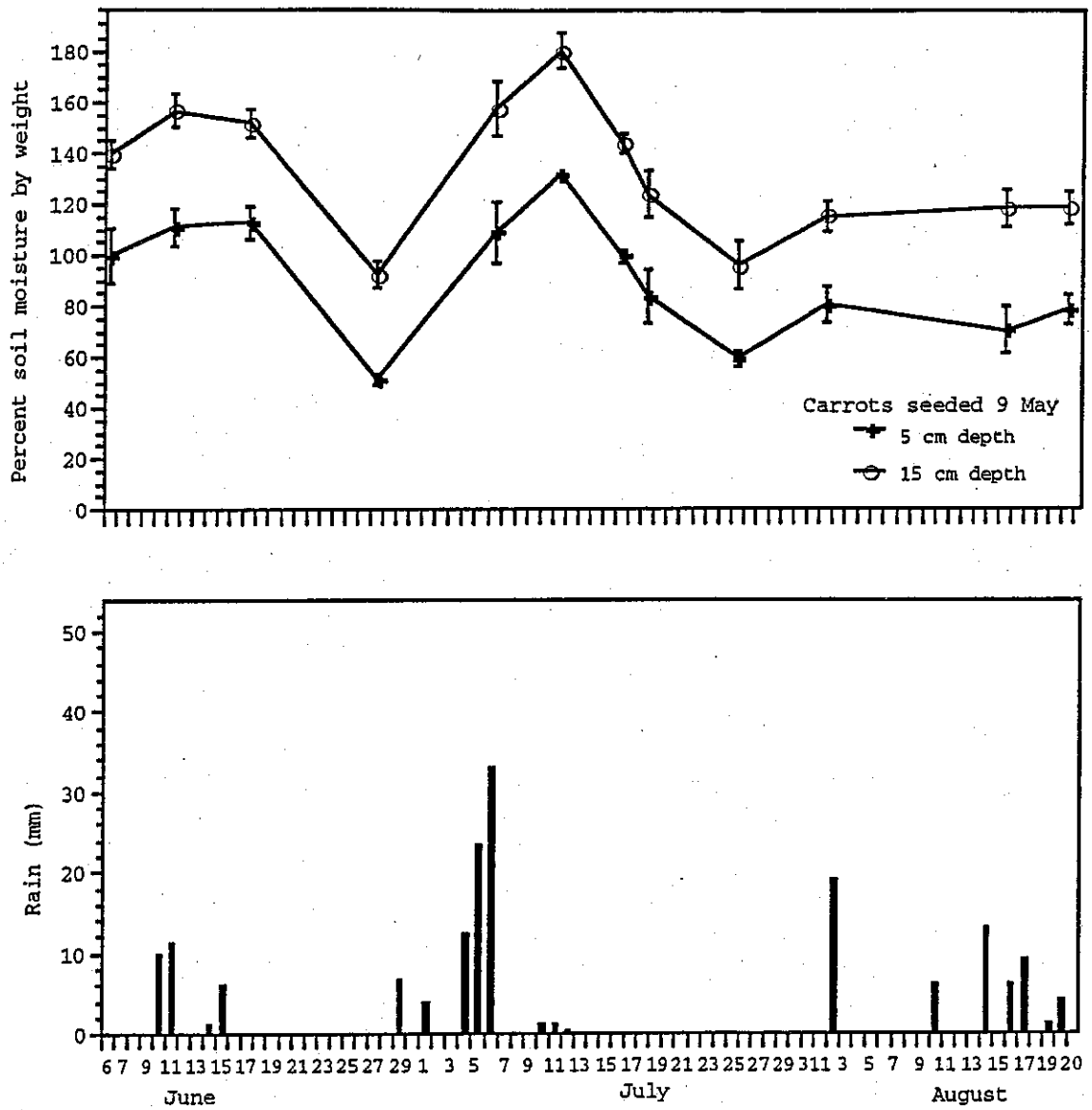

Figure 4. Rainfall and soil moisture content of organic soil at 5 and 15 cm depths in carrot plots seeded 9 May.

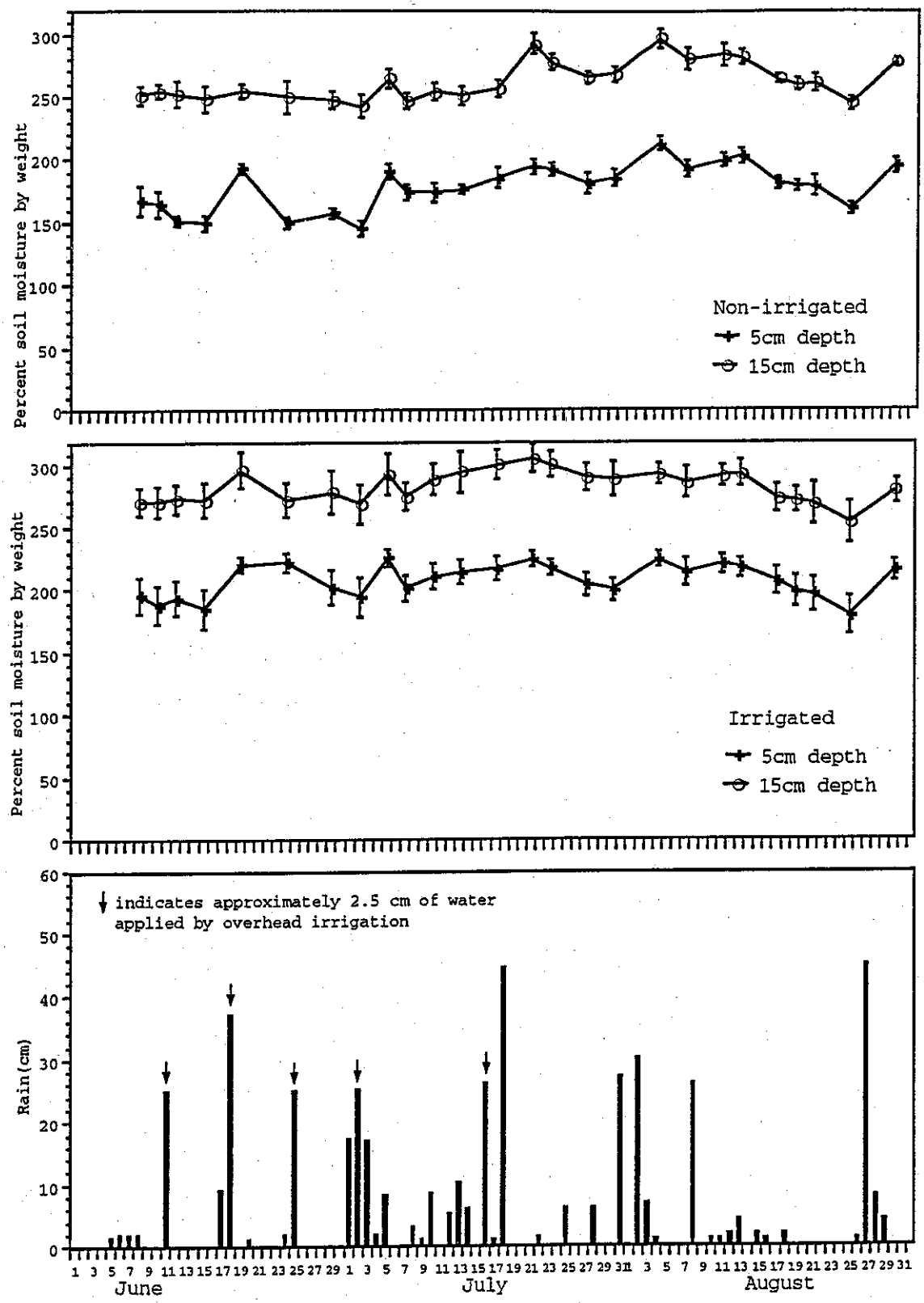

Figure 5. Rainfall plus irrigation and soil moisture content of organic soil at 5 and 15 cm depths in carrot plots seeded in 1992.

content was higher in both the non-irrigated and irrigated plots. Maximum levels were 297 and 305 percent soil moisture by weight, in the non-irrigated and irrigated plots, respectively (Figure 5). In the non-irrigated plot, soil moisture content increased following rainfall events and decreased during periods of low ($\leq$ 10 mm) or no rainfall, but changes in moisture content were smaller than those during the 1991 season.

Maximum moisture content increased in the non-irrigated plot on 21 July after 44.4 mm of rainfall on 18 July and on 4 August after 27.1 and 30.3 mm of rain on 31 July and 2 August, respectively (Figure 5). A small but distinct increase in soil moisture was observed on 5 July after a total of 17.1 mm rain on 3 and 4 July. However, 17.3 mm of rainfall occurred on 1 July and did not result in a corresponding increase in soil moisture when TDR readings were taken on 2 July. Another increase in soil moisture was detected at the 5 cm depth on 19 June after a total of 21.2 mm of rain on 17 and 18 July, but no increase in moisture content was detected in the soil at 15 cm depth. The soil moisture content at 15 cm depth fell slightly from 21 to 27 July nine days after the 18 July rain when total rainfall was 14.3 mm, and during the period from 13 to 25 August when the maximum rainfall on any day was 4.1 mm or less (Figure 5).

Soil moisture levels in the irrigated plot followed much the same pattern as those in the non-irrigated plot, except that the moisture content was approximately 12 to 25 percentage points higher during the first half of the monitoring period (8 June to 15 July) when irrigation was applied. Soil moisture at the 15 cm depth changed little during the monitoring period and decreased after 13 August when rainfall was less than 5 mm per day for several days. Soil moisture at 5 cm depth increased after 37 mm irrigation plus rainfall was received on 18 June and also following 58 mm of rainfall and irrigation from 1 to 3 July. Soil moisture remained constant for the duration of the monitoring period, decreased by 25 August, then increased by 30 August following 46 mm of rainfall on 27 August (Figure 5). Soil moisture content never fell below

245% and 254% at the 15 cm depth in the non-irrigated and irrigated plots, respectively (Figure 5).

DISCUSSION

The present study was the first to examine the epidemiology of cavity spot of carrot in relation to plant age, rainfall and soil temperature. A preliminary investigation of rainfall in relation to the soil moisture content of organic soil was conducted using time domain reflectometry.

Cavity spot incidence increased with increasing plant age and cumulative rainfall, and decreasing soil temperature. However, none of these parameters provided a consistently reliable prediction of cavity spot incidence.

Increases in cavity spot incidence sometimes followed within nine to thirty nine days of rainfall exceeding 20 mm when these occurred before November. Decreases in incidence were usually preceded by periods of little (< 5 mm) or no rainfall for several (>13) days. Soil temperature did not appear to be directly related to changes in incidence. Early season rainfall (zero to eight weeks after seeding) was not closely related to AUDPC or maximum levels of cavity spot on susceptible cultivars, but low early season soil temperatures (16-17.5°C) during this period had some association with high levels of cavity spot, especially AUDPC (r^2=0.43). High (20-22°C) soil temperatures in the six weeks after seeding occurred during years where AUDPC levels were low. However, early season soil temperature was not the only factor associated with high levels of cavity spot. Moderate rainfall during the growing season (approximately 550 mm) also had some association with high AUDPC (r^2=0.28).

The moisture content (percent by weight) of organic soil in the carrot plots increased quickly when rain fell and decreased within nine days of dry weather (< 5 mm rain/day). Time domain reflectometry provided a convenient and non-destructive means of determining the moisture content of organic soil.

Regression analysis of several environmental parameters and days after seeding on cavity spot incidence and increments of AUDPC indicated that days after seeding was the parameter most often related to changes in cavity spot, although the coefficient of determination (r^2) ranged from insignificant to 0.82. Disease incidence often levelled off by October. However, the disease progress curves exhibited a number of peaks and valleys even during seasons where the incidence of cavity spot increased to the final harvest date, as in 1986 and 1990. During 1991 and 1992, maximum disease incidence occurred before the final harvest date.

Regression analyses demonstrated that cumulative rainfall and average soil temperature at 5 cm depth were also related to changes in cavity spot. However, these parameters were highly related to days after seeding and it was not possible to determine their individual effects over the course of an epidemic. Examination of the other rainfall parameters (total rainfall in the one, two, three, five or seven weeks or the preceding four weeks with rainfall) did not show strong relationships with changes in cavity spot. Regressions of total rain in the one, two, or three weeks preceding assessment were often not significant or described by quadratic equations indicating that both high and low levels of rainfall had a similar effect on cavity spot. Cavity spot levels increased with increasing rainfall five and seven weeks preceding assessment in 1986 but decreased with increasing rainfall during these periods in 1987, 1991 and 1992 Appendix III Table 10). The r^2 values for these regressions were high in 1986 (0.70 and 0.54) but low for the other years (0.14 to 0.49, Table 10).

Regression analyses provided few indications of environmental parameters that were associated with the development of cavity spot, even though several reports in the literature suggested that high levels of rainfall or wet soil were associated with increased cavity spot (Guba et al. 1961, Perry and Harrison 1979b, Soroker et al. 1984). Other parameters, other than high soil moisture throughout the season, must be

involved.

To further examine the relationship between environmental parameters and cavity spot development, disease incidence was plotted against daily rainfall and daily soil temperature at 5 cm depth. The occurrence of at least 20 mm of rainfall was the only environmental factor that was sometimes related to increases in incidence, while decreases followed periods of little (> 5 mm each day) or no rainfall. The response to rainfall was distinct in 1986. Increases in incidence followed 14-19 days after rainfall events for Chanton, but occurred 27 and 28 days after the rain on Six Pak. However, in 1992 the time from rainfall to an increase in incidence was the same for Six Pak and the other cultivars, even very susceptible Huron.

The length of time from rainfall until an increase in incidence was observed may represent the incubation period (the length of time from the arrival of inoculum on a host until visible symptoms appear (Vanderplank 1975)). However, it is still not certain whether the increase in incidence represents lesions that resulted from new infections or whether asymptomatic or localized infection existed and changes in the environment resulted in a change to symptomatic or progressive infections. It is likely that new infections occurred in response to the rainfall and the changes in disease incidence do reflect the length of the incubation period.

The observed time periods between rainfall and increased incidence only provide an estimate of the incubation period. Carrots were sampled on a weekly basis from 24 August to 8 October in 1986, but approximately once every two to three weeks in subsequent years. Sampling in 1992 was done every three weeks. Thus, the estimates of the incubation period also incorporate the sampling interval. There is no indication whether the increase in incidence actually occurred near the beginning or the end of the sampling period. However, an estimate of the minimum incubation period can be obtained from the disease progress curves. In 1991, the

incidence on Cellobunch carrots seeded 7 June decreased from 22 August to 5 September, 25 days after rainfall events exceeding 20 mm of rain. However, on Chancellor, seeded 7 June, an increase in incidence followed 10 days after rainfall on 12 August. An increase also occurred by 17 October which may have been associated with rainfall on 8 October, nine days before the increase. Thus, the incubation period appears to require at least nine to ten days, but may be considerably longer on some cultivars and under certain conditions. Sampling at weekly intervals rather than once every two to three weeks would have provided better information on the duration of the incubation period.

Cavity spot lesions developed within three days on mature carrot roots inoculated with mycelial plugs of Pythium violae (Montfort and Rouxel 1988). However, the development of cavity spot on carrots grown in growth media in pots generally required three to four weeks for symptom development (Perry and Harrison 1979b, Soroker et al. 1984, Vivoda et al. 1991) indicating that the incubation period was longer than on carrots that were inoculated with mycelium. Montfort and Rouxel (1988) also demonstrated that the rate of lesion expansion was slower at 5°C and 25°C than at 15°C when carrots were directly inoculated. The incubation period on field-grown carrots would be expected to vary with soil temperature. Thus the incubation period would change during the growing season. This may explain the low r^2 values for the regressions of rainfall in the preceding weeks and cavity spot. If rainfall in the preceding two weeks resulted in an increase in incidence during part of the season but three weeks were required to initiate an increase after rainfall during another part of the season then there would be no strong correlation with either of the parameters throughout the entire season. Inoculum density can also affect the incubation period (Vanderplank 1982). However, it has not been possible to isolate P. violae from soil to determine the inoculum density (Phelps et al. 1991).

In field soils, sporangia and oogonia of many Pythium spp. are

exogenously dormant but can germinate rapidly when stimulated by an exogenous source of nutrients (Stanghellini 1974). Soil moisture and soil temperature may limit successful host colonization. Each species has an optimum temperature for maximum activity, but wet soils (0 to -0.3 bar matric water potential) have been associated with increased incidence of Pythium-incited disease. Conditions of high soil moisture provide the water needed for zoospore production and motility (Stanghellini 1974).

Hancock (1977) studied Pythium development on cotton leaves in soil and found that water-saturated soils did not support Pythium development. Populations increased substantially at water potentials between -0.3 and -8.0 bars but did not increase at water potentials below -9 to -11 bars. Lyons and White (1992) concluded that neither P. violae nor P. sulcatum had an asexual reproductive stage in their life cycles. In addition, Liddell et al. (1989) conducted studies on Pythium root dieback and reported that their isolates of P. ultimum and P. irregulare did not produce zoospores and could infect carrots at soil matric potentials of -30 kPa. Thus several of the Pythium species that have been identified as important causal agents of cavity spot do not require saturated soil conditions to stimulate infection via zoospores.

It is likely that increases in soil moisture content increase the germination and infection of Pythium propagules by increasing the exudation of nutrients from roots and allowing these nutrients to diffuse further into the surrounding soil. Dormant resting structures of Pythium spp. are capable of a high percentage of germination in soil in a short period of time, once they have been stimulated by exogenous nutrients (Stanghellini 1974). Carrot roots exude sugars and other nutrients when held in water. Perry (1983) found that carrot roots immersed in water exuded more glucose in a 24 hour period than roots immersed in aerated water. Soroker et al. (1984) reported that the exudates from carrot roots were composed of 70% sugars plus proteins, amino acids, lipids and minerals. Leakage of the electrolytes was enhanced in carrots immersed in

water and at temperatures of 30°C and above. Thus a rainfall event could stimulate the germination of Pythium propagules and the subsequent infection of carrot roots, even if the soil was saturated for only a short time. Rainfall may also stimulate root growth and a concurrent increase in exudates.

Moisture content of soils in the field plots in 1991 and 1992 were found to be very different. The percent soil moisture content at 15 cm depth varied from 100 to 185% (by weight) in 1991, a dry year, and from 240 to 300% in 1992. Total rainfall during the period from seeding to harvest was 428 mm in 1991 and 567 and 720 mm for the non-irrigated and irrigated plots in 1992. Irwin (1986) reported that field capacity of Bradford muck soil occurred at approximately 265% soil moisture by weight and the permanent wilting point occurred at 44% moisture. He also indicated that muck soil, once dried, loses some of its capability to hold water. This may explain why the soil at 5 cm depth never had as high a moisture content as the soil at 15 cm depth.

In 1991, the soil moisture content of soil in the field plot never reached field capacity (265% moisture) during the three months when moisture content was monitored. In contrast, moisture content of the soil in the non-irrigated plot was near field capacity until 18 July when field capacity was exceeded for almost a month. Soil moisture content in the irrigated plot was above field capacity for most of the monitoring period.

Cavity spot incidence in 1991 rose slightly 29 days after the rainfall on 2 August on SR-481 seeded 30 May. The moisture content of the soil increased following the 2 August rainfall. The rain from 10 to 20 August was only enough to maintain the soil moisture level at approximately 120% at 15 cm depth. Disease incidence increased further on this cultivar by 18 September even though there was little rainfall (<5 mm each day).

Soil moisture levels in the carrot plots in 1992 were high throughout June and July in both the non-irrigated and irrigated plots and reached a maximum in these plots on 4 August and 21 July, respectively. Cavity spot

incidence on all cultivars increased by 4 August in response to rainfall on 18 July and a concurrent peak in soil moisture. The soil moisture content in both plots decreased by 25 August to slightly below field capacity (265%). However, the incidence of cavity spot increased on some cultivars but decreased on others by 25 August. These changes were not consistently associated with cultivar or irrigation, although decreases occurred on Red Core Chantenay in both the non-irrigated and irrigated plot. Incidence decreased after 25 August on all cultivars despite a heavy rainfall on 27 August that increased the soil moisture content except at 15 cm depth in the irrigated plot.

A decrease in cavity spot in response to high soil moisture was unusual, but soil moisture levels were also unusually high in 1992. Perhaps the excessively high soil moisture inhibited the Pythium spp. which cause cavity spot. Alternatively, the several days of high moisture levels may have exhausted all of the inoculum within the root zone and inhibited root growth, such that the roots were not penetrating soil with a fresh supply of inoculum.

The measurement of soil moisture content using time delay reflectometry was non-destructive, rapid and efficient. Topp et al. (1984) report that calibrations were not needed for different soil types (although a calibration curve for muck soils did have to be established). The soil moisture content readings reflected expected changes in moisture content in response to rainfall and periods of dry weather. Time domain reflectometry appears to be an important tool for determining the moisture content of muck soils for the study of soil-borne plant diseases. The only drawback to this method is the initial cost. A portable TDR costs in excess of $10,000.00 (Tektronix, Barrie, ON).

A disease forecasting system based on rainfall rather than soil moisture measurements would be cheaper and easier to implement, since daily rainfall data is inexpensive to obtain with the use of funnel-type rain gauges. The moisture content of muck soil did increase in

conjunction with rainfall and decrease during periods of no rain, but it would be difficult to predict the relative increase or decrease from the rainfall data alone, without knowing the soil moisture content prior to the rainfall event. An exact determination of soil moisture may not be necessary to predict cavity spot, since an increase in incidence followed rains in 1991 that did not increase the moisture content to field capacity or saturation. Further studies are required to study the relationship between rainfall, soil moisture content and cavity spot incidence for the duration of the epidemic. Calculations of evapotranspiration in conjunction with rainfall data may provide a better estimate of soil moisture than rainfall data alone.

Soil temperature appeared to have little effect on cavity spot development under Ontario conditions, except in the eight weeks after seeding. Cavity spot developed over a range of temperatures (3-22°C) that were often below the optima for the individual Pythium species identified as causal agents of cavity spot (20°C and 35°C for Pythium sulcatum and P. aphanidermatum, respectively). However, Hancock (1977) in his study of P. ultimum, concluded that the optimal environmental conditions for P. ultimum were different in nature than in culture, and this probably holds true for other Pythium spp. There were no indications from the present study that 15°C was the optimum temperature for cavity spot development as reported by Montfort and Rouxel (1988) and Vivoda et al. (1991).

Low soil temperatures (16-17.5°C) in the six to eight weeks after seeding were associated with higher cavity spot incidence (AUDPC) than were high soil temperatures (20-22°C) during the same period. Soil moisture did not appear to be a limiting factor during this stage of disease development perhaps because moisture levels that are sufficient for seed germination and growth are also sufficient for germination and growth of Pythium propagules. There may also be more nutrients exuded from the rapidly growing seedling roots than from more mature roots later in the season. Generally, Pythium species such as P. ultimum and P.

irregulare cause more damping-off and root rot at low temperatures (Hendrix and Campbell 1973).

Decreases in cavity spot incidence may be as important as increases, especially if the decreases could be predicted. Decreases in disease incidence appear to be the result of wound healing, in the absence of new infections and when little or no rainfall occurs over a period of several days. Soil temperature was not associated with decreases in cavity spot incidence. Decreases occurred early in the season when soil temperatures preceding the decrease were over 20°C (i.e. Red Core Chantenay, 4-10 August, 1988) and late in the season when the average temperature was 3.8°C (i.e. Red Core Chantenay, 17 November to 8 December, in the non-irrigated plot in 1992). The conditions which lead to the decreases in incidence remain unclear. In 1992, the incidence on cv. Eagle grown in the non-irrigated plot decreased from 17 November to 8 December while the incidence on the same cultivar in the irrigated plot remained constant, even though the growing conditions were similar.

Garrod et al. (1982) studied the phenomenon of wound repair on carrot roots. The repair process involved structural changes such as lignification and suberization of surface cells as well as the accumulation of antifungal substances. They found that all cells in the surface layer became suberized within 12 and 48 hours at 25°C and 15°C, but little suberization occurred within 240 hours at 3.5°C. Lignification commenced later and reached a maximum in 168 hours at 25 and 15°C. Even though wound repair occurs more rapidly at warmer temperatures, mature carrot roots are capable of wound repair at temperatures approaching 0°C under moist conditions (Lewis and Garrod 1984).

Carrot roots increase in diameter through secondary growth. The periderm cells are sloughed off as the root grows. Over time, the dark linified cells of the superficial cavities may be sloughed off and replaced by unblemished periderm.

The present study demonstrated that cavity spot incidence after mid

October on later-seeded (younger) carrots was equal to or higher than that on earlier-seeded (older) carrots of the same cultivar. These results do not support those of Perry and Harrison (1979b) who found a higher incidence of cavity spot on five-month-old than on four or three-month-old carrots. Vivoda et al. (1991) also reported that five month-old carrots were more susceptible to cavity spot than younger carrots, but they found no differences in incidence among the carrots of different ages. Older carrots in their trial had a greater number of lesions per carrot, an assessment which was not done in the present study.

The results of the present study indicate that a forecasting system for cavity spot of carrot must include: information on the relative resistance of the carrot cultivar grown; soil temperatures in the eight weeks after seeding; and rainfall from seeding to mid-October with observations on the relative moisture content of the soil, particularly if the soil is at or near saturation for more than one or two days. Cavity spot incidence would be high during a season where soil temperatures were low early in the season, and there was heavy rainfall several times before mid-October, but no periods of two or more weeks of dry weather, or where the soils were very wet for several days. Delaying the seeding date in the spring so the soil will be warmer does not appear to be an effective method for avoiding cavity spot, since the incidence at harvest was the same or higher on the younger carrots. Delaying seeding also increases the risk of other production problems, including poor germination because of dry soils and burn-off of the seedlings in the heat.

CONCLUSIONS

The present study demonstrated that the incidence of cavity spot on carrots grown in organic soil in Ontario reached a maximum between 8 August and 31 October each year. The only exceptions were in 1990 on Cellobunch carrots seeded 9 July and Chancellor seeded 7 June and when cavity spot levels were very low (Six Pak and SR-481 carrots seeded on 21

June 1991). An increase in soil moisture content, as the result of rainfall or irrigation, was the environmental parameter most often associated with an increase in disease incidence. Further field and controlled-environment trials are needed to further elucidate the effects of soil temperature, rainfall and periodic soil saturation on the incidence and severity of cavity spot. A preliminary forecasting system for the disease was outlined.

Cultivar resistance was the most important factor affecting the maximum and final levels of cavity spot, although environmental factors had an effect on the pattern of disease development. Low soil temperatures (16-17.5°C) during the six to eight weeks after seeding were related to a higher AUDPC while specific increases in incidence followed within nine to thirty nine days of rainfall events greater than 20 mm when these occurred before 15 October. Decreases in cavity spot incidence followed periods of little (<5 mm) or no rainfall for a minimum of 13 days. Reductions in incidence may have been the result of wound healing in the absence of further infections. Increases and decreases in incidence occurred at soil temperatures ranging from 3.0 to 21.9°C.

The results of the present study suggest that cavity spot incidence will be high when a susceptible cultivar is grown and low soil temperatures in the first six to eight weeks after seeding are followed by several periodic rainfalls of over 20 mm before mid-October. To predict the disease incidence that will occur during a season, a better understanding is needed of the environmental factors that contribute to an increase and decrease in cavity spot. A measurement of the inoculum density in the field is also required.

Coakley (1988) indicated that a minimum of eight to twelve years of disease data collected from fields with a natural inoculum source were necessary to identify with certainty what the controlling climatic factors may be. Thus, the present study represents only half of the data required to identify the major environmental factors affecting cavity spot

development. Continued research is required.

A major disadvantage to the study of cavity spot is the inability to isolate P. violae from soil (except by using carrots as bait). An ability to determine the inoculum density in field plots would increase the scope and accuracy of the epidemiological studies and would increase the usefulness of the disease forecasting system, once it is fully developed. Perhaps the competition ELISA technique developed by Lyons and White (1992) for identifying Pythium violae and P. sulcatum will be available for detecting and quantifying Pythium spp. in soil samples by the time a predictive system for cavity spot is ready for field use.

CHAPTER 5

EVALUATION OF FUNGICIDES, PLANT GROWTH-PROMOTING RHIZOBACTERIA, AND CULTIVAR RESISTANCE FOR THE CONTROL OF CAVITY SPOT

INTRODUCTION

In the Holland-Bradford Marsh area of Ontario, cavity spot is one of the most serious diseases affecting carrots, and few measures are available to manage this disease. Growers are advised to avoid fields with a history of severe cavity spot, choose cultivars that have some resistance to the disease and to avoid over-fertilizing the fields (Ontario Ministry of Agriculture and Food 1992b). These measures often fail to provide satisfactory disease control. Growers normally avoid growing carrots in heavily-infested fields but this is sometimes not possible because of the need for crop rotation. Many of the cultivars reported to have partial resistance to cavity spot may develop unacceptable levels of cavity spot and research linking cavity spot to excesses of soil potassium or ammonium have failed to prove the relationship (Maynard et al. 1963, Scaife et al. 1980). Other potential management methods for cavity spot include the application of selective fungicides and biological control with plant growth-promoting rhizobacteria. In 1984, Lyshol et al. reported control of cavity spot by fungicides that were selective for fungi in the Class Oomycetes. Control of cavity spot by the acylalanide fungicide, metalaxyl, has been widely confirmed (Lyshol et al. 1984, White 1986, Sweet et al. 1989, Davis et al. 1991, Walker 1991). The acyl phosphonate fungicide, fosetyl-Al, has also been evaluated for cavity spot control (Gladders and Crompton 1984, Lyshol et al. 1984, Walker 1991). These fungicides reduce the incidence of cavity spot but the efficacy may vary from year to year or site to site (Davis et al. 1991, Sweet et al. 1989). Neither metalaxyl nor fosetyl-Al are currently registered in Canada for the control of cavity spot of carrot and trials to determine the most effective materials, rates and methods of application are required to support the application for Minor Use Registration and to ensure that recommendations for use are available

when the products become registered. Registration of selective fungicides for cavity spot control will increase the disease management options for carrot growers, but the general public is demanding a reduction in pesticide use, and alternative control methods are also needed. Biological control of cavity spot with plant growth-promoting rhizobacteria (PGPR) may be an effective alternative to fungicide application. A number of plant growth-promoting rhizobacteria have been identified that provide biological control of Pythium-incited diseases (Weller 1988). Most of these PGPR's are isolates of Pseudomonas putida or P. fluorescens (Kloepper et al. 1988). The potential of PGPR's for the control of cavity spot has not been investigated.

The use of resistant cultivars can be an effective and economical method of disease management. Partial resistance can be considered as a substitute for the bulk of fungicide use (Bruin and Edgington 1983). Considerable variation in carrot susceptibility to cavity spot has been found, but no cultivars are completely resistant (National Institute of Agricultural Botany 1991, McDonald et al. 1991). Cultivar resistance needs to be studied further to determine the levels of resistance in commercial cultivars and whether there are cultivar by fungicide interactions that would influence the effective rate of fungicide applications (Fry 1975).

The goal of the present study was to evaluate methods of managing cavity spot, including selective fungicides, PGPR's, and resistant cultivars, to provide the groundwork for integrated management strategies for the disease in carrots grown on organic soils in Ontario.

The objectives were to evaluate disease progress curves and levels of cavity spot on specific harvest dates:

a) to determine the most effective rate, timing and method of application of the selective fungicides metalaxyl and fosetyl-Al.

b) to evaluate selected PGPR's for the control of cavity spot and compare the efficacy of PGPR's to that of selective

fungicides.

c) to identify and characterize cultivar resistance to cavity spot in the field and in storage.

d) to determine whether there is an interaction between cultivar resistance and the efficacy of fungicides and PGPR's.

e) to test the hypothesis that older carrots were more susceptible to cavity spot by seeding carrots on different dates and assessing disease development.

f) to study the development of cavity spot in storage to determine whether cultivar resistance or fungicide treatment affect the storage phase of the disease.

Field trials were conducted over a period of six years to address these objectives. Portions of the results have been published (McDonald et al. 1987, McDonald and Edgington 1988, McDonald and Sutton 1992).

MATERIALS AND METHODS

Field trials were conducted yearly from 1986-1992, except 1989, with carrots seeded in organic soil at the Bradford Muck Research Station with a history of cavity spot.

Cultivars

Carrot cultivars used in the trials were Chantenay Comet (Nickerson Zwaan B.V., Gilroy, CA), Chanton, Red Core Chantenay, Chancellor, Cellobunch, XPH-3507 (Asgrow Seed Co., Newmarket, ON), SR-481 Huron and Six Pak. Seeding rates were previously outlined in Chapter 4. The specific cultivars used in the various trials are summarized in Table 12.

Field plots

All trials were conducted at the Muck Research Station. Fertilizer was applied each spring and incorporated prior to seeding in accordance

Table 12. Field trials to assess the effects of cultivar, seeding date, fungicide and plant growth-promoting rhizobacteria on cavity spot in 1986-1992.

Year	Cultivar	Seeding date	Treatment[1]	Application method	Rate kg ai/ha	Time of application (week after seeding)
1986	Chanton		metalaxyl	seed dressing	0.012	0
	Chantenay Comet	3 June	benalaxyl-thiram	seed dressing	0.002/0.004	0
	Six Pak[2]		metalaxyl	granular	0.2-4.0	0
			untreated check			
1987	Red Core	26 May	metalaxyl	seed dressing	0.012,0.06	0
	Chantenay		benalaxyl-thiram	seed dressing	0.002/0.004, 0.01/0.02, 0.02/0.1	0
			untreated check			
1987	Red Core	26 May	metalaxyl+mancozeb	drench	2.00	0,2,4,6,8
	Chantennay		metalaxyl+mancozeb	spray	1.2,3.6	12,17
			fosetyl-Al	spray	1.6,3.2,4.8	12,17
			phosphorous acid	spray	1.6,3.2,4.8	12,17
			untreated check			
1988	Red Core	2 June	metalaxyl+mancozeb	drench	2.0	0,2,4,6
	Chantenay		untreated check			
1988	Red Core	2 June	metalaxyl	seed dressing	0.06	0
	Chantenay		metalaxyl	drench	0.50	0
	Chanton		metalaxyl	seed furrow	0.50	0
	Six Pak		PGPR 1-102	seed treatment		0
			PGPR 31-12	seed treatment		0
			PGPR GR12-2	seed treatment		0
			untreated check			

.../ continued

Table 12. - continued

Year	Cultivar	Seeding date	Treatment	Application Method	Rate kg ai/ha	Time of application (week after seeding)
1990	Chancellor Cellobunch Six Pak	7 June, 9 July 7 June only				
1991	SR-481 Six Pak	9, 30 May 21 June, 12 July				
1992	Red Core Chantenay SR-481 or Huron Eagle Six Pak	22, 25 May	metalaxyl+mancozeb fosetyl-Al	drench drench	2.0 4.0	0 0

1 Formulations of metalaxyl were: seed dressing-Apron 35 SD (35% metalaxyl), spray and drench-Ridomil MZ 72WP (8% metalaxyl and 64% mancozeb) and granular seed furrow application-Subdue 5G (5% metalaxyl). The benalaxyl-thiram (5% benalaxyl and 10% thiram) is not available in a commercial formulation. Fosetyl-Al is formulated as Aliette (80% fosetyl-Al). The phosphorous acid was technical grade (95% pure, Fisher Scientific). The three PGPR's were Serratia proteamaculans isolate 1-102, Pseudomonas fluorescens isolate 31-12 and P. putida isolate GR12-2 and were obtained from Allelix Inc., Mississauga, Ontario (now Esso Ag Biologicals, Saskatoon, Saskatchewan).

2 Six Pak included as untreated check only.

with soil analyses (Ontario Ministry of Agriculture and Food 1992b, Appendix IV, Table 12). Carrots were seeded with a V-belt hand operated seeder, except in 1987, when pelleted seed of Red Core Chantenay was sown with a tractor-drawn Stan-Hay precision seeder. Recommended insecticides and herbicides were applied as needed (Ontario Ministry of Agriculture and Food 1992b). Fungicides were not applied, except those used as treatments. Plots in all trials were arranged in a randomized complete block design with four replications per treatment. Each replicate plot consisted of a single 6 m row (1986-88), or a single bed 1.7 by 6 m (1990-1992) with three or four rows of carrots per bed.

Carrot storage

Carrots selected for studies in storage were placed in clean plastic pots, one pot per replication and in mesh onion bags in 1990 and 1992, respectively. Carrots were placed in a pallet box in a temperature-controlled Filacell storage at 1.0°C $\pm$ 1.0°C and 90% $\pm$ 5% relative humidity.

Assessment of disease and yield

The emergence of carrots in field plots was rated by counting the number of carrots in the center one metre of row of each replication.

Ten adjacent carrots were sampled from each replicate plot of selected treatments at two to three week intervals during the cropping season. In 1986, four adjacent carrots of each replication were sampled and all were pooled for assessment. In 1988, three adjacent carrots per replication were harvested for assessment on the first four sampling dates (27 July - 8 Sept.), and ten adjacent carrots per replication were harvested and assessed on subsequent sampling dates. For all treatments, the center one or two metres of row, which had been excluded from destructive sampling during the season, was harvested in late fall. In 1986 and 1987, the center two metres of row of each replication were

harvested on 8 October and 2 November, respectively. In 1988, 1990, 1991 and 1992, one metre of row at the center of each replicate plot was harvested on 1 November, 31 October, 31 October and 9 November, respectively. Assessment of disease incidence and the cavity spot index was described in Chapter 3.

Area under the disease progress curve (AUDPC) was calculated using the midpoint rule for area estimation (Campbell et al. 1980). The sum of the average disease rating between two consecutive sample dates was divided by two and multiplied by the number of days that lapsed between the two sample dates. The AUDPC values for each sample period were summed to obtain the total AUDPC. The first sample date in the calculation was the date with a disease rating of zero which was just prior to a disease rating greater than zero. Area under the disease progress curve was calculated based on cavity spot index (area under cavity spot index curve or AUCSIC) and also disease incidence (area under disease incidence curve or AUDIC). Preliminary studies indicated that the AUDPC based on disease incidence provided a better indication of the effectiveness of the control measures. The AUDPC values refer to area under the disease incidence curve.

Fungicide treatments

Seed dressings

Fungicide seed dressings were applied to carrot seed in 1986, 1987 and 1988. Treatments were applied to ten gram aliquots of seed which were placed in plastic bags. Seed dressing was spread inside each bag above the seed, and the bag was closed and shaken by hand until seeds were uniformly covered (about five minutes). The seed was treated the day before seeding. Metalaxyl (Apron 35SD, Ciba-Geigy Canada Ltd., Mississauga, Ontario) was applied at a rate of 1 or 5 g per 100 g seed (0.012 and 0.06 kg ai/ha respectively) and benalaxyl + thiram was applied at a rate of 9, 45 or 90 ml/100 g seed (0.002, 0.01 or 0.2 kg ai/ha

benalaxyl plus 0.004, 0.02 or 0.1 kg ai/ha thiram, respectively). Five grams of Apron 35SD was the maximum amount that would adhere to 100 g of carrot seed.

Furrow, drench and spray applications

Several methods were used to apply the fungicides metalaxyl, metalaxyl plus mancozeb, fosetyl-Al and phosphorous acid to the carrot plots. The granular formulation of metalaxyl, Subdue 5G (5% metalaxyl, Ciba-Geigy Canada Ltd.) was applied in the seed furrow. Ridomil MZ 72WP (8% metalaxyl, 64% mancozeb, Ciba-Geigy Canada Ltd.) was applied as a drench in the equivalent of 2,000 L/ha of water (1987, 1988) or 1,000 L/ha (1992), in an 8 cm wide band over the seed row. Ridomil MZ 72WP, Aliette (80% fosetyl-Al, Rhone-Poulenc Canada Inc.) or phosphorous acid (technical grade, Fisher Scientific Canada, Don Mills, Ontario) were applied as foliar sprays in the equivalent of 550 L/ha of water with a single nozzle Unico 113u hand can sprayer. When applying the foliar sprays, plastic sheeting was erected on each side of a row to prevent spray drift onto adjacent rows.

Effect of irrigation on fungicide efficacy

To evaluate the effect of irrigation on cavity spot development and fungicide efficacy, two plots were established 100 m apart in 1992. The irrigated plot received 2.5 cm of water once a week from 11 June to 2 July and again on 16 July and 17 September. During the other weeks, natural rainfall was high and soil was near saturation.

Plant growth-promoting rhizobacteria

The plant growth-promoting rhizobacteria (PGPR) were as described in Chapter 3. Rifampicin-resistant isolates of the three PGPR were used to determine if the bacteria survived and colonized carrot roots. Suspensions of rifampicin-resistant isolates were received on 6 June, 1988

and carrot seed was inoculated and seeded as previously described (Chapter 3). Non-inoculated seed of each cultivar was also included. Cultivar Six Pak only received treatment with rifampicin resistant Pp-2, as there was not enough fungicide-free seed to conduct this test with all three PGPR. Carrot seedlings (five per treatment) treated with the rifampicin-resistant PGPR were harvested on 28 June, 26 days after seeding and washed in running tap water. The roots were placed individually in test tubes of 10 ml sterile water, shaken on a Vortex for ten seconds, a 1 ml aliquot from each tube was transferred to another test tube with 9 ml sterile water, shaken and 0.1 ml samples of the resulting suspensions were streaked onto selective media (Difco Ps.f. agar with 100 ppm rifampicin, 50 ppm benomyl (Benlate), and 50 ppm cycloheximide. Suspensions from seedlings treated with PGPR Pp-2 were plated on a similar medium without cycloheximide. Length of the tap root and major secondary roots of each seedling was measured. The number of bacterial colonies per plate was counted 48 hours after inoculation.

Cavity spot development in storage

In 1990, 15 carrots were selected from each replicate plot harvested on 16 November such that there were three carrots per severity class from one (widest cavity < 0.1 cm in vertical width) to five (widest cavity $\geq$ 1.0 cm). The total number of lesions in each size category was also recorded. Carrots were placed in storage 19 November 1990, and were removed from storage on 17 April 1991 when they were again rated for number and size of lesions.

On 9 November 1992, 20 carrots were harvested from each replicate plot of the check and metalaxyl treatments of Six Pak and Red Core Chantenay. The number of cavities per carrot in each severity class was recorded. The carrots were placed in storage and cavities were rated again on 15 January and 7 June 1993. Disease severity, mean number of cavities per carrot and mean number of large (severity class four and

five) lesions per carrot were calculated.

Statistical analysis

One-way analysis of variance (ANOVA), analysis of covariance, and simple linear regression analyses were performed using the PARASTAT program written by Terry James, Department of Environmental Biology, University of Guelph. N-way analysis of variance was performed using SAS, Version 6.03. Mean separations for simple and main effects of factors were performed using Duncan's New Multiple Range Test on SAS. Where there were no interactions and main effects were examined, LSD values were calculated for the simple effects to allow comparisons between adjacent means. Linear and polynomial regression analyses were run using Statview (Abacus Concepts, Berkley, CA) on a MacIntosh 2E. Transformations based on growth models were used to linearize the data. Means were transformed and plotted against time using the following formulas: monomolecular or simple interest $\ln\{1/(1-y)\}$, polycyclic, compound interest or logistic $\ln\{y/(1-y)\}$, logarithmic or exponential $\ln(y)$, and Gompertz - $\ln[-\ln(y)]$, where y=proportion of infected plants (Campbell and Madden 1990). Calculations and regression analyses were done using the Epimodel program developed by Nutter and Worawitilikit (1990) with the highest observed disease intensity used as the maximum value, as recommended by Neher and Campbell (1992). The slopes and elevations of disease progress curves were compared using analysis of covariance (Wright and Sutton 1990) run on Parastat.

Mean separations were performed using Duncan's New Multiple Range Test or a Protected Least Significant Difference Test (Protected LSD). If there were missing data points in any of the data sets, the analysis was done on SAS, using the PROC GLM (General Linear Models) procedure. Non parametric statistics (Wilcoxon Signed Rank Test) were performed on the 1990/91 data on cavity spot development in storage because the carrots were selected such that there were three carrots in each severity class,

thus the distribution was not normal nor the sample randomly selected.

RESULTS

Efficacy of fungicides

Seed dressings

In 1986 and 1988, the effects of fungicide seed dressings on emergence of carrots, harvest weight and cavity spot index were analyzed as a factorial experiment with two factors, cultivar and treatment. The simple effects for 1986 are presented in Table 13a, and those for 1988, in Tables 15a and 16. There were no interactions (Appendix IV Tables 13, 15, 16) so main effects of significant factors were examined (Tables 13b, 15b for 1986 and 1988, respectively). In 1987, the effects of different rates of fungicide seed dressings were analyzed as a two-factorial experiment. Simple effects are presented in Table 14a. There was no interaction (Appendix IV Table 14) so the main effects of rate were examined (Table 14b).

In 1986, the benalaxyl plus thiram seed dressing significantly (P=0.05) reduced the cavity spot index on Chanton, but not on Comet while metalaxyl failed to suppress cavity spot on either cultivar (Table 13a). The seed dressings did not affect seedling emergence or harvest weight.

In 1987, metalaxyl and benalaxyl plus thiram at five times the recommended rate reduced the cavity spot index (Table 14b). Seed dressings applied at the recommended rate (1 g and 9 ml/100 g seed for metalaxyl and benalaxyl plus thiram, respectively) were ineffective. In 1988, (Table 15a) a metalaxyl seed dressing at the rate of 5 g product per 100 g seed did not significantly affect emergence, cavity spot index, disease incidence or weight at harvest (Table 16).

Furrow (granular) treatments

Several rates of metalaxyl applied as furrow granular treatments were evaluated for effects on emergence of carrots, harvest weight and cavity

Table 13a. Effect of seed dressing and granular metalaxyl on emergence, yield and cavity spot index of carrot cv.'s Chanton and Comet in 1986.

Treatment	Product[2]	Rate (kg ai/ha)	Emergence (carrots/m)		Harvest weight (kg/m)		Cavity spot index (0-100)	
			Chanton	Comet	Chanton	Comet	Chanton	Comet
Check	Check		24 abc[1]	30 ab	4.0	3.0	56.1 a	27.5 b
Seed Dressing	Apron 35SD	0.012	19 b-e	28 abc	3.6	3.4	57.0 a	15.9 bcd
	Benalaxyl+ thiram	0.002 0.004	17 b-e	37 a			21.4 bc	21.1 bc
Granular	Subdue 5G	0.2	24 abc	27 a-d	4.5	3.4	22.0 bc	9.6 cd
		0.5	26 abc	27 a-d	4.4	3.6	24.9 bc	13.4 bcd
		1.0	21 bcd	15 cde	4.5	2.8	18.5 bcd	12.2 bcd
		2.0	21 bcd	15 cde	3.8	2.1	21.1 bc	12.5 bcd
		4.0	14 de	6 e	2.8	1.3	22.7 bc	3.2 d
LSD (P=0.05)					0.84	0.84		

1 Values in a group followed by the same letter are not significantly different at P=0.05, Duncan's New Multiple Range Test.

2 Apron 35 SD (35% metalaxyl), Subdue 5G, (5% metalaxyl), benalaxyl plus thiram (5% benalaxyl plus 10% thiram).

Table 13b. Main effects of seed dressings and granular metalaxyl on harvest weight of carrot cv.'s Chanton and Comet

Fungicide	Rate (kg ai/ha)	N[1]	Weight (kg/m)
Check		8	7.4 a[2]
Apron 35 SD	0.012	8	4.9 bc
Subdue 5G	0.2	8	7.9 a
	0.5	8	7.9 a
	1.0	8	7.3 a
	2.0	8	5.9 b
	4.0	8	4.0 c

1 Number of replication per mean.

2 Values in a column followed by the same letter are not significantly different at P=0.05, Duncan's New Multiple Range Test.

Table 14a. Evaluation of fungicide seed dressings for the control of cavity spot in 1987.

Seed dressings Product	Rate per 100g seed (X recommended rate)	Rate kg ai/ha	Cavity spot index[1] (0-100)
Check	-	-	18.4 a[2]
Apron 35 SD[3]	1 g (1x)	0.012	17.4 ab
Apron 35 SD	5 g (5x)	0.06	10.5 b
Benalaxyl + thiram	9 ml (1x)	0.002 0.004	18.8 a
Benalaxyl + thiram	45 ml (5x)	0.01 0.02	12.7 ab
Benalaxyl + thiram	90 ml (10x)	0.02 0.04	18.2 a
LSD (P=0.05)			7.2

1 Cavity spot index assessed at harvest on 2 November.

2 Values in a column followed by the same letter are not significantly different at P=0.05, Protected LSD Test.

3 Apron 35 SD (35% metalaxyl)

Table 14b. Main effects of rate of fungicide seed dressings for the control of cavity spot in 1987.

Rate of fungicide	N[1]	Cavity spot index (0-100)
0	4	18.4 a
1x	8	18.1 a
5x	8	11.6 b
10x	4	18.1 a

1 Number of replications per mean.

2 Values in a column followed by the same letter are not significantly different at P=0.05, Duncan's New Multiple Range Test.

Table 15a. Evaluation of cultivar and formulations of metalaxyl, metalaxyl plus mancozeb and of plant growth-promoting rhizobacteria (PGPR) on carrot emergence and cavity spot index and incidence at harvest in 1988.

Cultivar	Fungicide formulation[1] and rate (kg ai/ha)	PGPR[2] (5.0×10^7 cfu/10 g seed)	Emergence[3] (carrots/m)	Cavity spot	
				Index (0-100)	Incidence (%)
Six Pak	Check		87.0	13.0 a[4]	48 abc
	Seed dressing (0.06)		59.0	14.0 a	52 a
	Drench (0.5)		68.2	9.5 a	30 cd
	Granular (0.5)		70.5	12.0 a	26 d
		Sp-102	80.0	12.0 a	50 a
		Pf-12	77.0	14.5 a	44 abcd
		Pp-2	77.5	12.0 a	44 abcd
Chanton	Check		27.8	30.0 ab	80 ab
	Seed dressing (0.6)		19.5	28.0 abc	78 ab
	Drench (0.5)		21.5	20.0 bc	70 abc
	Granular (0.5)		26.5	18.0 c	55 c
		Sp-102	25.5	22.0 bc	68 abc
		Pf-12	27.5	38.0 a	86 a
		Pp-2	22.0	24.0 bc	70 abc
Red Core Chantenay	Check		30.8	30.0 ab	71 a
	Seed dressing (0.6)		36.2	19.0 bcd	61 ab
	Drench (0.5)		35.0	16.0 cd	52 b
	Granular (0.5)		29.0	17.0 d	32 c
		Sp-102	36.5	32.0 a	86 a
		Pf-12	40.2	28.0 ab	66 ab
		Pp-2	30.0	26.0 abc	73 a
LSD P=0.05			N.S.	11.2	20.7

.../ continued

Table 15a. - continued

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1 Seed dressing was Apron 35 SD (35% metalaxyl), drench was Ridomil MZ (8% metalaxyl plus 64% mancozeb) and granular was Subdue 5G (5% metalaxyl). Carrots harvested on 1 November, 1988 (152 days after seeding).

2 Plant growth-promoting rhizobacteria (PGPR Sp-102, Pf-12 and Pp-2 were isolate 1-102 of Serratia proteamaculans, isolate 31-12 of Pseudomonas fluorescens and isolate GR12-2 of P. putida, respectively, obtained from Allelix Inc.

3 Emergence was rated on 29 June, 27 days after seeding. Seeding rates for Six Pak, Chanton and Red Core were 112, 50 and 48 seeds/m, respectively.

4 Values for a cultivar in a column followed by the same letter are not significantly different at P=0.05, Protected LSD Test.

Table 15b. Main effects of formulations of metalaxyl, metalaxyl plus mancozeb and of plant growth-promoting rhizobacteria on cavity spot index and incidence on 1 November, 1988.

Fungicide formulation[1] and rate (kg ai/ha)	PGPR[2] (5.0×10^7 cfu/10g seed)	N[3]	Cavity spot index (0-100)	Cavity spot incidence (%)
Check		12	24.5 ab[4]	66.2 a
Seed dressing (0.06)		12	18.2 bc	59.0 ab
Drench (0.5)		12	15.5 c	50.9 ab
Granular (0.5)		12	15.8 c	38.3 c
	Sp-102	12	22.0 abc	69.5 a
	Pf-12	12	26.8 a	65.4 a
	Pp-2	12	20.7 abc	62.3 ab

1 Metalaxyl dressing was Apron 35 SD (35% metalaxyl), drench was Ridomil MZ (8% metalaxyl plus 64% mancozeb) and granular was Subdue 5G (5% metalaxyl). Carrots harvested on 1 November, 1988 (152 days after seeding).

2 Plant growth-promoting rhizobacteria (PGPR Sp-102, Pf-12 and Pp-2 were isolate 1-102 of Serratia proteamaculans, isolate 31-12 of Pseudomonas fluorescens and isolate GR12-2 of P. putida, respectively.

3 Number of replications per mean.

4 Values in a column followed by the same letter are not signifiantly different at P=0.05, Duncan's New Multiple Range Test.

Table 15c. Main effects of cultivar on cavity spot index and incidence on 1 November, 1988.

Cultivar	N[1]	Cavity spot index (0-100)	Cavity spot incidence (%)
Six Pak	28	12.4 b[2]	42.1 c
Chanton	28	26.0 a	72.3 a
Red Core Chantenay	28	23.2 a	61.1 b
LSD P=0.05		4.22	7.8

1 Number of replications per mean.

2 Values in a column followed by the same letter are not significantly different at P=0.05, Duncan's New Multiple Range Test.

Table 16. Effect of metalaxyl and metalaxyl plus mancozeb treatments and plant growth-promoting rhizobacteria on carrot yield, carrot weight and number of carrots/m at harvest in 1988.

Cultivar	Fungicide[1] formulation and rate (kg ai/ha)	PGPR[2] (5.0×10^7 cfu/10g seed)	Yield/m[3] of row (kg)	Mean weight/ carrot(g)	Mean number of carrots/m
Six Pak	Check		4.12[4]	54	80
	Seed dressing(0.06)		3.72	66	67
	Drench (0.50)		4.26	58	74
	Granular (0.50)		3.80	52	76
		Sp-102	4.02	56	72
		Pf-12	4.18	65	66
		Pp-2	3.34	57	63
Chanton	Check		3.46	248	16
	Seed dressing(0.06)		3.47	224	16
	Drench (0.50)		3.94	232	18
	Granular (0.50)		4.24	197	22
		Sp-102	3.64	170	22
		Pf-12	3.77	249	16
		Pp-2	3.54	180	20
Red Core Chantenay	Check		3.78	134	30
	Seed dressing(0.06)		4.30	136	32
	Drench (0.50)		3.82	135	28
	Granular (0.50)		4.17	112	38
		Sp-102	3.80	162	26
		Pf-12	3.70	108	30
		Pp-2	3.36	165	22

1 Seed dressing was Apron 35 SD (35% metalaxyl), drench was Ridomil MZ 72WP (8% metalaxyl plus 64% mancozeb, 0.50 kg ai/ha metalaxyl plus 4.0 kg ai/ha) applied in an 8 cm band over the seed row immediately after seeding. Granular application was Subdue 35 SD (35% metalaxyl) applied in the seed furrow.

2 Plant growth-promoting rhizobacteria (PGPR) Sp-102, Pf-12 and Pp-2 were isolate 1-102 of *Serratia proteamaculans* isolate 31-12 of *Pseudomonas fluorescens* and isolate GR12-2 of *P. putida*.

3 Carrots harvested on 1 November, 152 days after seeding.

4 There were no significant differences (P=0.05) among treatments for any of the cultivars.

spot index in 1986, as part of the two-factor factorial experiment described for the seed dressings above. The simple effects and main effects on harvest weight are presented in Tables 13a and b, respectively. Because several rates were used, the relationship between rates and the dependent variables emergence, harvest weight and cavity spot index was examined using simple linear regression, as was the association between cavity spot index and harvest weight (Appendix IV Table 13).

Granular applications of metalaxyl at rates of 0.2 to 4.0 kg ai/ha significantly reduced the cavity spot index on cv. Chanton, but only rates of 0.2, 2.0 and 4.0 reduced cavity spot on cv. Comet (Table 13). Increasing rates of metalaxyl were associated with decreasing emergence (r^2=0.17 and 0.53 for Chanton and Comet, respectively), decreasing harvest weight (r^2=0.29 and 0.63 for Chanton and Comet, respectively), and decreasing cavity spot index r^2=0.22 and 0.30 for Chanton and Comet, respectively). The cavity spot index was not related to harvest weight r^2=0.01) but harvest weight was associated with emergence r^2=0.35, Appendix IV Table 13). The decrease in emergence and harvest weight with increasing rates of metalaxyl indicated that Subdue 5G was phytotoxic to carrots, especially at rates of 2.0 and 4.0 kg ai/ha. Emergence and yield of Comet was reduced more by high rates of metalaxyl than was emergence and yield of Chanton (r^2=0.17, 0.53, 0.29 and 0.63, respectively Appendix IV Table 13).

In 1988, the effects of the granular formulation of metalaxyl were examined as part of the two-factor factorial experiment described for the seed dressings above. Granular metalaxyl applied at 0.5 kg/ha did not affect seedling emergence, but reduced cavity spot index on cv.'s Chanton and Red Core Chantenay and disease incidence on all three cultivars (Table 15a). There were no significant interactions between cultivar and treatment for either cavity spot index or incidence (P=0.0864 and 0.0692, respectively, Appendix IV Table 15). Analysis of main effects showed that the granular treatment significantly reduced both cavity spot index and

incidence, compared to the untreated check (Table 15b). The 0.5 kg ai/ha rate did not affect seedling emergence (Table 15a) or yield, mean weight/carrot or mean number of carrots (Table 16).

Drench applications

In the 1988 trial, analysis of main effects of metalaxyl formulation on cavity spot index and incidence demonstrated that the drench application of metalaxyl plus mancozeb at 0.5 kg ai/ha was as effective as the same rate of granular metalaxyl in reducing cavity spot index but did not reduce the incidence of cavity spot compared to the untreated check (Table 15b).

In 1992, the effects of drench applications of metalaxyl plus mancozeb and fosetyl-Al on cavity spot were analyzed as a factorial experiment with two factors, fungicide and cultivar. Cavity spot was assessed as index, incidence, AUCSIC and AUDIC. Simple effects are presented in Table 17a. There were no interactions when cavity spot was assessed as index, AUCSIC or incidence so the main effects of the factors were examined (Tables 17b, c, d, respectively). There was a cultivar by fungicide interaction for AUCSIC (P=0.0426, Appendix IV Table 17) and simple effects were examined (Table 17a).

Metalaxyl plus mancozeb drench treatments suppressed cavity spot index (Table 17b), AUCSIC (Table 17c), and disease incidence (Table 17d). Area under the disease incidence curve was also suppressed on all cultivars except Six Pak (Table 17a). The fosetyl-Al drench application was ineffective (Tables 17a-d). Cavity spot index, AUCSIC, incidence, and AUDIC at harvest were lower on Six Pak then Huron (Tables (17a-d).

Effects of plant-growth promoting rhizobacteria (PGPR)

The effects of PGPR's on cavity spot levels was evaluated in 1988 as part of the two-factor factorial experiment that included several formulations of metalaxyl as discussed above. There were no interactions

Table 17a. Effect of cultivar and metalaxyl plus mancozeb or fosetyl-Al treatment on cavity spot on carrots grown in a non-irrigated plot in 1992.

Cultivar	Fungicide[1]	Rate (kg ai/ha)	Cavity spot rating: Cavity spot[2] index (0-100)	AUCSIC[3] (index days)	Incidence (%)	AUDIC[4] (incidence days)	
Six Pak	Check		9.5	767.2	17.5	1485.0	def
	Metalaxyl	2.0	8.0	582.8	13.2	1080.4	ef
	Fosetyl-Al	4.0	1.5	518.3	2.5	984.8	ef
Red Core Chantenay	Check		21.6	1790.0	35.0	3383.8	abc
	Metalaxyl	2.0	0	357.0	0	525.0	f
	Fosetyl-Al	4.0	13.0	1584.2	26.2	3274.0	abc
Eagle	Check		12.0	1764.8	20.0	2908.5	bcd
	Metalaxyl	2.0	3.5	297.8	5.0	678.8	ef
	Fosetyl-Al	4.0	17.3	2023.0	27.2	3541.0	ab
Huron	Check		29.4	2562.0	48.8	4745.0	a
	Metalaxyl	2.0	9.3	994.2	15.5	2060.0	cd
	Fosetyl-Al	4.0	23.8	1682.0	40.5	3108.0	bc
LSD (P=0.05)			16.8	861.5	17.5	1521.1	

1 Metalaxyl plus mancozeb treatment was Ridomil MZ 72WP (8% metalaxyl plus 64% mancozeb), fosetyl-Al treatment was Aliette (80% fosetyl-Al). Both were applied as a drench in an 8 cm band over the seed row immediately after seeding.

2 Cavity spot index and incidence were rated on 8 December, 1992, 184 days after seeding.

3 AUCSIC - area under the cavity spot index curve.

4 AUDIC - area under disease incidence curve.

5 Values in a column followed by the same letter are not significantly different at P=0.05, Protected LSD Test.

Table 17b. Main effects of cultivar and fungicide on cavity spot index in non-irrigated carrots in 1992.

Cultivar	N[1]	Cavity spot index (0-100)	Fungicide	N	Cavity spot index (0-100)
Huron	12	20.8 a[2]	Check	16	18.1 a
Red Core Chantenay	12	11.5 ab	Fosetyl-Al	16	13.9 a
Eagle	12	10.9 ab	Metalaxyl	16	5.2 b
Six Pak	12	6.4 b			

1 Number of replications per mean.

2 Values in a column followed by the same letter are not significantly different at P=0.05, Duncan's New Multiple Range Test.

Table 17c. Main effects of cultivar and fungicide on area under the cavity spot index curve in non-irrigated carrots in 1992.

Cultivar	N[1]	Mean AUCSIC	Fungicide	N	Mean AUCSIC
Huron	12	1746.2 a[2]	Check	16	1721.1 a
Eagle	12	1361.8 ab	Fosetyl-Al	16	1450.8 a
Red Core Chantenay	12	1242.2 ab	Metalaxyl	16	557.9 b
Six Pak	12	622.8 c			

1 Number of replications per mean.

2 Values in a column followed by the same letter are not significantly different at P=0.05, Duncan's New Multiple Range Test.

Table 17d. Main effects of cultivar and fungicide on cavity spot incidence in non-irrigated carrots in 1992.

Cultivar	N[1]	Incidence (%)
Huron	12	34.9 a[2]
Red Core Chantenay	12	20.4 b
Eagle	12	17.4 b
Six Pak	12	11.1 b

Fungicide	N	Incidence (%)
Check	16	30.3 a
Fosetyl-Al	16	24.1 a
Metalaxyl	16	8.4 b

1 Number of replications per mean.

2 Values in a column followed by the same letter are not significantly different at P=0.05, Duncan's New Multiple Range Test.

when cavity spot was assessed as index or incidence (P=0.0864 and 0.0692, respectively, Appendix IV Table 15), so main effects were examined (Table 15b). Treatment of carrots with PGPR's did not suppress cavity spot incidence or index on carrots harvested on 1 November, 1988 (Table 15b).

These assessments were based on carrots harvested from a 2 m length of row on a single harvest date (1 November, 1988). Assessments based on area under the disease progress curve revealed more significant effects of metalaxyl and the PGPR treatments over the entire development of the epidemic (Table 18a). When cavity spot was assessed as area under the cavity spot index curve, analysis of main effects demonstrated that Pp-2 significantly suppressed cavity spot compared to the untreated check and the effect was equivalent to that of the metalaxyl plus mancozeb drench treatment (Table 18b).

Analysis of the AUDIC's revealed a significant cultivar by treatment interaction (Appendix II Table 18). The PGPR treatments Sp-102 and Pp-2 were effective on Chanton but not on Six Pak or Red Core Chantenay.

Recovery of rifampicin-resistant PGPR

Rifampicin-resistant bacteria were not found on roots of untreated carrot seedlings, but were isolated from all samples of the seedlings grown from bacterized seed, with the exception of Red Core Chantenay treated with Pp-2. The wrong selective medium was used for this treatment. Levels of recovery were low, ranging from 2.02-0.22 x 10^3 cfu/cm root. This study was not replicated, therefore no statistics were performed on the data.

Timing of fungicide applications

The efficacy of drench applications of metalaxyl plus mancozeb applied at different times after seeding was analyzed as one factor of a three-factor factorial experiment in 1987 and as a single factor experiment in 1988 (Appendix IV Table 19). No interactions were

Table 18a. Effect of cultivar and metalaxyl plus mancozeb application and plant growth-promoting rhizobacteria on area under the disease progress curve of 3 carrot cultivars in 1988.

Cultivar Incidence	Treatments: Metalaxyl+ mancozeb 2.0 (kg ai/ha)	Treatments: PGPR[1] (5.0×10^7 cfu/10 g seed)	Area under disease progress curve: Cavity spot index (index days)	Area under disease progress curve: Incidence (incidence days)
Six Pak	Check		1053	3780 cf[3]
	Drench[2]		564	2006 g
		Sp-102	986	2818 efg
		Pf-12	711	2733 efg
		Pp-2	619	2438 efg
Chanton	Check		2793	7638 a
	Drench		1943	6078 abc
		Sp-102	2022	4571 cd
		Pf-12	2290	6280 ab
		Pp-2	1393	4026 cde
Red Core Chantenay	Check		1830	4881 bcd
	Drench		1156	3656 def
		Sp-102	1981	5156 bcd
		Pf-12	1612	4492 cd
		Pp-2	1559	4538 cd
LSD (P=0.05)			687.8	1497.2

1 Plant growth-promoting rhizobacteria (PGPR): SP-102 was isolate 1-102 of Serratia proteamaculans, Pf-12 was isolate 31-12 of Pseudomonas fluorescens and Pp-2 was isolate GR12-2 to P. putida.

2 Drench application was Ridomil MZ 72WP (8% metalaxyl plus 64% mancozeb) applied in an 8 cm band over the seed row immediately after seeding.

3 Values followed by the same letter are not significantly different at P=0.05, Duncan's New Multiple Range Test.

Table 18b. Main effects of metalaxyl plus mancozeb, plant growth-promoting rhizobacteria and cultivar on area under the cavity spot index curve (AUCSIC) in 1988.

Treatment	N[1]	Mean AUCSIC
Check	12	1892 a[2]
Sp-102	12	1663 a
Pf-12	12	1538 ab
Pp-2	12	1191 b
Metalaxyl+ mancozeb	12	1221 b

Cultivar	N	Mean AUCSIC
Chanton	20	2089 a
Red Core Chantenay	20	1628 b
Six Pak	20	786 c

1 Number of replications per mean.

2 Values in a column followed by the same letter are not significantly different P=0.05, Duncan's New Multiple Range Test.

identified by the analysis of the 1987 data. Effects of the timing of the fungicide application are presented in Table 19. Because there were several levels of the factor time, the association between time of application and cavity spot incidence was examined with simple linear regression. (Appendix IV Table 19).

Drench applications of metalaxyl plus mancozeb (2.0 kg plus 7.0 ai/ha) applied zero, two, four, six or eight weeks after seeding in 1987 and zero, two, four or six weeks after seeding in 1988 significantly reduced the cavity spot index and incidence compared to the untreated check (Table 19). No cavity spot lesions were visible on carrots sampled at the time of fungicide application eight weeks after seeding (Figure 6). In 1988, a drench of 2.0 kg ai/ha metalaxyl plus mancozeb was equally effective when applied zero, two, four, or six weeks after seeding (Table 19). Incidence was not correlated to time of fungicide application in either year (r^2=0.15 P=0.0863, r^2=0.1 P=0.6700 for 1987 and 1988, respectively, Appendix IV Table 19).

All treatments suppressed cavity spot compared to the untreated check (Table 20b). The metalaxyl drench applied zero to eight weeks after seeding, was more effective than spray applications of metalaxyl, fosetyl-Al or phosphorous acid (Table 20b). Fungicides applied as sprays provided similar levels of control. Three-fold increases in application rates of the fungicide did not further suppress cavity spot (Table 20c).

Metalaxyl drenches applied zero to six weeks after seeding were more effective in reducing cavity spot than were foliar sprays applied 12 or 17 weeks after seeding (Table 20d). A drench application eight weeks after seeding reduced cavity spot as effectively as fungicide sprays applied 12 weeks after seeding. However, the incidence of cavity spot on carrots sprayed 12 weeks after seeding was higher than that on carrots that received the metalaxyl drench.

In 1987, the effects of foliar applications of metalaxyl plus mancozeb, fosetyl-Al and phosphorous acid applied at 12 and 17 weeks after

Table 19. Timing of drench applications of metalaxyl plus mancozeb on the control of cavity spot on cv. Red Core Chantenay in 1987 and 1988.

Metalaxyl[1] + mancozeb (kg ai/ha)	Time of application (week after seeding)	Cavity Spot incidence (%)	
		1987[2]	1988
-	-	66 a[3]	71 a
2.0	0	14 c	44 b
2.0	2	24 bc	38 b
2.0	4	14 c	48 a
2.0	6	22 bc	34 b
2.0	8	32 b	-

1 Metalaxyl plus mancozeb (Ridomil MZ 72WP, 8% metalaxyl plus 64% mancozeb, 0.5 and 2.0 kg ai/ha metalaxyl plus 4.0 and 16.0 kg ai/ha mancozeb) applied as a drench in an 8 cm band over the seed row.

2 In 1987 and 1988 carrots were harvested on 1 November and 2 November, 160 and 152 days after seeding, respectively.

3 Values in a column followed by the same letter are not significantly different at P=0.05, Duncan's New Multiple Range Test.

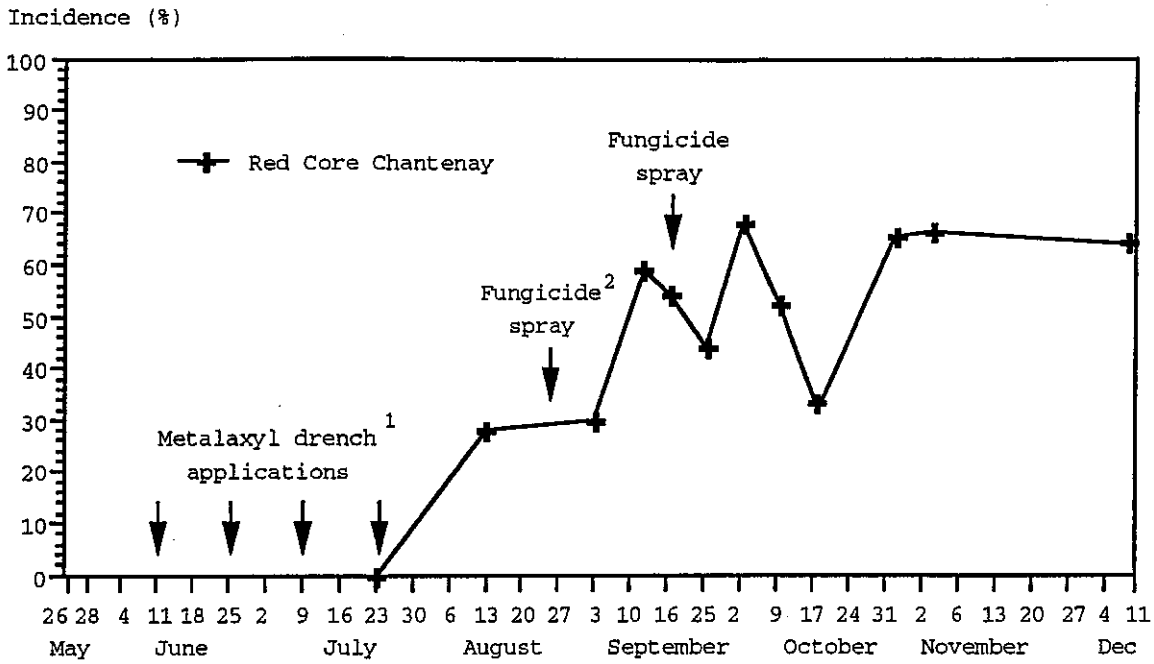


Figure 6. Cavity spot development on untreated Red Core Chantenay in relation to fungicide applications in 1987.

1 Metalaxyl drench was Ridomil mz 72 WPC (16% metalaxyl plus 56% mancozeb) applied at 2.0 kg ai/ha (drench).

2 Fungicide sprays were: Metalaxyl (Ridomil mz 72wp, 16% metalaxyl plus 56% mancozeb) applied at 1.2 or 3.6 kg metalaxyl plus 4.2 or 11.2 kg ai/ha; fosetyl-Al (Aliette, 80% fosetyl-Al) 1.6, 3.2 and 4.8 kg ai/ha; phosphorous acid (95% technical grade) 1.6, 3.2 and 4.8 kg/ha.
Carrots seeded 26 May.

Table 20a. Evaluation of fungicides, rates and time of application for the control of cavity spot on carrot cv. Red Core Chantenay in 1987.

Fungicide[1]	Rate (kg ai/ha)	Application[2] Method	Time of application (wk after seeding)	Cavity spot incidence (%)
Check	-	-	-	66
Ridomil MZ	2.0	Drench	0	14
	"	"	2	24
	"	"	4	14
	"	"	6	22
	"	"	8	32
Aliette	1.6	Spray	12	46
	"	"	17	52
Aliette	3.2	"	12	40
	"	"	17	46
Aliette	4.8	"	12	44
	"	"	17	54
Phosphorous Acid	1.6	"	12	46
	"	"	17	44
Phosphorous Acid	3.2	"	12	39
	"	"	17	41
Phosphorous Acid	4.8	"	12	42
	"	"	17	52
Ridomil MZ	1.2	"	12	44
	"	"	17	44
Ridomil MZ	3.6	"	12	36
	"	"	17	44
LSD(P=0.05)				10.8

1 Ridomil MZ 72WP contains 8% metalaxyl plus 64% mancozeb rates of 2.0, 1.2 and 3.6 kg ai/ha metalaxyl include 16.0, 9.6 and 28.8 kg ai/ha mancozeb, respectively. Aliette contains 80% fosetyl-Al. The phosphorous acid was technical grade, 95% phosphorous acid.

2 Drench applications were applied in an 8 cm band over the seed row. Spray applications were applied with a single nozzle sprayer.

Table 20b. Main effects of fungicides on control of cavity spot on Red Core Chantenay in 1987.

Treatment	Method of application	N[1]	Disease incidence (%)
Check		4	66.0 a[2]
Fosetyl-Al	spray	24	47.0 b
Phosphorous acid	spray	24	44.2 b
Metalaxyl + Mancozeb	spray	16	42.2 b
Metalaxyl + Mancozeb	drench	20	21.3 c

1 Number of replications per mean.

2 Values in a column are not significantly different at P=0.05, Duncan's Multiple Range Test.

Table 20c. Main effects of 3 rates of fungicide spray applications on control of cavity spot on Red Core Chantenay in 1987.

Fungicide rate (X recommended rate)	N[1]	Disease incidence (%)
0	4	66.0 a[2]
1X	24	45.6 b
2X	16	45.8 b
3X	24	46.0 b

1 Number of replications per mean.

2 Values in a column followed by the same letter are not significantly different at P=0.05, Duncan's New Multiple Range Test.

Table 20d. Main effects of time of fungicide application on control of cavity spot on Red Core Chantenay in 1987.

Time of fungicide application (week after seeding)	N[1]	Disease incidence (%)
No application	4	66.0 a[2]
0	4	14.8 d
2	4	24.0 cd
4	4	14.5 d
6	4	21.8 cd
8	4	31.5 c
12	32	42.3 b
17	32	47.3 b

1 Number of replications per mean.

2 Value in a column followed by the same letter are not significantly different at P=0.05, Duncan's New Multiple Range Test.

seeding on disease incidence were compared to the variously timed drench applications of metalaxyl plus mancozeb. This was a three-factor factorial experiment. Simple effects are presented in Table 20a. There were no two or three factor interactions (Appendix IV Table 20) so main effects of the factors were examined (Tables 20b, c, d). No cavities were apparent on carrots sampled on 23 July, eight weeks after seeding (Figure 6). At the time the first fungicide sprays were applied on 21 August, 12 weeks after seeding, the cavity spot index was approximately 6.6%, and the disease incidence was about 29%. On 22 September, 17 weeks after seeding, when the second fungicide sprays were applied, the disease index was approximately 16.5% and incidence was 47.3%, based on interpolation from the disease progress curve (Figure 2).

The carrot foliage was examined for necrosis or other signs of phytotoxicity following the foliar fungicide applications. The high (3X) rates of metalaxyl and fosetyl-Al left visible residues on the leaves, but no phytotoxicity was observed following any of the treatments.

Effect of cultivar, fungicide and irrigation on progress curves of cavity spot

Six Pak and Chanton - 1986

In 1986, in the susceptible cultivar Chanton, cavity spot was first observed in mid August, remained at about the same level for a month and increased again in September. Cavity spot incidence was consistently lower in Six Pak (Figure 7). At harvest, incidence of Six Pak carrots with cavities was 50% of that for Chanton (Table 21). The AUDPC for Six Pak was approximately 17% than that of Chanton.

Red Core Chantenay in 1987

In 1987, cavities were first apparent in mid-August on Red Core Chantenay. Cavity spot increased rapidly to 11 September, then remained relatively constant throughout the season, with occasional decreases in incidence occurring (Table 22 and Figure 6).

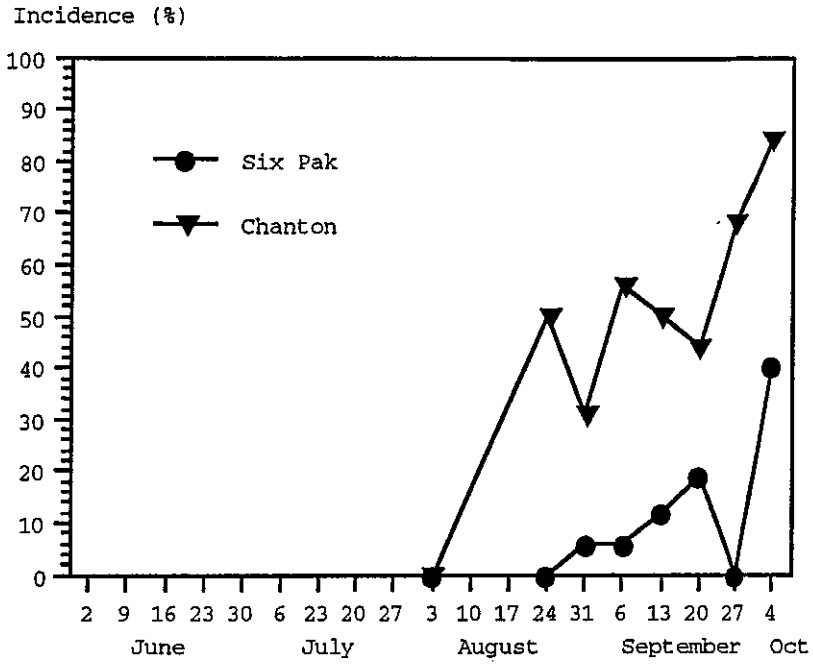


Figure 7. Development of cavity spot on cv.'s Six Pak and Chanton in 1986.

Table 21. Cavity spot development on cv.'s Chanton and Six Pak in 1986.

Harvest date	Days after seeding	Cavity spot rating	
		Chanton	Six Pak
		Incidence (%)	Incidence (%)
22 July	49	0	0
7 August	65	0	0
24 August	82	50	0
1 September	90	31	6
8 September	97	56	6
16 September	105	50	12
22 September	111	44	19
29 September	118	68	0
8 October	127	84	40
AUDPC[1]		2912	476

1 AUDPC - area under disease progress curve.

This trial was not replicated, therefore, no statistical analyses were performed.

Table 22. Development of cavity spot on cv. Red Core Chantenay in 1987.

Harvest date	Days after seeding	Disease Rating Incidence (%)
23 July	59	0
13 August	80	28
29 August	96	30
11 September	109	59
16 September	114	54
25 September	123	44
2 October	130	68
9 October	137	52
17 October	144	33
31 October	158	65
2 November	160	66
11 December	199	64
AUDPC[1]		5844

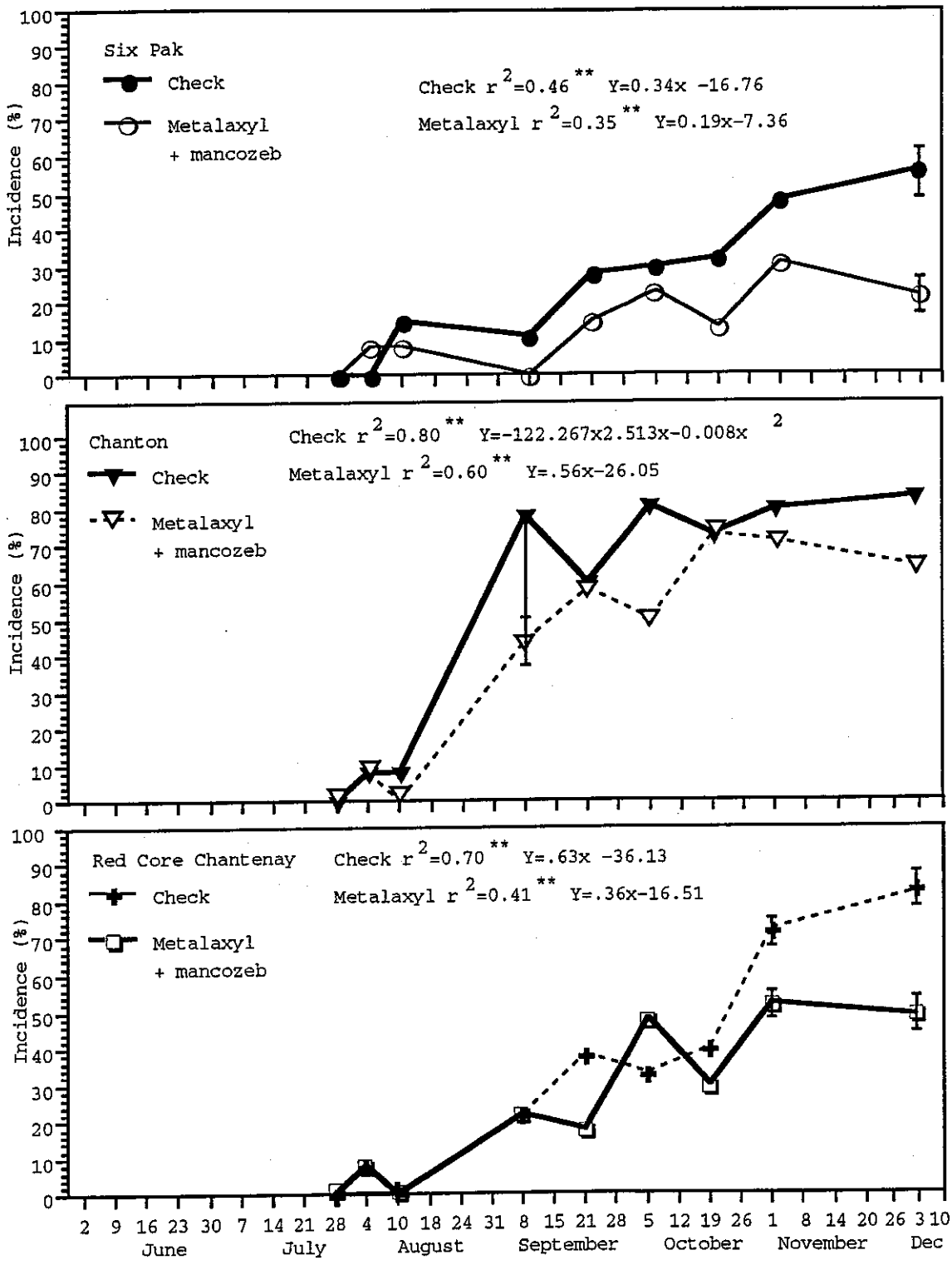
1 AUDPC-area under disease progress curve.

Six Pak, Chanton and Red Core Chantenay in 1988.

In 1988, cavities were first observed in early August (63 days after seeding) on Six Pak, Chanton, and Red Core Chantenay (Tables 23a, b, c). Cavity spot index and incidence increased with time but the magnitude of the increases varied with cultivar, fungicide and PGPR treatment.

For Six Pak, a resistant cultivar, cavity spot lesions were observed on carrots treated with metalaxyl plus mancozeb one week before they were found on carrots in the untreated check (Figure 8). Lesions were first observed on 4 August on untreated and fungicide-treated Chanton and Red Core Chantenay (Figure 8). Metalaxyl plus mancozeb treatment reduced cavity spot incidence late in the season on Six Pak and Red Core Chantenay but did not affect the incidence on Chanton even though the disease progress curve appeared to be lower. On Chanton and Red Core Chantenay the change in incidence on metalaxyl-treated carrots appeared to lag behind the check by on average, one sample interval (Figure 8). The effects of cultivar and metalaxyl plus mancozeb and PGPR treatments on cavity spot development were analyzed as a two-factor factorial experiment for each sample date and the AUDPC. No cultivar by treatment interactions were found for data from individual sample dates but there was a significant interaction (P=0.028) for the AUDPC data (Appendix IV Table 23). Simple effects of the factors on incidence are presented in Tables 24a, b, and c and simple effects of the factors on AUDPC are summarized in Table 23e. Main effects of cultivar and treatment on incidence are summarized in Tables 23d and f.

Treatment of carrots with metalaxyl plus mancozeb reduced disease incidence carrots sampled on 1 November and 3 December, while PGPR treatments did not reduce incidence compared to the untreated check (Table 23d). Examination of the simple effects of treatment on AUDPC shows that metalaxyl plus mancozeb suppressed cavity spot on Six Pak but not on Chanton or Red Core Chantenay (Table 23e). Application of PGPR's Sp-102 and Pp-2 suppressed cavity spot on Chanton but not on the other cultivars.



** Linear regression significant at P=0.01

Figure 8. Cavity spot incidence on untreated and metalaxyl treated carrots cv.'s Six Pak, Chanton and Red Core Chantenay in 1988.

Standard error bars were included only where points were significantly different at P=0.05, Duncan's New Multiple Range Test.

Table 23a. Effect of metalaxyl plus mancozeb drench and plant growth-promoting rhizobacteria on disease incidence of cv. Six Pak in 1988.

Sample date	Incidence (%) Check	Metalaxyl + mancozeb[1] (2.0 kg ai/ha)	PGPR[2] SP-102	PGPR[2] Pf-12	PGPR[2] Pp-2	LSD[3] (P=0.05)
27 July	0	0	-	-	-	N.S.
4 Aug.	0	8	-	-	-	N.S.
10 Aug.	15	8	0	-	-	N.S.
8 Sept.	11	0	-	11	-	49.6
21 Sept.	28	15	-	28	33	26.3
5 Oct.	30	23	33	-	-	29.7
19 Oct.	32	13	48	38	43	28.8
1 Nov.	48	31	60	44	39	19.7
3 Dec.	56	22	48	43	35	25.8
AUDPC[5]	3780 c-f[4]	2006 g	2818 efg	2733 efg	2439 efg	1497.2

1 Metalaxyl plus mancozeb (Ridomil MZ 72WP, 8% metalaxyl plus 64% mancozeb, applied at a rate of 2.0 kg ai/ha metalaxyl plus 16.0 kg ai/ha mancozeb, in an 8 cm band over the seed row immediately after seeding.

2 Plant growth-promoting rhizobacteria (PGPR) Sp-102, Pf-12 and Pp-2 were isolate 1-102 of Serratia proteamaculans, isolate 31-12 of Pseudomonas fluorescens and isolate GR12-2 of P. putida respectively.

3 Protected LSD value were calculated for the three cultivars x five treatment factorial analysis.

4 Examination of simple effects: values in a row followed by the same letter are not significantly different at P=0.05, Duncan's New Multiple Range Test

5 AUDPC-area under the disease progress curve.

Table 23b. Effect of metalaxyl plus mancozeb drench and plant-growth promoting rhizobacteria on cavity spot incidence of cv. Chanton in 1988.

Sample date	Incidence (%)					
	Check	Metalaxyl + mancozeb[1] (2.0 kg (ai/ha)	PGPR[2] Sp-102	PGPR[2] Pf-12	PGPR[2] Pp-2	LSD[3] P=0.05
27 July	0	0	-	-	-	N.S.
4 Aug.	8	8	-	-	-	N.S.
10 Aug.	8	0	0	-	-	N.S.
8 Sept.	78	44	-	67	-	48.6
21 Sept.	60	58	-	70	62	26.3
5 Oct.	81	50	90	-	-	29.7
19 Oct.	73	73	68	73	58	28.8
1 Nov.	80	71	68	87	70	19.7
3 Dec.	83	64	83	85	53	25.8
AUDPC[5]	7638 a[4]	6078 abc	4571 cd	6280 ab	4026 cde	1497.2

1 Metalaxyl plus mancozeb (Ridomil MZ 72WP, 8% metalaxyl plus 64% mancozeb, applied at a rate of 2.0 kg ai/ha metalaxyl plus 16.0 kg ai/ha mancozeb, in an 8 cm band over the seed row immediately after seeding.

2 Plant growth-promoting rhizobacteria (PGPR) Sp-102, Pf-12 and Pp-2 were isolate 1-102 of *Serratia proteamaculans*, isolate 31-12 of *Pseudomonas fluorescens* and isolate GR12-2 of *P. putida* respectively.

3 Protected LSD values were calculated for the three cultivars x five treatment factorial analysis.

4 Examination of simple effects: values in a row followed by the same letter are not significantly different at P=0.05, Duncan's New Multiple Range Test.

5 AUDPC-area under the disease progress curve.

Table 23c. Effect of metalaxyl plus mancozeb drench and plant growth-promoting rhizobacteria on cavity spot incidence of cv. Red Core Chantenay in 1988.

Sample date	Incidence (%)					LSD[3] (P=0.05)
	Check	Metalaxyl + mancozeb[1] (2.0 kg ai/ha)	PGPR[2] Sp-102	PGPR[2] Pf-12	PGPR[2] Pp-2	
27 July	0	0	-	-	-	N.S.
4 Aug.	8	8	-	-	-	N.S.
10 Aug.	0	0	8	-	-	N.S.
8 Sept.	22	22	-	11	-	48.6
21 Sept.	38	18	-	62	44	26.3
5 Oct.	33	48	70	-	-	29.7
19 Oct.	40	30	70	68	70	28.7
1 Nov.	72	52	79	66	73	19.7
3 Dec.	83	49	83	69	85	25.8
AUDPC[5]	4881 bcd[4]	3656 def	5156 bcd	4493 cd	4538 cd	1497.2

1 Metalaxyl plus mancozeb (Ridomil MZ 72WP, 8% metalaxyl plus 64% mancozeb, applied at a rate of 2.0 kg ai/ha metalaxyl plus 16.0 kg ai/ha mancozeb, in an 8 cm band over the seed row immediately after seeding.

2 Plant growth-promoting rhizobacteria (PGPR) Sp-102, Pf-12 and Pp-2 were isolate 1-102 of Serratia proteamaculans, isolate 31-12 of Pseudomonas fluorescens and isolate GR12-2 of P. putida respectively.

3 Protected LSD values were calculated for the three cultivars x five treatment factorial analysis.

4 Examination of simple effects: values in a row followed by the same letter are not significantly different at P=0.05, Duncan's New Multiple Range Test.

5 AUDPC-area under the disease progress curve.

Table 23d. Main effects of treatment with metalaxyl plus mancozeb and plant growth-promoting rhizobacteria on cavity spot incidence in 1988.

Treatment	N[1]	Incidence (%) Sample date 21 Sept.	5 Oct.	19 Oct.	1 Nov.	3 Dec.
Check ab	12	41.6 ab[2]	47.7 ab	48.0 ab	24.5 ab	73.8
Sp-102	12		64.2 a	61.7 a	22.0 abc	87.5 a
Pf-12	12	53.0 a		59.3 a	26.8 a	65.5 bc
Pp-2	12	46.4 a		56.7 a	20.7 bc	62.7 bc
Metalaxyl[3]+ mancozeb	12	30.0 b	42.5 b	35.8 b	15.5 c	44.5 c

1 Number of replications per mean.

2 Values in a column followed by the same letter are not significantly different at P=0.05, Duncan's New Multiple Range Test.

3 Ridomil MZ 72WP (8% metalaxyl plus 64% mancozeb).

Table 23e. Simple effects of treatment with metalaxyl plus mancozeb and plant growth-promoting rhizobacteria on area under the disease incidence curve (AUDPC) in 1988.

	Mean AUDPC (percent days)				
		Metalaxyl+ mancozeb	PGPR		
Cultivar	Check	(2.0 kg ai/ha)	Sp-102	Pf-12	Pp-2
Six Pak	3780 c-f	2006 g	2818 efg	2733 efg	2439 fg
Chanton	7638 a	6078 abc	4571 cd	6280 ab	4026 cde
Red Core Chantenay	4881 bcd	3656 def	5156 bcd	4492 cd	4538 cd

1 Values followed by the same letter are not significantly different P=0.05, Duncan's New Multiple Range Test.

Table 23f. Main effects of cultivar on cavity spot incidence in 1988.

	Incidence (%)					
Treatment	8 Sept.	21 Sept.	5 Oct.	19 Oct.	1 Nov.	3 Dec.
Six Pak	5.5 b[2]	25.8 c	28.3 c	34.4 b	42.1 c	40.6 b
Chanton	47.2 a	62.4 a	76.0 a	67.0 a	72.3 a	82.3 a
Red Core Chantenay	13.9 b	40.1 b	50.0 b	55.5 a	61.1 b	78.5 a

1. Values in a column followed by the same letter are not significantly different at P=0.05, Duncan's New Multiple Range Test.

The three cultivars differed in susceptibility to cavity spot. Cavity spot incidence was consistently low (5.5-42.1%) on Six Pak and high (47.2-82.3%) on Chanton (Table 23f). Incidence on Red Core Chantenay was significantly higher than on Six Pak but lower than that on Chanton on 21 September, 5 October and 1 November sample dates (Table 23f). Similar results were found when cavity spot was assessed as AUDPC. Chanton had a higher AUDPC than either Six Pak or Red Core Chantenay (Table 23e).

Application of metalaxyl plus mancozeb to Six Pak reduced AUDPC more effectively than any other cultivar and treatment combination. Treatment of susceptible Chanton with metalaxyl plus mancozeb, Sp-102 or Pp-2 reduced the AUDPC to the equivalent of untreated resistant cultivar Six Pak.

Six Pak, Red Core Chantenay, Eagle, Huron and SR-481 in 1992

In 1992, cavity spot was first observed on 17 July (50 days after seeding) or 4 August (71 days after seeding) on carrots of all cultivars and treatments, except for Red Core Chantenay carrots treated with metalaxyl plus mancozeb in the non-irrigated plot, where lesions were first observed on 6 October (Tables 24a, b, c, d, e).

The effects of fungicide application and cultivar resistance on incidence of cavity spot and AUDPC were analyzed as a two-factor factorial experiment. Cavity spot incidence in the non-irrigated and irrigated plots were analyzed separately. Significant cultivar by fungicide interactions were found for incidence on carrots sampled on 4 August and 6 October from the non-irrigated plot (P=0.0014, 0.0112, respectively Appendix IV, Table 24) and for carrots sampled on 4 August from the irrigated plot (P=0.0362, Appendix IV Table 24). There was also a significant cultivar by fungicide interaction for AUDPC in both the non-irrigated and irrigated plots (P=0.0426, 0.0317, respectively Appendix IV Table 24). Simple effects were examined for data where interactions were found (Tables 24a-e). Where there were significant effects of the factors

Table 24a. Effect of metalaxyl plus mancozeb or fosetyl-Al on cavity spot incidence of cv. Six Pak grown in irrigated and non-irrigated plots in 1992.

Date	Days after seeding	Cavity spot index (0-100)							
		Non-irrigated				Irrigated			
		Check	Metalaxyl+[1] mancozeb (2.0 kg ai/ha)	Fosetyl-Al[1] (4.0 kg ai/ha)	LSD[2] (P=0.05)	Check	Metalaxyl+ mancozeb (2.0 kg ai/ha)	Fosetyl-Al (4.0 kg ai/ha)	LSD (P=0.05)
17 July	50	0.0	0.0	3.0	N.S.	5.0	0.0	3.0	N.S.
4 Aug.	71	8.0 cd	9.0 cd	3.0 d	16.8	20.0 abc	3.0 bc	8.0 bc	16.2
25 Aug.	92	18.0	16.0	11.0	N.S.	5.0	4.0	15.0	N.S.
15 Sept.	113	0.0	0.0	3.0	N.S.	3.0	8.0	0.0	N.S.
6 Oct.	134	5.0 ab	0.0 b	5.0 ab	20.6	0.0	0.0	0.0	8.8
27 Oct.	155	15.0	15.0	10.0	36.4	24.0	20.0	8.0	30.6
7 Nov.	176	18.0	5.0	13.0	29.3	13.0	8.0	18.0	34.4
8 Dec.	197	18.0	13.0	3.0	17.5	13.0	13.0	15.0	23.5
AUDPC[4]		1485.0 c	1080.4 c	984.8 c	1521.1	1548.0 de	993.8 e	1187.2 e	1040.3

1 Metalaxyl plus mancozeb treatment was Ridomil MZ 72WP (8% metalaxyl plus 64% mancozeb), fosetyl-Al treatment was Aliette (80% fosetyl-Al). Both treatments were applied as a drench in an 8 cm band over the seed row immediately after seeding.

2 LSD values were calculated for the three cultivars x three treatment factorial analysis.

3 Examination of simple effects: values in a row followed by the same letter are not significantly different at P=0.05, Duncan's New Multiple Range Test.

4 AUDPC-area under the disease progress curve.

Table 24b. Effect of metalaxyl plus mancozeb or fosetyl-Al on cavity spot incidence of cv. Red Core Chantenay grown in irrigated and non-irrigated plots in 1992.

Date	Days after seeding	Cavity spot index (0-100)							
		Non-irrigated				Irrigated			
		Check	Metalaxyl+[1] mancozeb (2.0 kg ai/ha)	Fosetyl-Al[1] (4.0 kg ai/ha)	LSD[2] (P=0.05)	Check	Metalaxyl+ mancozeb (2.0 kg ai/ha)	Fosetyl-Al (4.0 kg ai/ha)	LSD (P=0.05)
17 July	50	0.0	0.0	0.0	N.S.	0.0	3.0	5.0	N.S.
4 Aug.	71	23.0 bc[3]	0.0 d	10.0 cd	16.8	30.0 a	3.0 c	13.0 ab	16.2
25 Aug.	92	20.0	0.0	13.0	N.S.	21.0	20.0	23.0	N.S.
15 Sept.	113	3.0	0.0	8.0	N.S.	10.0	0.0	23.0	N.S.
6 Oct.	134	0.0 b	3.0 ab	8.0 ab	20.6	5.0	18.0	5.0	8.8
27 Oct.	155	73.0	8.0	46.0	36.4	68.0	30.0	39.0	30.6
17 Nov.	176	28.0	15.0	60.0	29.3	49.0	25.0	38.0	34.4
8 Dec.	197	35.0	0.0	26.0	17.5	51.0	8.0	34.0	23.5
AUDPC[4]		3383.8 ab	525.0 c	3274.0 ab	1521.1	4363.8 ab	1752.8 de	3365.2 bc	1040.3

1 Metalaxyl plus mancozeb treatment was Ridomil MZ 72WP (8% metalaxyl plus 64% mancozeb), fosetyl-Al treatment was Aliette (80% fosetyl-Al). Both treatments were applied as a drench in an 8 cm band over the seed row immediately after seeding.

2 LSD values were calculated for the three cultivars x three treatment factorial analysis.

3 Examination of simple effects: values in a row followed by the same letter are not significantly different at P=0.05, Duncan's New Multiple Range Test.

4 AUDPC-area under the disease progress curve.

Table 24c. Effect of metalaxyl plus mancozeb or fosetyl-Al on cavity spot incidence of cv. Eagle grown in irrigated and non-irrigated plots in 1992.

Date	Days after seeding	Cavity spot index (0-100)							
		Non-irrigated				Irrigated			
		Check	Metalaxyl+[1] mancozeb (2.0 kg ai/ha)	Fosetyl-Al[1] (4.0 kg ai/ha)	LSD[2] (P=0.05)	Check	Metalaxyl+ mancozeb (2.0 kg ai/ha)	Fosetyl-Al (4.0 kg ai/ha)	(P=0.05)
17 July	50	0.0	0.0	3.0	N.S.	8.0	0.0	3.0	N.S.
4 Aug.	71	13.0 cd[3]	3.0 d	33.0 a		20.0 abc	8.0 bc	25.0 ab	16.2
25 Aug.	92	23.0	0.0	5.0	N.S.	18.0	0.0	33.0	N.S.
15 Sept.	113	5.0	3.0	10.0	N.S.	5.0	13.0	28.0	N.S.
6 Oct.	134	3.0 ab	3.0 ab	8.0 ab	20.6	3.0	5.0	5.0	8.8
27 Oct.	155	50.0	5.0	58.0	36.4	48.0	27.0	58.0	30.6
17 Nov.	176	49.0	18.0	43.0	29.3	48.0	30.0	38.0	34.4
8 Dec.	197	20.0	5.0	27.0	17.5	48.0	28.0	53.0	23.5
AUDPC[4]		2908.5 b	678.8 c	3541.0 ab	1521.1	3581.2 abc	1994.0 de	4521.0 a	1040.3

1 Metalaxyl plus mancozeb treatment was Ridomil MZ 72WP (8% metalaxyl plus 64% mancozeb), fosetyl-Al treatment was Aliette (80% fosetyl-Al). Both treatments were applied as a drench in an 8 cm band over the seed row immediately after seeding.

2 LSD values were calculated for the three cultivars x three treatment factorial analysis.

3 Examination of simple effects: values in a row followed by the same letter are not significantly different at P=0.05, Duncan's New Multiple Range Test.

4 AUDPC-area under the disease progress curve.

Table 24d. Effect of metalaxyl plus mancozeb or fosetyl-Al on cavity spot incidence of cv. Huron grown in a non-irrigated plot in 1992.

Date	Days after seeding	Disease incidence (%) Check	Metalaxyl+[1] mancozeb (2.0 kg ai/ha	Fosetyl-Al[1] (4.0 kg ai/ha)	LSD[2] (P=0.05)
17 July	50	0.0	0.0	0.0	N.S.
4 Aug.	71	30.0 b[3]	5.0 cd	17.0 a-d	16.8
25 Aug.	92	15.0	8.0	33.0	N.S.
15 Sept.	113	18.0	0.0	10.0	N.S.
6 Oct.	134	25.0 a	3.0 ab	3.0 ab	20.6
27 Oct.	155	59.0	18.0	15.0	36.4
17 Nov.	176	57.0	35.0	54.0	29.3
8 Dec.	197	49.0	16.0	40.0	17.5
AUDPC[4]		4745.0 a	2060.0 bc	3108.0 ab	1521.1

1 Metalaxyl plus mancozeb treatment was Ridomil MZ (8% metalaxyl plus 64% mancozeb), fosetyl-Al treatment was Aliette (80% fosetyl-Al). Both treatments were applied as a drench in an 8 cm band over the seed row immediately after seeding.

2 LSD values were calculated for the three cultivars x three treatment factorial analysis.

3 Examination of simple effects: values in a row followed by the same letter are not significantly different at P=0.05, Duncan's New Multiple Range Test.

4 AUDPC-area under the disease progress curve.

Table 24e. Effect of metalaxyl plus mancozeb or fosetyl-Al on cavity spot incidence of cv. SR-481 grown in an irrigated plot in 1992.

Date	Days after seeding	Disease Incidence (%) Check	Metalaxyl+[1] mancozeb (2.0 kg ai/ha)	Fosetyl-Al (4.0 kg ai/ha)	LSD[2] (P=0.05)
17 July	50	3.0	0.0	0.0	N.S.
4 Aug.	71	13.0 ab[3]	8.0 b	15.0 ab	16.2
25 Aug.	92	25.0	8.0	13.0	N.S.
15 Sept.	113	18.0	5.0	18.0	N.S.
6 Oct.	134	3.0	5.0	0.0	8.8
27 Oct.	155	27.0	14.0	17.0	30.6
17 Nov.	176	28.0	17.0	30.0	34.4
8 Dec.	197	28.0	2.0	24.0	23.5
AUDPC[4]		2660.0 cd	1332.0 e	2161.0 de	1040.3

1 Metalaxyl plus mancozeb treatment was Ridomil MZ 72WP (8% metalaxyl plus 64% mancozeb), fosetyl-Al treatment was Aliette (80% fosetyl-Al). Both treatments were applied as a drench in an 8 cm band over the seed row immediately after seeding.

2 LSD values were calculated for the three cultivars x three treatment factorial analysis.

3 Examination of simple effects: values in a row followed by the same letter are not significantly different at P=0.05, Duncan's New Multiple Range Test.

4 AUDPC-area under the disease progress curve.

and no interaction, main effects were examined (Tables 24f, g).

Examination of the main effects of fungicide indicated that metalaxyl plus mancozeb treatment reduced cavity spot incidence on carrots harvested on 27 October, 17 November and 8 December in both non-irrigated and irrigated plots (Table 24f). The effects of fungicide treatment varied with cultivar on the 4 August and 6 October harvest dates. Application of metalaxyl plus mancozeb suppressed cavity spot incidence on Red Core Chantenay and Huron harvested on 4 August (Tables 24b, d) and on Six Pak carrots harvested on 6 October from the non-irrigated plot (Table 24a). The effects of metalaxyl plus mancozeb on AUDPC also varied with cultivar. This treatment was effective on Red Core Chantenay, Eagle, Huron and SR-481, but not on Six Pak.

Treatment of carrots with fosetyl-Al occasionally suppressed cavity spot on carrots grown in the non-irrigated plot. Incidence was reduced on carrots harvested on 27 October, and on Red Core Chantenay carrots harvested on 4 August (Tables 24f, b). In addition, AUDPC was suppressed on Huron carrots (Table 24g).

Differences in cultivar susceptibility were apparent in this trial, although the susceptibility ranking sometimes changed with sample date. Six Pak consistently had the lowest incidence of cavity spot, except for carrots harvested 6 October from the non-irrigated plot. On this date Red Core Chantenay was the only cultivar with a significantly lower incidence (0%) than Huron (25%) (Tables 24b, d, Figure 9). Among carrots grown in the non-irrigated plot Red Core Chantenay had a higher incidence than Six Pak on 27 October, Huron on 8 December and Red Core Chantenay, Eagle and Huron all had a higher incidence than Six Pak on 8 December (Figure 10). When carrots were grown in the irrigated plot, cavity spot incidence on SR-481 was similar to that on Six Pak. Red Core Chantenay had a higher incidence than Six Pak on 6 October and both Red Core Chantenay and Eagle had a higher incidence of cavity spot on 27 October, 17 November and 8 December (Table 24h, Figure 10).

Table 24f. Main effects of metalaxyl plus mancozeb and fosetyl-Al on cavity spot incidence on carrots grown in irrigated and non-irrigated plots in 1992.

Sample date	N[1]	Non-irrigated			Irrigated		
		Check	Metalaxyl[2]+ mancozeb (2.0 kg ai/ha)	Fosetyl-Al[2] (4.0 kg ai/ha)	Check	Metalaxyl+ mancozeb (2.0 kg ai/ha)	Fosetyl-Al (4.0 kg ai/ha)
27 Oct.	16	49.2 a[3]	11.2 b	26.5 b	41.7 a	22.5 b	30.2 ab
17 Nov.	16	37.6 a	18.1 b	42.4 a	34.1 a	19.9 b	30.7 ab
8 Dec.	16	30.3 a	8.4 b	24.1 a	34.8 a	12.6 b	31.2 a

1 Number of replications per mean.

2 Metalaxyl plus mancozeb treatment was Ridomil MZ 72WP (8% metalaxyl plus 64% mancozeb), fosetyl-Al treatment was Aliette (80% fosetyl-Al). Both treatments were applied as a drench in an 8 cm band over the seed row immediately after seeding.

3 Values in a row for non-irrigated or irrigated plot followed by the same letter are not significantly different at P=0.05, Duncan's New Multiple Range Test.

Table 24g. Effect of cultivar and metalaxyl plus mancozeb or fosetyl-Al on area under the disease progress curve (AUDPC) on cavity spot in carrots grown in a non-irrigated and irrigated plot in 1992.

Cultivar	Fungicide[1]	Rate (kg ai/ha)	Non-irrigated AUDPC	Irrigated AUDPC
Six Pak	Check		1485.0 def[2]	1548.0 de
	Metalaxyl+ mancozeb	2.0 7.0	1080.4 ef	993.8 e
	Fosetyl-Al	4.0	984.8 ef	1187.2 de
Red Core Chantenay	Check		3383.8 abc	4363.8 a
	Metalaxyl+ mancozeb	2.0 7.0	525.0 f	1752.8 cde
	Fosetyl-Al	4.0	3274.0 abc	3365.2 b
Eagle	Check		2908.5 bcd	3581.2 ab
	Metalaxyl+ mancozeb	2.0 7.0	678.8 ef	1994.0 cde
	Fosetyl-Al	4.0	3541.0 ab	4521.0 a
Huron	Check		4745.0 a	
	Metalaxyl+ mancozeb	2.0 7.0	2060.0 cd	
	Fosetyl-Al	4.0	3108.0 bc	
SR-481	Check			2660.0 bc
	Metalaxyl+ mancozeb	2.0 7.0		1332.0 de
	Fosetyl-Al	4.0		2161.0 cd
LSD (P=0.05)			1521.1	1040.3

1 Metalaxyl plus mancozeb treatment was Ridomil MZ 72WP (8% metalaxyl plus 64% mancozeb), fosetyl-Al treatment was Aliette (80% fosetyl-Al). Both treatments were applied as a drench in an 8 cm band over the seed row immediately after seeding.

2 Values in a column followed by the same letter are not significantly different at P=0.05, Duncan's New Multiple Range Test.

Table 24h. Main effects of cultivar on cavity spot incidence on carrots grown in irrigated and non-irrigated plots in 1992.

Sample date	N[1]	Non-irrigated				Irrigated			
		Six Pak	Red Core Chantenay	Eagle	Huron	Six Pak	Red Core Chantenay	Eagle	SR-481
6 Oct.	12					0 b	39.2 a	5.0 ab	2.5 b
27 Oct.	12	13.6 b[2]	42.0 a	29.9 ab	30.7 ab	17.1 b	45.6 a	44.1 a	19.1 b
17 Nov.	12	6.2 b	18.3 a	21.6 a	25.5 a	12.5 c	37.2 ab	38.4 a	24.8 bc
8 Dec.	12	11.1 b	20.4 b	17.4 b	34.9 a	13.2 c	30.9 ab	43.0 a	17.8 bc

1 Number of replications per mean.

2 Values in a row for the non-irrigated or irrigated plot, followed by the same letter are not significantly different at P=0.05, Duncan's New Multiple Range Test.

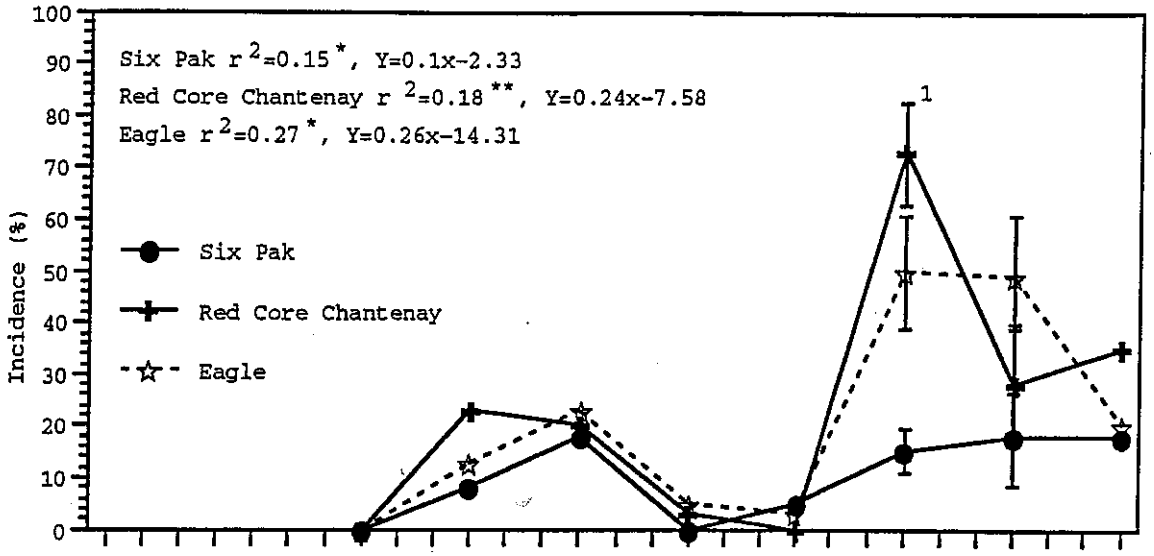


Figure 9. Cavity spot incidence on cv.'s Six Pak, Red Core Chantenay and Eagle in the non-irrigated plot in 1992.

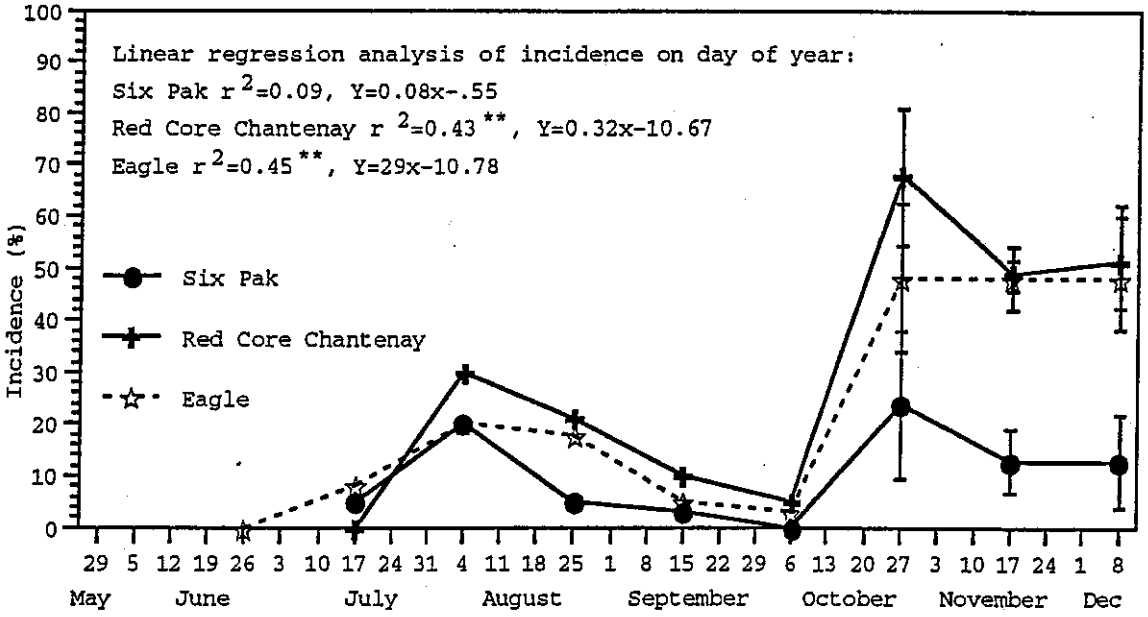


Figure 10. Cavity spot incidence on cv.'s Six Pak, Red Core Chantenay and Eagle in the irrigated plot in 1992.

* Linear regression significant at P=0.05

** Linear regression significant at P=0.01

1 Standard error bars were included only where points were significantly different at P=0.05, Duncan's New Multiple Range Test.

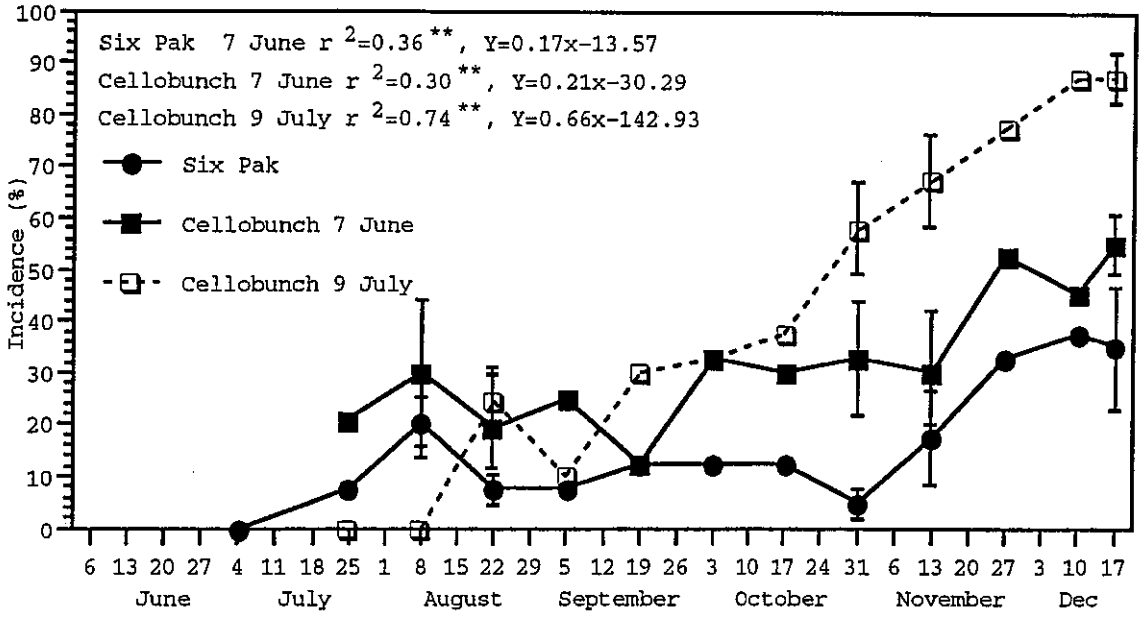
Differences in susceptibility among the untreated checks were also found when cavity spot was assessed as AUDPC. In the non-irrigated plot, AUDPC was higher on Red Core Chantenay and Huron than on Six Pak. In the irrigated plot, Red Core Chantenay, Eagle and SR-481 all had higher AUDPC's than Six Pak (Table 24g).

Effect of cultivar and seeding date on cavity spot development

In 1990, the first cavity spot lesions were observed on 25 July and 22 August on carrots seeded (Figure 11, Table 25a) on 7 June and 9 July (48 and 44 days after seeding, respectively). Cavity spot increased more rapidly on the later seeded (younger) carrots, such that the final levels were equal to, or higher than, those of earlier seed carrots of the same cultivar. There was a high positive correlation between incidence and days after seeding (r^2=0.74 and 0.76) for Cellobunch and Chancellor, respectively, seeded on 9 July (Appendix II Table 25-2). Disease progress of carrots seeded 7 June was not as closely associated with days after seeding (r^2=0.36, 0.30 and 0.50 for Six Pak, Cellobunch and Chancellor, respectively, Appendix II Table 25-2). Despite the positive correlation between plant age (as determined by days after seeding) and disease incidence, there was no evidence that the older carrot roots were more susceptible to cavity spot.

The effects of plant age, estimated by seeding date, and cultivar on cavity spot incidence in 1990 were analyzed in a two-factor factorial experiment. Significant cultivar by seeding date interactions were found on 22 August, 19 December and for AUDPC (P=0.0026, 0.0110 and 0.0262, respectively, Appendix IV Table 25-1). The simple effects are presented in Table 25a. No interactions were found for incidence on 8 August, 31 October and 16 November and main effects for the significant factors are presented in Tables 25b and c.

Cavity spot incidence in relation to plant age varied with sample date, and cultivar was sometimes an important factor. Early in the



** Linear regression significant at P=0.0001

Figure 11. Cavity spot incidence on cv.'s Six Pak and Cellobunch seeded 7 June and Cellobunch seeded 9 July, 1990.

Table 25a. Effect of cultivar and two seeding dates on cavity spot incidence in 1990.

	Cultivar					
	Six Pak	Cellobunch		Chancellor		LSD
	Cavity spot incidence (%)	Cavity spot incidence (%)		Cavity spot incidence (%)		(P=0.05)
Sample Date	7 June	7 June	9 July	7 June	9 July	
25 July	7.5	20.0	0	30.0		N.S.
8 August	12.5	27.5	0	17.5	0	19.8
22 August	7.5 cd	19.5 bc	24.5 ab	35.0 a	2.5 d	13.7
5 Sept.	7.5	25.0	10.0	15.0	15.0	N.S.
19 Sept.	12.5	12.5	30.0	32.5	20.0	N.S.
3 Oct.	12.5	32.5	32.5	17.5	27.5	N.S.
17 Oct.	12.5	30.0	37.5	42.5	52.5	N.S.
31 Oct.	5.0	32.5	57.5	32.5	50.0	23.99
16 Nov.	17.5	30.0	67.5	32.5	57.5	24.68
28 Nov.	32.5	52.5	77.5	62.5	52.5	N.S.
13 Dec.	37.5	45.0	87.5	70.0	70.0	N.S.
19 Dec.	35.0 c	55.0 bc	87.5 a	57.5 bc	70.0 ab	27.0
AUDPC	2348 c	4626 b	5789 a	5208 ab	4746 b	771.6

1 Values in a row followed by the same letter are not significantly different at P=0.05, Duncan's New Multiple Range Test.

Table 25b. Main effects of seeding date on incidence of cavity spot in 1990.

Seeding date	N[1]	Incidence (%) Sample date 8 Aug.	31 Oct.	16 Nov.
7 June	12	19.1 a[2]	23.3 b	26.7 b
9 July	8	0 b	53.8 a	62.5 a

1 Numbers of replications per mean.

2 Values in a column followed by the same letter are not significantly different at P=0.05, Duncan's New Multiple Range Test.

Table 25c. Main effects of cultivar on cavity spot in 1990.

Cultivar	N[1]	Incidence (%) 31 Oct.
Six Pak	4	5.0 b[2]
Cellobunch	8	45.0 a
Chancellor	8	41.2 a

1 Number of replications per mean.

2 Values in a column followed by the same letter are not significantly different at P=0.05, Duncan's New Multiple Range Test.

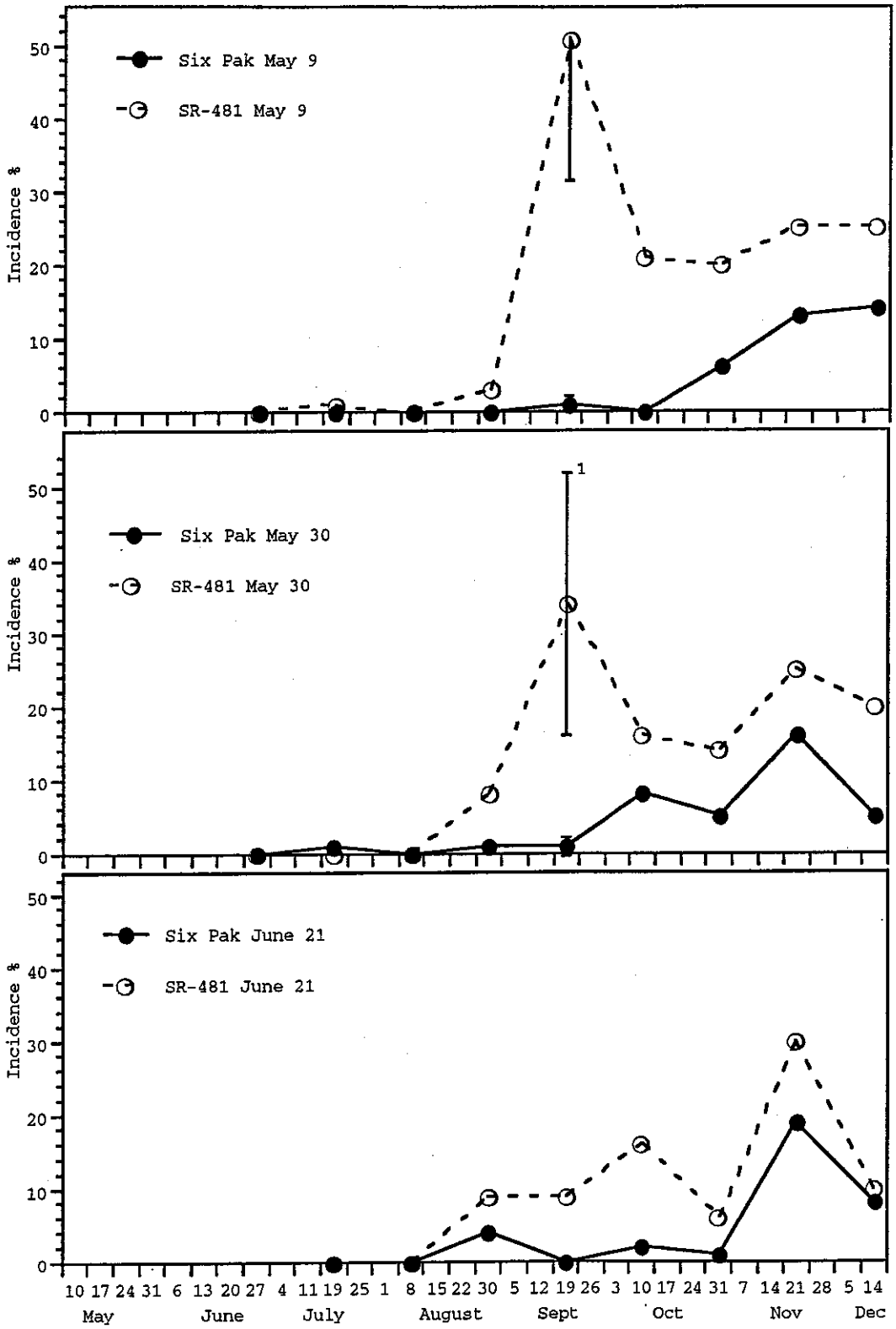
season, on the 8 August sample date, there was a higher incidence of cavity spot on carrots seeded 7 June than on those seeded 9 July (Table 25b). As the season was nearing the end (31 October and 16 November), incidence was higher on carrots seeded 9 July than on those seeded 7 June. Very late in the season, (19 December), incidence was higher on Cellobunch carrots seeded on 9 July than on those seeded 7 June, but seeding date did not affect incidence on Chancellor carrots (Table 25a). Cultivar also had an effect on the AUDPC in relation to seeding date. Cellobunch carrots seeded on 9 July had a higher AUDPC than carrots of the same cultivar seeded one month earlier, on 7 June, while Chancellor carrots had equivalent AUDPC values, despite the different seeding dates (Table 25a).

Cultivar effects on incidence were only found on one sample date, 31 October, where Six Pak had a lower incidence than Cellobunch or Chancellor (Table 25c). Differences in cultivar susceptibility did affect the AUDPC. Six Pak carrots, seeded 7 June, had the lowest AUDPC of all the treatments (Table 25a).

In 1991, the first cavity spot lesions were observed on 19 July on both SR-481 carrots seeded 9 May and Six Pak carrots seed 30 May. Six Pak carrot seeded 9 May did not develop lesions until 19 September (133 days after seeding) while SR-481 carrots seeded 30 May first developed lesions on 30 August (92 days after seeding). The carrots of both cultivars seeded 21 June and 12 July first developed lesions on the same dates (30 August and 10 October) 70 days after seeding, respectively (Table 26a).

Cavity spot incidence increased slowly in all seedings of Six Pak and reached a maximum on 21 November. Disease incidence on SR-481 carrots seeded 9 and 30 May reached the highest levels on 19 September, while carrots seeded 21 June or 12 July had the highest incidence on 21 November, similar to the Six Pak treatments (Figure 12).

The 1991 data were analyzed as a two-factor factorial experiment, as were the 1990 data above. Significant effects of the factors cultivar and seeding date were found only for incidence on the 19 September sample



1 Standard error bars included only where points were significantly different at P=0.05, Duncan's New Multiple Range Test.

Figure 12. Cavity spot incidence on carrot cv.'s Six Pak and SR-481 seeded on 9 May, 30 May, 21 June, 1991

Table 26a. Effect of cultivar and seeding date on cavity spot incidence in 1991.

Sample date	Disease incidence (%)								LSD (P=0.05)
	Six Pak Seeding date				SR-481 Seeding date				
	9 May	30 May	21 June	12 July	9 May	30 May	21 June	12 July	
6 June	0	-	-	-	0	-	-	-	N.S.[1]
27 June	0	0	-	-	0	0	-	-	N.S.
19 July	0	1	0	-	1	0	0	-	N.S.
8 Aug.	0	0	0	0	0	0	0	0	N.S.
30 Aug.	0	1	4	0	3	8	9	0	N.S.
19 Sept.	1	1	0	0	51	34	9	0	30.8
10 Oct.	0	8	2	10	21	16	16	15	N.S.
31 Oct.	6	5	1	8	20	14	6	3	N.S.
21 Nov.	13	16	19	21	25	25	30	33	N.S.
11 Dec.	14	5	8	16	25	20	10	10	N.S.
AUDPC[3]	578	723	591	829	2456	2120	1598	1239	1637.7

1 N.S. indicates not significant at P=0.05, Protected LSD Test.

2 AUDPC-area under the disease progress curve.

Table 26b. Main effects of carrot cultivar on incidence of cavity spot on 30 September sample date and area under the disease progress curve (AUDPC) in 1991.

Cultivar	N[1]	Incidence (%)	N	AUDPC (percent days)
SR-481	16	10.7 a[2]	16	1853 a
Six Pak	16	0.2 b	16	760 b

1 Number of replications per mean.

2 Values in a column followed by the same letter are not significantly different at P=0.05, Duncan's New Multiple Range Test.

date and for the AUDPC data. The two factor interactions were not significant (P=0.0884 and 0.2274, respectively, Appendix IV Table 26.1). Thus, main effects were examined (Table 26b).

Seeding date had no effect on cavity spot incidence or AUDPC when carrots were seeded on four dates at three week intervals (Table 26a). Analysis of main effects indicated that Six Pak carrots had a lower incidence of cavity spot of 19 September and a lower AUDPC, as compared to SR-481 carrots (Table 26b).

The effect of cultivar and fungicide treatment on start of the cavity spot epidemic, estimated as the number of days from seeding until lesions were first observed, was analyzed as a two-factor, factorial experiment for both the 1988 and 1992 data. There were no significant differences in the 1988 data (Appendix IV Table 27a). Analysis of the 1992 data showed a significant cultivar by treatment interaction (P=0.0413, Appendix IV Table 27a) in the data from the non-irrigated plot. Simple effects of the factors were examined (Table 27a). There was no cultivar by fungicide interaction (P=0.2163, Appendix IV Table 27a) in the data from the irrigated plot so main effects were examined (Table 27b).

The effect of cultivar and seeding date on the start of the epidemic were in 1990 and 1991 analyzed as a two-factor factorial experiment. No significant effects were found in the 1990 data (Appendix IV Table 27c) but there was a significant interaction of the 1991 data (P=0.0399, Appendix IV Table 29c). The simple effects of cultivar and seeding date were examined (Table 27c).

Comparison of the cavity spot epidemics

Start of the epidemic

The start of the cavity spot epidemic was not affected by cultivar in any of the trials (Tables 27a, 27c). The number of days from seeding until the first cavities were observed increased on carrots treated with metalaxyl plus mancozeb and grown in the non-irrigated plot in 1992 except

Table 27a. Effect of cultivar, irrigation, and treatment with metalaxyl plus mancozeb or fosetyl-Al on the initial observance of cavity spot lesions in 1988 and 1992.

Year	Cultivar	Fungicide[1] (kg ai/ha)	Day cavities first observed[2] Non-irrigated plot	Irrigated plot
1988	Six Pak	Check	87	
		Metalaxyl (2.0)+ mancozeb (7.0)	89	
	Chanton	Check	93	
		Metalaxyl (2.0)+ mancozeb (7.0)	89	
	Red Core Chantenay	Check	99	
		Metalaxyl (2.0)+ mancozeb (7.0)	103	
LSD (P=0.05)			N.S.	
1992	Six Pak	Check	92 b[3]	61
		Metalaxyl (2.0)+ mancozeb (7.0)	139 ab	134
		Fosetyl-Al (4.0)	82 b	92
	Red Core Chantenay	Check	71 b	66
		Metalaxyl (2.0)+ mancozeb (7.0)	155 a	76
		Fosetyl-Al (4.0)	82 b	66

.../continued

Table 27a. continued.

Year	Cultivar	Fungicide[1] (kg ai/ha)	Day cavities first observed[2] Non-irrigated plot	Irrigated plot
1992	Eagle	Check	92 b	61
		Metalaxyl (2.0)+ mancozeb (7.0)	145 a	92
	Eagle	Fosetyl-Al (4.0)	66 b[3]	66
	Huron	Check	71 b	
		Metalaxyl (2.0)+ mancozeb (7.0)	71 b	
		Fosetyl-Al	92 b	
	SR-481	Check		71
		Metalaxyl (2.0) mancozeb (7.0)		71
		Fosetyl-Al (4.0)		71
LSD (P=0.05)			45.9	38.9

1 Metalaxyl plus mancozeb application was Ridomil MZ 72WP (8% metalaxyl plus 64% mancozeb), fosetyl-Al was Aliette (80% fosetyl-Al). Both treatments were applied as a drench in an 8 cm band over the seed row immediately after seeding.

2 Days after seeding that cavities were first observed on harvested roots. Carrots were harvested at two to three week intervals throughout the growing season.

3 Values in a column for each year followed by the same letter are not significantly different at P=0.05, Duncan's New Multiple Range Test.

Table 27b. Main effects of treatment with metalaxyl plus mancozeb or fosetyl-Al on the initial observance of cavity spot lesions in the irrigated plot in 1992.

Fungicide[1] (kg ai/ha)	N[2]	Days cavities first observed[3]
Check	16	93 a[4]
Metalaxyl (2.0)+ mancozeb (7.0)	16	74 b
Fosetyl-Al (4.0)	16	64 b

1 Metalaxyl plus mancozeb application was Ridomil MZ 72WP (8% metalaxyl plus 64% mancozeb), fosetyl-Al was Aliette (80% fosetyl-Al). Both were applied as a drench in an 8 cm band over the seed row immediately after seeding.

2 Days after seeding that cavities were first observed on harvested roots. Carrots were harvested at 2-3 week intervals throughout the growing season.

3 Values in a column for each year followed by the same letter are not significantly different at P=0.05, Duncan's New Multiple Range Test.

Table 27c. Effect of cultivar and seeding date on the initial observance of cavity spot lesions in 1990 and 1991.

Year	Cultivar	Seeding date	Day cavities first observed[1]
1990	Six Pak	7 June	66
	Cellobunch	7 June	52
		9 July	44
	Chancellor	7 June	48
		9 July	62
LSD (P=0.05)			N.S.
1991	Six Pak	9 May	170 a[2]
		30 May	97 b
		21 June	122 b
		12 July	78 b
	SR-481	9 May	112 b
		30 May	101 b
		21 June	90 b
		12 July	111 b
LSD (P=0.05)			45.5

1 Days after seeding that cavities were first observed on harvested roots. Carrots were harvested at two to three week intervals throughout the growing season.

2 Values in a column for each year followed by the same letter are not significantly different at P=0.05, Duncan's New Multiple Range Test.

on Six Pak and Huron (Table 27a). When carrots were grown in the irrigated plot, both metalaxyl plus mancozeb and fosetyl-Al treatment delayed the start of the epidemic (Table 27b). There were no significant effects of cultivar or metalaxyl plus mancozeb treatment on the start of the epidemic in the 1988 trial. The cavity spot epidemics started at much the same time in both years (87 and 92 days after seeding for Six Pak in 1988 and 1992, respectively).

Similarly, seeding date within any season had no effect on the time when lesions were first observed, with the exception of Six Pak seeded 9 May, 1991 (Table 27c). This was the only combination which significantly delayed the start of the epidemic. The cavity spot epidemic began somewhat earlier in 1990 than in 1991 (66 vs 97 days after seeding for cavity spot seeded 7 June 1990 and 30 May, 1991, respectively).

Shape of the disease progress curves

Simple linear regression best described the shape of the disease progress curves of carrots in 1986, 1987, 1988 and 1990, when these curves were derived from the mean cavity spot incidence on each date, regressed against days after seeding (Table 28). The coefficient of determination (r^2) was greater than 0.60 for all regressions, except for Six Pak in 1986 (r^2=0.499 and 0.467 for cavity spot index and incidence, respectively) and Red Core Chantenay in 1987 (r^2=0.583 for cavity spot incidence, Table 28). In most cases the r^2 values were greater than 0.75. Cultivar Chanton was the major exception to this pattern. In 1988, disease progress assessed as cavity spot incidence was best described by the Gompertz model. Simple linear regression best described the progress of cavity spot on carrots treated with metalaxyl plus mancozeb for all cultivars.

The shapes of the disease progress curves for carrots grown in 1991 and 1992 were considerably different from those of carrots grown in previous years (Table 28). In 1991, most of the curves were best described by the logarithmic growth model, except Six Pak, seeded on 9

Table 28. Linear regression statistics of transformed disease progress curves in relation to carrot cultivar, seeding date and treatment with metalaxyl plus mancozeb in 1986, 1988, 1990, 1991 and 1992.

Year	Cultivar	Seeding date	Metalaxyl+ mancozeb (2.0 kg ai/ha)	Linear regression analysis Best fit transformation	r^2
1986	Six Pak	3 June	Check	Linear	0.467
				Monomolecular	0.438
	Chanton	3 June	Check	Linear	0.763*
				Logistic	0.756*
1987	Red Core Chantenay	26 May	Check	Linear	0.583*
				Logistic	0.501
1988	Six Pak	2 June	Check	Linear	0.911**
				Logistic	0.834**
1988	Six Pak	2 June	Drench	Linear	0.605
				Logistic	0.431
1988	Chanton	2 June	Check	Linear	0.755*
				Gompertz	0.850**
1988	Chanton	2 June	Drench	Linear	0.807**
				Logistic	0.685*
1988	Red Core Chantenay	2 June	Check	Linear	0.931**
				Logistic	0.885**
1988	Red Core Chantenay	2 June	Drench	Linear	0.771*
				Logistic	0.675*
1990	Six Pak	7 June	Check	Linear	0.586*
				Logistic	0.641*
1990	Chancellor	7 June	Check	Linear	0.684**
				Logistic	0.653*
		9 July	Check	Linear	0.947**
				Logistic	0.901**
1990	Cellobunch	7 June	Check	Linear	0.748**
				Logistic	0.693**
		9 July	Check	Linear	0.954**
				Logistic	0.867**
1991	Six Pak	9 May	Check	Linear	0.859*
				Logistic	0.830*
		30 May	Check	Linear	0.511
				Logarithmic	0.720

...../continued

Table 28. - continued.

Year	Cultivar	Seeding date	Metalaxyl+ mancozeb (2.0 kg ai/ha)	Linear regression analysis Best fit transformation	r^2
1991	Six Pak	21 June	Check	Linear	0.390
				Logarithmic	0.502
		12 July	Check	Linear	0.220
				Logarithmic	0.486
1991	SR-481	9 May	Check	Linear	0.371
				Logarithmic	0.709
		30 May	Check	Linear	0.257
				Logarithmic	0.446
1991	SR-481	21 June	Check	Linear	0.320
				Logarithmic	0.433
		12 July	Check	Linear	0.220
				Logarithmic	0.486
Non-irrigated					
1992	Six Pak	25 May	Check	Linear	0.395
				Logistic	0.385
			Drench	Linear	0.082
				Logarithmic	0.137
1992	Red Core Chantenay	25 May	Check	Linear	0.259
				Logarithmic	0.228
			Drench	Linear	0.089
				Monomolecular	0.124
1992	Eagle		Check	Linear	0.347
				Logarithmic	0.405
			Drench	Linear	0.405
				Logarithmic	0.544
1992	Huron		Check	Linear	0.703
				Logistic	0.590
			Drench	Linear	0.520
				Logistic	0.451
Irrigated					
1992	Six Pak		Check	Linear	0.064
				Monomolecular	0.051

.../ continued

Table 28. - continued.

Year	Cultivar	Seeding date	Metalaxyl+ mancozeb (2.0 kg ai/ha)	Linear regression analysis Best fit transformation	r^2
Irrigated					
1992	Six Pak		Drench	Linear	0.438
				Logarithmic	0.294
1992	Red Core Chantenay		Check	Linear	0.482
				Logarithmic	0.438
			Drench	Linear	0.245
				Logarithmic	0.189
1992	Eagle		Check	Linear	0.545
				Monomolecular	0.692
			Drench	Linear	0.758*
					0.708*
1992	SR-481		Check	Linear	0.424
				Monomolecular	0.697
			Drench	Linear	0.147
				Logistic	0.276

*, ** r^2 Value significant at 0.05 and 0.01, respectively, simple linear regression.

May. None of the r^2 values was significant and in several instances, they were below 0.50, indicating that less than 50% of the variation in the data could be accounted for by the logarithmic transformation of the data. Low and non-significant r^2 values were also common in the 1992 data, and there were a variety of growth models that described disease progress on the different cultivars. Most of the disease progress curves of carrots in the irrigated plot treated with metalaxyl plus mancozeb were linear, but again several of the r^2 values were very low (i.e. 0.245 for incidence on Red Core Chantenay, Table 28). It is interesting to note that out of 68 disease progress curves, only three were best described by the monomolecular growth model. This model describes the progress of diseases with only one cycle per growing season and is often considered to be the model that describes the progress of soilborne plant diseases (Vanderplank 1968, Campbell and Madden 1990).

Equality of slopes and elevations

Cultivar resistance had a significant effect on the elevation of disease progress curves, but not on the slope (Tables 29a, c). Disease incidence curves (represented by simple linear regression) of resistant Six Pak were significantly lower than those of susceptible cultivars Chanton in 1988 and Huron in 1992 (Table 29a), as well as Chancellor in 1990 and SR-481 seeded on 9 May and 21 June in 1991 (Table 29c). The slopes of these curves were equivalent except for those of Six Pak and SR-481 seeded 9 May, 1991 (Table 29c). When these two cultivars were seeded on 30 May, 1991, the slopes were different but the elevations were not.

Neither the slopes nor elevations of the curves was affected by treatment of carrots with metalaxyl plus mancozeb drench in 1988 and 1992 (Table 29a) or when the plots were irrigated (Table 29b), even though the fungicide treatment significantly reduced the AUDPC (Tables 23e, 24g).

Seeding date also had a significant effect on the elevations of the disease progress curves (Table 29c). In 1990, carrots seeded on 9 July

Table 29a. Equality of slopes and elevations of linear regressions of cavity spot incidence for carrot cultivars untreated and treated with metalaxyl plus mancozeb and grown in a non-irrigated or irrigated plot in 1988 and 1992.

	Non-irrigated plot				Irrigated plot			
			F Value				F Value	
Year	Regression 1	Regression 2	Slope	Elevation	Regression 1	Regression 2	Slope	Elevation
1988	Six Pak	Chanton	3.39	11.16**				
	Six Pak	Red Core Chantenay	1.00	1.49				
	Six Pak Check	Six Pak Drench[1]	0.02	3.08				
	Chanton Check	Chanton Drench	0.01	1.75				
	Red Core Chantenay Check	Red Core Chantenay Drench	0.00	1.63				
1992	Six Pak	Red Core Chantenay	0.87	0.67	Six Pak	Red Core Chantenay	1.03	2.17
	Six Pak	Eagle	0.53	0.73	Six Pak	Eagle	1.66	1.60
	Six Pak	Huron	0.43	4.52*	Six Pak	SR-481	0.98	0.29
	Six Pak Check	Six Pak Drench	1.44	0.04	Six Pak Check	Six Pak Drench	1.59	0.68
	Red Core Chantenay Check	Red Core Chantenay Drench	2.00	1.65	Red Core Chantenay Check	Red Core Chantenay Drench	0.06	2.44

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Table 29a. - continued.

Year	Non-irrigated plot				Irrigated plot			
			F Value				F Value	
	Regression 1	Regression 2	Slope	Elevation	Regression 1	Regression 2	Slope	Elevation
1992	Eagle Check	Eagle Drench	1.93	1.94	Eagle Check	Eagle Drench	0.84	2.44
	Huron Check	Huron Drench	1.47	1.86	SR-481 Check	SR-481 Drench	0.51	0.61

*, ** Slope or elevation of regression lines 1 and 2 are significantly different at P=0.05 and 0.01, respectively, analysis of covariance.

Table 29b. Equality of slopes and elevations of linear regressions of cavity spot incidence of carrots grown in a non-irrigated and irrigated plot as affected by cultivar and treatment with metalaxyl plus mancozeb in 1992.

Cultivar	Metalaxyl[1] + mancozeb (2.0 kg ai/ha)	F Value[2]	
		Slope	Elevation
Six Pak	Check	1.45[3]	0.01
	Drench	1.59	0.01
Red Core Chantenay	Check	0.32	0.78
	Drench	1.17	1.23
Eagle	Check	0.37	0.46
	Drench	0.41	2.46

1 Metalaxyl plus mancozeb was applied as Ridomil MZ 72WP (8% metalaxyl plus 64% mancozeb, 2.0 kg ai/ha metalaxyl plus 7 kg ai/ha mancozeb) in an 8 cm band over the seed row immediately after seeding.

2 Regression 1 was data from non-irrigated plot and Regression 2 from irrigated plot.

3 None of the slopes or elevations were significantly different at P=0.05 and 0.01, respectively, analysis of covariance.

Table 29c. Equality of slopes and elevations of linear regressions of cavity spot incidence on various carrot cultivars seeded on different dates in 1990 and 1991.

Year	Cultivar and seeding date		F Value	
	Regression 1	Regression 2	Slope	Elevation
1990	Six Pak 7 June	Chancellor 7 June	1.26	8.02**
	Six Pak 7 June	Cellobunch 7 June	3.01	2.94
	Chancellor 7 June	Chancellor 9 July	0.01	11.58**
	Cellobunch 7 June	Cellobunch 9 July	0.69	119.38**
1991	Six Pak 9 May	SR-481 9 May	7.73*	7.38*
	Six Pak 30 May	SR-481 30 May	6.76*	0.01
	Six Pak 21 June	SR-481 21 June	2.12	5.21*
	Six Pak 12 July	SR-481 12 July	0.30	0.01
	Six Pak 9 May	Six Pak 30 May	0.01	15.86**
	Six Pak 9 May	Six Pak 21 June	56.94**	167.04**
	Six Pak 9 May	Six Pak 12 July	13.32**	42.90**
	Six Pak 30 May	Six Pak 21 June	17.17**	50.01**
	Six Pak 30 May	Six Pak 12 July	7.76*	2.49
	Six Pak 21 June	Six Pak 12 July	5.62*	128.74**
1991	SR-481 9 May	SR-481 30 May	2.97	71.31**
	SR-481 9 May	SR-481 21 June	2.57	104.58**

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Table 29c. - continued.

Year	Cultivar and seeding date		F Value	
	Regression 1	Regression 2	Slope	Elevation
1991	SR-481 9 May	SR-481 12 July	0.13	6.22*
	SR-481 30 May	SR-481 21 June	2.36	113.91**
	SD-481 30 May	SD-481 12 July	0.47	3.31
	SR-481 21 June	SR-481 12 July	0.91	108.66**

*, ** Slope or elevation of regression lines 1 and 2 are significantly different at P=0.05, and 0.01, respectively, analysis of covariance.

Table 29d. Equality of slopes and elevations of linear regressions of cavity spot incidence of Red Core Chantenay and Six Pak in different years.

Cultivar and year		F Value	
Regression 1	Regression 2	Slope	Elevation
Red Core Chantenay 1987	Red Core Chantenay 1988	0.05	1.09
Red Core Chantenay 1987	Red Core Chantenay 1992	0.12	1.52
Red Core Chantenay 1988	Red Core Chantenay 1992	0.19	5.30*
Six Pak 1988	Six Pak 1990	0.81	4.73*
Six Pak 1988	Six Pak 1991[1]	4.99*	7.96*
Six Pak 1988	Six Pak 1992	0.35	6.96*
Six Pak 1990	Six Pak 1991[1]	2.39	2.59
Six Pak 1990	Six Pak 1992	0.01	1.40
Six Pak 1991	Six Pak 1992	1.75	0.19

*, ** Slope or elevation of regression lines 1 and 2 are significantly different at P=0.05 and P=0.01, respectively, analysis of covariance.

1 Six Pak seeded 30 May, 1991.

had equivalent slopes but higher elevations than carrots of the same cultivar seeded 7 June. In 1991, seeding date affected the elevation of disease progress curves of both Six Pak and SR-481, but only the slope of disease progress on Six Pak. The pattern of disease progress was not consistent with that of the 1990 trial. The curve for SR-481 seeded on 9 May had a steeper slope and higher elevation than those of the later-seeded carrots, while the disease progress curve of Six Pak carrots seeded on 12 July had a steeper slope and higher elevation, followed by those of 9 May, 21 June and 30 May.

The disease progress curves for cultivars Red Core Chantenay and Six Pak did not change significantly from year to year, except in 1988 (Table 29d). The elevation of the disease curve for Red Core Chantenay was higher in 1988 than in 1992, and that of Six Pak was higher in 1988 than in 1990, 1991, and 1992.

Major factors affecting disease progress

Cultivar effects

Six Pak had lower cavity spot ratings than any other cultivar during all years of the trial. Cultivar Chanton had the highest AUCSIC and AUDIC ratings in the same trial. The AUDPC for Chanton in 1986 was 580 percent greater than that of Six Pak (2912 and 498 incidence days, respectively Table 21), and was more than 200% higher in 1988 (7638 and 3780 percent days, respectively, Table 23e). In the 1992 trial, Huron had the highest AUDPC rating (4745.0 incidence days), Red Core Chantenay an intermediate rating (3383.8 percent days) and Six Pak had the lowest (1485.0 percent days). Eagle and SR-481 all had AUDPC's that were higher than Six Pak (Table 24d, b, a). Red Core Chantenay developed less cavity spot than Chanton in 1988 (Table 23e) but more than SR-481 in 1992 (Table 24g).

Metalaxyl plus mancozeb

A metalaxyl plus mancozeb drench at seeding suppressed cavity spot

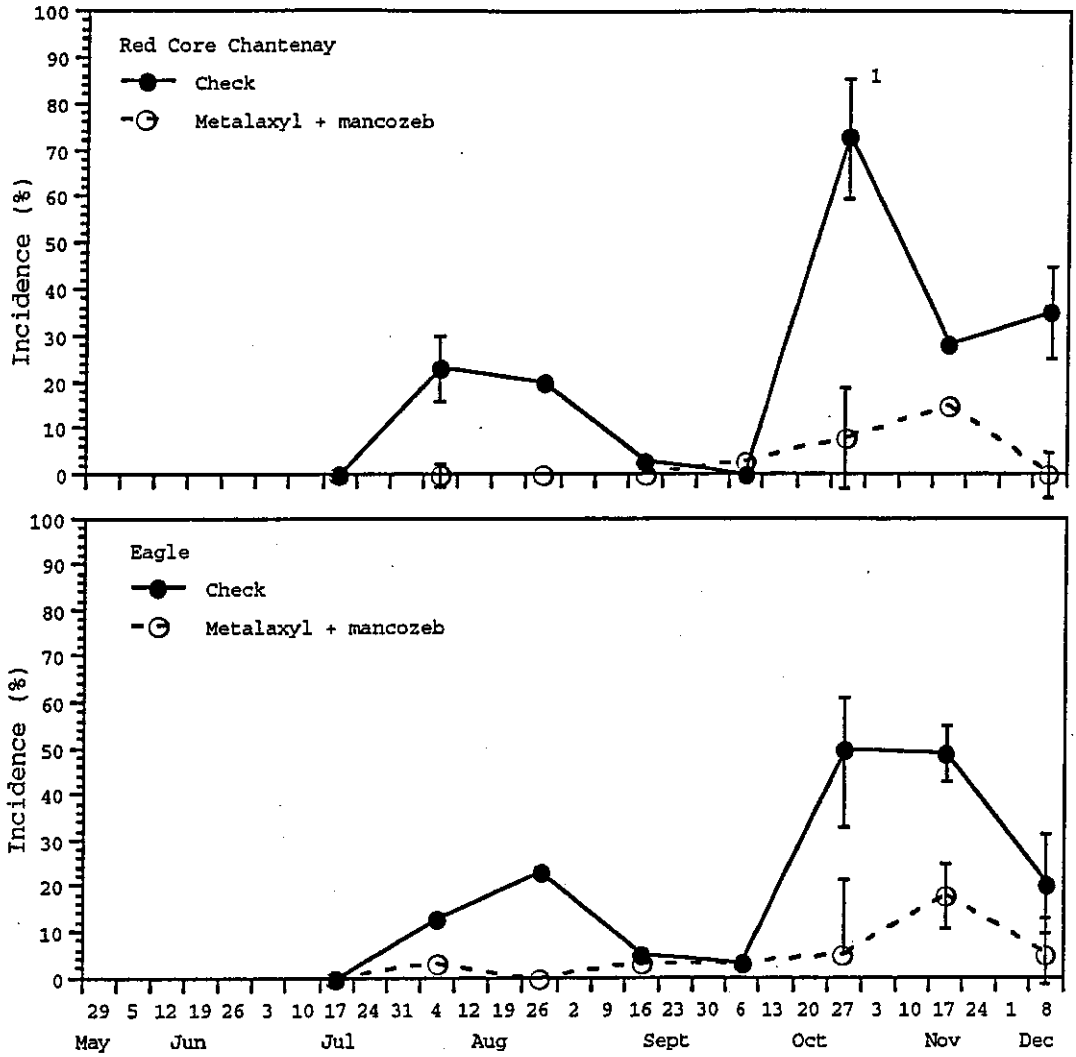
incidence and AUDPC of treated carrots in both 1988 (Table 23d) and 1992 (Table 24g). This fungicide treatment also delayed the start of the epidemic on non-irrigated carrots in 1992, but not in 1988 (Table 27a). There were no differences between the slopes and elevations of disease progress curves of untreated and metalaxyl plus mancozeb treated carrots (Table 29a).

Cultivar in relation to fungicide and PGPR efficacy

The choice of cultivar had a significant effect on the efficacy of metalaxyl plus mancozeb, PGPR and fosetyl-Al treatments in 1988 and 1992 when cavity spot was assessed as AUDPC (Table 23e, Appendix IV Table 24) In the 1988 trial, the metalaxyl plus mancozeb drench significantly reduced the AUDPC on Six Pak and Chanton but not Red Core Chantenay (Table 23e). The PGPR's Sp-102 and Pp-2 were effective only on Chanton. None of the PGPR treatments significantly reduced cavity spot on the other two cultivars (Table 23e). In 1992, there was a significant cultivar by fungicide interaction for AUDPC of carrots grown in the non-irrigated and irrigated plots (P=0.0426 and 0.0317, respectively, Appendix IV Table 24). Again, Six Pak had the lowest AUDPC. Fungicide treatment did not suppress cavity spot on Six Pak but treatment with metalaxyl plus mancozeb was effective on the other cultivars. Two examples are presented in Table 13a. Fosetyl-Al treatment reduced the AUDPC on the cultivars with the highest AUDPC's: Huron grown in the non-irrigated plot and on Red Core Chantenay grown in the irrigated plot.

Cavity spot development in storage

The development of cavity spot in storage was assessed by two methods. The change in number of lesions and large lesions per carrot from one assessment date to another was analyzed using the Wilcoxan Rank Test (Table 30) and Paired T Test (Table 31). In addition the effect of the treatments on numbers of lesions and large lesions/carrot was analyzed



1 Standard error bars were included only where points were significantly different at P=0.05, Duncan's New Multiple Range Test.

Figure 13. Cavity spot incidence on untreated and metalaxyl plus mancozeb treated Red Core Chantenay and Eagle in the non-irrigated plot in 1992.

Table 30. Effect of cultivar and seeding date on number and size of cavity spot lesions in storage from December 1990 to April 1991.

Cultivar	Seeding date	Lesions/carrot		Large lesions/[1] carrot 7.5mm	
		21 Dec.	17 Apr.	21 Dec.	17 Apr.
Chancellor	7 June	2.73	1.86	0.21	0.15
Chancellor	9 July	3.82	2.63	0.12	0.27
XPH-3507	7 June	3.71	2.41	0.18	0.55
XPH-3507	9 July	2.16	1.86	0.09	0.41
Cellobunch	7 June	2.66	1.88	0.11	0.21
Cellobunch	9 July	4.23	2.38	0.15	0.29
Six Pak	7 June	1.75	1.48	0.04	0.12
Mean		3.00	2.92	0.13	0.28
Wilcoxon Rank Test[2]		P=0.0001		P=0.0001	

1 Large lesions over 5 mm in vertical width.

2 The change in lesions/carrot and large lesions/carrot over the storage period was tested using the nonparametric Wilcoxon signed Rank Test.

Table 31. Effect of cultivar and metalaxyl treatment on the number and size of cavity spot lesions in storage in November 1992 and January 1993 and June 1993.

Cultivar	Metalaxyl+ mancozeb (2.0 kg ai/ha)	Lesions/carrot			Large lesions/[1] carrot		
		9 November	15 January	7 June	9 November	15 January	7 June
Six Pak	Check	0.25 b[2]	0.14 b	0.5 b	0.09 b	0.01	0.01 b
	Metalaxyl	0.13 b	0.09 b	0.3 b	0 c	0	0 b
Red Core Chantenay	Check	0.55 a	0.41 a	3.0 a	0.32 a	0.06	0.26 a
	Metalaxyl	0.09 b	0.06 b	0.2 b	0.03 bc	0.01	0.06 b
Mean		0.23	0.18	1.06	0.11	0.02	0.08
Paired T Test[3]		P=0.027	P=0.015		P=0.157	P=0.196	

1 Large lesions over 5 mm in vertical width.

2 Values in a column followed by the same letter are not significantly different at P=0.05, Duncan's New Multiple Range Test.

3 P values for the Paired T Test are for consecutive assessment dates. P values for the change from 9 November to 7 June are P=0.02 and P=0.29 for lesions/carrot and large lesions/carrot, respectively.

with analysis of variance to determine if the effects of the treatments changed over time (Table 31). The mean number of lesions per carrot decreased while carrots were kept in cold storage in 1990/1991 and increased in 1992/93. The change in number of large lesions (<5 mm width) per carrot also varied depending on the year (Tables 30, 31). During the 1990/91 storage period, the number of large lesions per carrot increased (Table 30) while there was no significant change during the 1992/93 storage period (Table 31). Cultivars or treatments that had the highest numbers of lesions at the start of the storage period also had the highest numbers of lesions at the end of the storage period.

In 1990/91, the mean number of lesions per carrot on 17 April was approximately 2/3 of the number of lesions on 21 December, except on Six Pak carrots where the decrease was less. The number of large lesions per carrot doubled over the storage period on Chancellor carrots seeded 9 June 1990, and Cellobunch, and tripled on carrots of XPH-3507 and Six Pak. The resistant cultivar Six Pak had the lowest number of lesions and large lesions per carrot throughout the storage period, even though the number of large lesions tripled while the carrots were in storage (Table 30).

On 9 November 1992 and on 15 January and 7 June 1993, untreated carrots of Red Core Chantenay had the highest number of lesions per carrot while there were no differences among the numbers of lesions per carrot on untreated Six Pak, and Six Pak and Red Core Chantenay carrots treated with metalaxyl plus mancozeb (Table 31). These results are similar to the comparison of the cavity spot incidence of these treatments at harvest on 27 October (155 days after seeding) (Tables 24a, e). Untreated Red Core Chantenay carrots also had the highest number of large lesions/carrot. The number of lesions/carrot decreased while the carrots were in storage from 9 November, 1992 to 15 January 1993, then increased by 7 June 1993. The number of lesions/carrot approximately doubled on carrots of all treatments that had low numbers of lesions on 9 November (Six Pak and Red Core Chantenay treated with metalaxyl plus mancozeb, Table 31) while the

increase on the untreated Red Core Chantenay was over 500 percent. There were no significant changes in the number of large lesions/carrot during the storage period. Untreated Red Core Chantenay had both the greatest number of lesions/carrot and large lesions/carrot.

DISCUSSION

This is the first study to systematically describe the disease progress of cavity spot on field-grown carrots and the first to examine the influence of cultivar resistance, treatment with metalaxyl plus mancozeb and plant growth-promoting rhizobacteria and seeding date, on the shape and magnitude of the disease progress curves. The present study is also the first to identify a PGPR as a potential biological control agent for cavity spot, to demonstrate that older carrots were not more susceptible to the disease than younger carrots, and to document a marked decrease in cavity spot incidence late in the season.

Various levels of resistance to cavity spot were found among the carrot cultivars tested. Six Pak was most resistant, while SR-481, Eagle and Red Core Chantenay had intermediate levels of resistance and Chanton and Huron were most susceptible. Disease progress of cavity spot was generally best described by a straight line although logistic and Gompertz transformations were highly correlated to disease progress in several instances.

Fungicide efficacy

Metalaxyl

The present study confirmed that the selective fungicide, metalaxyl, significantly reduced the incidence of cavity spot on carrots grown on organic soil in Ontario. Metalaxyl was most effective when applied as a furrow granular treatment or as a drench with mancozeb, within six weeks of seeding. The granular formulation of metalaxyl reduced cavity spot at

rates of 0.2 to 4.0 kg ai/ha, however, the 4.0 kg ai/ha rate was phytotoxic. Rates of 1.0 and 2.0 kg ai/ha also reduced seedling emergence on cv. Comet. Drench applications of metalaxyl were effective at rates of 0.5 or 2.0 kg ai/ha. Foliar applications of metalaxyl plus mancozeb at 1.2 and 3.6 kg ai/ha were applied 12 and 17 weeks after seeding and were not as effective as early season (zero to six weeks after seeding) drench applications at 2.0 kg ai/ha. Seed dressings with metalaxyl or benalaxyl plus thiram resulted in inconsistent control.

Several researchers also have reported reductions in cavity spot with metalaxyl applied at similar rates. Lyshol et al. (1984) found that a spray application of 2.0 kg ai/ha metalaxyl at seeding suppressed cavity spot. Davis et al. (1991) reported that a post-plant application at 2.24 kg ai/ha was more effective than a 1.12 kg ai/ha rate but eight split applications totalling 1 or 2 lb ai/acre provided the best control. A pre-plant granular application at 4.48 kg ai/ha was as effective as the 22.4 kg ai/ha spray, and did not reduce yields. Walker (1991) reported that granular metalaxyl applied at rates of 0.43 to 4.8 kg ai/ha controlled cavity spot, but a rate of 0.21 kg ai/ha did not. He also determined that a granular formulation of metalaxyl, Ridomil 50G, and Ridomil 72WP were equally effective, and no additional benefit was provided by the mancozeb present in Ridomil 72WP.

These trials were all conducted on carrots growing in sandy loam mineral soils. Gladders and McPherson (1986) tested metalaxyl on both organic and mineral soils in Britain and found that a rate of 1.2 kg ai/ha consistently suppressed cavity spot and there was no benefit to split applications.

Application of a metalaxyl plus mancozeb drench at seeding reduced the number of carrots with cavities, and the AUDPC, however, this treatment did not significantly affect the shape, slope, or elevation of the cavity spot incidence curve. On several occasions, the metalaxyl plus mancozeb drench resulted in a significant delay in the start of the

epidemic and was associated with a lag of two to three weeks in symptom expression. Often there was a marked late-season decrease in the incidence of cavity spot on carrots that had received the metalaxyl plus mancozeb drench.

The effect of metalaxyl plus mancozeb on the progress of cavity spot has not been reported in the literature. A delay in the start of the epidemic may indicate that the fungicide treatment provided complete protection from infection for a certain time, or that it reduced the infection efficiency of the inoculum to an extremely low rate. The start of the epidemic on treated carrots may occur once the metalaxyl begins to degrade and become less effective, although the levels of cavity spot remained lower on treated than on untreated carrots throughout the epidemic. Kannwischer and Mitchell (1978) found that metalaxyl (CGA 48988) treatment delayed the start of the black shank epidemic on tobacco, but after the initial delay, the epidemic progressed more rapidly on treated plants. The rapid increase in disease was thought to correspond to a reduction in efficacy of the fungicide at that time. However, this does not satisfactorily explain the changes in the progress of cavity spot.

The decrease in incidence in November and December have not been reported prior to this study. These effects suggest that metalaxyl has a direct effect on the host since the fungicide concentration in the soil decreases over time and would be lower at this stage of growth than earlier in the season. The half-life of metalaxyl in Bradford muck soil is eight weeks (Sharom and Edgington 1982).

Fosetyl-Al and phosphorous acid

Fosetyl-Al and phosphoric acid were as effective as metalaxyl when applied as foliar sprays 12 or 17 weeks after seeding, but fosetyl-Al did not suppress cavity spot when applied as a drench over the seed furrow, except on the susceptible cultivars, Huron and Red Core Chantenay. Walker

(1991) found that phosphonate, (equivalent to phosphoric acid), did not control cavity spot at rates of 10 or 16 kg ai/ha when applied four, six, eight, ten or twelve weeks after seeding. However, application at 25 kg ai/ha 14 weeks after seeding was effective. These rates were much higher than those used in the present trial (1.6 to 4.8 kg ai/ha). Lyshol et al. (1984) found that fosetyl-Al reduced cavity spot incidence as effectively as metalaxyl when applied to carrots in pots. However, the effective rate of fosetyl-Al was 53 times greater than the effective rate of metalaxyl. This corresponds to the difference in rates used by Walker (1991).

The low rates of fosetyl-Al and phosphoric acid used in the present trial were as effective as 1.2 or 3.6 kg ai/ha of metalaxyl when applied as foliar sprays. Fosetyl-Al has a half-life of 16 weeks in soil, but is very soluble in water (Cohen and Coffey 1986) and could quickly leach out of soil. Thus, fosetyl-Al may be more effective if applied during the season when high levels of infection are taking place rather than applied early for season-long control. Walker's (1991) data on timing of fungicide applications suggested that the cavity spot epidemic began about 14 weeks after seeding, and this was when the application of phosphonate was most effective. Earlier applications may have leached out of the root zone before conditions were correct for infection by Pythium propagules. However, there are some reports that phosphorous acid can persist in soil and plant tissues for several weeks or months (Cohen and Coffey 1986, Ouimette and Coffey 1989). Tests to determine the concentration of phosphorous acid in the soil and carrot roots would be needed to determine if leaching reduced the efficacy of phosphorous acid in Walkers's (1991) trial.

In the present trial, phosphoric acid was as effective as fosetyl-Al in reducing cavity spot. This was expected because phosphorous acid is the active metabolite of fosetyl-Al (Cohen and Coffey 1986).

Seed dressings

The fungicide seed dressings gave variable results when evaluated for effectiveness in reducing cavity spot. In 1986, benalaxyl plus thiram at 0.002 + 0.0004 kg ai/ha reduced cavity spot severity on cv. Chanton but not on Comet. In 1987, both seed dressings applied at 500 percent of the 1986 rate reduced cavity spot severity at harvest, while benalaxyl-thiram applied at 1,000 percent of the recommended rate (0.02 + 0.04 kg ai/ha) was ineffective. In the 1988 trial the 0.06 kg ai/ha rate of metalaxyl, which suppressed cavity spot in the 1987 trial, was not effective on the three cultivars tested.

The failure of the high rate (0.01 kg ai/ha) of benalaxyl plus thiram to reduce disease incidence compared to the untreated check may be related to the thiram in the formulation. While thiram does have some activity against Pythium, it is a broad-spectrum fungicide and may control other soil-borne fungi that compete with the Pythium spp. Soil treatment with iprodione, which does not control Pythium spp., actually increased the severity of cavity spot over that of the untreated check (Valk et al. 1986). In a similar experiment, Lyshol et al. (1984) found that iprodione, applied as a seed dressing or a spray, did not significantly reduce or increase cavity spot.

In other trials to evaluate the effectiveness of fungicide seed dressings for the control of cavity spot, Lyshol et al. (1984) found that neither metalaxyl at a rate of 1.4 g ai/kg seed nor fosetyl-Al at 9.6 g ai/kg seed significantly reduced the incidence of cavity spot in carrots grown in sandy loam soil in pots. White (1986), using the same rate of metalaxyl found a reduction in the incidence of cavity spot, but the control was not as great as when a metalaxyl soil drench (150 ml per pot of a solution containing 1.6 ai metalaxyl/L) was used in combination with the seed dressing. Walker (1991) did not find any differences in incidence of cavity spot between carrots grown from untreated seed and those grown from seed treated with 1.5, 3 or 6 g metalaxyl/kg seed.

The present trial was conducted in the field with carrots growing in organic soil where the other trials cited were conducted on carrots seeded in sandy loam soil in the field or in pots. However, the efficacy of the seed dressings in increasing seedling survival and reducing cavity spot was variable in all the trials.

Fungicide seed dressings did not have a significant effect on the emergence and survival of carrot seedlings in any of the trials nor did furrow granular or drench applications of metalaxyl. Similarly, Lyshol et al. (1984) found no significant differences in seedling emergence with the use of metalaxyl or fosetyl-Al seed dressings when carrots were grown in naturally infested sandy loam soil in pots. In carrot trials conducted on a sandy loam soil in Australia, Walker (1991) reported a significant increase in seedling survival when seed was dusted at rates of 1.5, 3 or 6 g metalaxyl/kg seed. These rates were within the range used by Lyshol et al. (1984) (1.4 g ai/kg seed) and in the present trial (3.5-17.5 g ai/kg seed). Walker also reported a significant reduction in mean root weight as a result of the seed treatments but attributes this to increased competition among plants rather than a phytotoxic effect of the fungicide.

Some mortality of seedlings after emergence does occur on carrots grown on muck soils. However, it is unknown how much of this seedling mortality can be attributed to Pythium-induced damping-off. In the 1988 trial, some of the mortality appeared to be the result of heat stress. Since none of the fungicide treatments significantly increased seedling survival, Pythium induced damping-off did not appear to be major contribution to seedling mortality in this trial.

Phytotoxicity

The highest rate of granular metalaxyl (Subdue 5G at 4.0 kg ai/ha) significantly reduced seedling emergence and appeared to be phytotoxic. There was a significant negative correlation between rate of Subdue 5G and carrot emergence for cv. Chanton but not Comet which suggests that rates

lower than 4.0 kg ai/ha may also be phytotoxic. Seedlings of Chanton may be more sensitive to metalaxyl than those of Comet. Wheatley et al. (1984) found that metalaxyl was phytotoxic and reduced plant stand when the fungicide was incorporated into a seeding gel at a rate of 6 mg/m row (approximately 1.12 kg ai/ha). Unbuffered phosphorous acid is reported to be phytotoxic to plants (Cohen and Coffey 1986) but no indications of phytotoxicity were seen on the carrot foliage.

Timing of fungicide applications

Metalaxyl was most effective when applied to carrots from zero to six weeks after seeding. Applications 12 or 17 weeks after seeding reduced cavity spot, but the level of control was not as great. Gladders and McPherson (1986), Walker (1991), and Davis et al. (1991) all reported similar results, although Gladders and McPherson (1986) found that application up to four weeks after seeding provided the best control, while Davis et al. (1991) concluded that application up to 59 days after seeding was effective. Walker (1991) found that metalaxyl provided good control of cavity spot when applied between four and fourteen weeks after seeding. None of these researchers harvested carrots from the plots during the growing season to follow disease progress, so it is not known whether lesions had started to develop at the time the metalaxyl was being applied. In the present study, there were no visible lesions on carrots harvested eight weeks after seeding, when the final metalaxyl drench was applied, but cavity spot developed on 31.5% of the carrots by harvest time.

Metalaxyl is relatively water soluble and leaches through sandy loam soil much faster than through organic soil (Sharom and Edgington 1982). In organic soils, metalaxyl is washed into the soil by rainfall but is carried back toward the soil surface by capillary action as water evaporates. Metalaxyl also has a longer half-life in organic than in mineral soil (eight weeks in Bradford muck vs. three weeks in Fox sandy

loam). Thus, the effective rate may vary with soil type and amount of rainfall or irrigation. In the Bradford area, metalaxyl applied to the soil would be expected to have a long half-life and remain in the top 0-20 cm of soil. Therefore, one application at seeding could provide season-long control of cavity spot. Where carrots are planted in sandy loam soil and receive high amounts of rainfall or irrigation during the growing season, split applications of metalaxyl may be required to replenish the fungicide that has degraded or leached out of the soil. However, in Australia (Walker 1991), a single application of metalaxyl at a rate 0.43 kg ai/ha provided season-long control of cavity spot on carrots grown on sandy loam soil.

Since early season applications of metalaxyl provide the best control of cavity spot, some infection of the carrot seedling must occur very early during the development of the carrot, certainly within the first four or six weeks after seeding. In this study and other reports (Montfort and Rouxel 1988, Vivoda et al. 1991) lesions were observed on carrots six weeks after seeding. The authors did not relate these observations to weather data or control with fungicides. Esau (1940) demonstrated that the root cortex of seedling carrots begins to rupture about 32 days after seeding, when the carrots had four true leaves, and by 39 days the cortex has been sloughed off, with only a few fragments remaining attached to the hypocotyl. Once the cortex is gone, periderm forms over the "root" (hypocotyl plus true tap root) surface. Perhaps the loss of the cortex provides additional nutrients to Pythium propagules in the surrounding soil and an increase in Pythium infections takes place at this stage. Another explanation is that any infections that occur prior to the time the cortex is lost are sloughed off with the cortical tissue. Thus, the efficacy of early-season fungicide treatments may be related to this physiological stage of growth. It appears that the seedling root must be protected by fungicide at this stage to effectively control cavity spot under Ontario conditions.

Some cavity spot lesions were visible when foliar fungicides were applied to carrots 12 and 17 weeks after seeding. Cavity spot incidence continued to increase on carrots sprayed 12 weeks after seeding (21 August) but not on those sprayed 17 weeks after seeding. The lesions that became visible after the fungicide applications could have resulted from infections that had taken place before the fungicide was applied but which had not produced visible lesions. However, this does not explain, why there was not further lesion development on the carrots sprayed on 22 September. Perhaps conditions were not favourable for infection prior to the second spray and no asymptomatic infections were present at that time. The relationship between soil moisture and temperature and cavity spot development was examined in Chapter 4. There are several reports (Perry and Harrison 1979b, Soroker et al. 1984, Vivoda et al. 1991) that suggest it may take four to six weeks for typical cavity spot lesions to develop on carrots at temperatures between 15 and 25°C. Therefore, the presence of asymptomatic infections at the time of fungicide application is possible.

Cultivar resistance

Cultivar Six Pak was more resistant to cavity spot than other cultivars in these trials and had significantly lower ratings for cavity spot incidence, and AUDPC. The slopes of the disease progress curves for Six Pak were also lower than those of cultivars Chanton, Chancellor and Huron, and of Red Core Chantenay grown in the irrigated plot in 1992. The number of lesions per carrot was not assessed, except in the storage trials. In the 1992/93 trial, Six Pak had fewer lesions per carrot than Red Core Chantenay.

Cultivar Chanton appeared to be the most susceptible cultivar evaluated. The AUDPC for Chanton was 580 percent greater than that of Six Pak in 1986 and 200 percent higher in 1988. Huron was also very susceptible. Red Core Chantenay, Chancellor, Cellobunch, SR-481, and

Eagle all appeared to be moderately susceptible to cavity spot when AUDPC values were compared to those of Six Pak and Chanton or Huron.

Eagle was originally included in the 1992 trial as a resistant cultivar based on the low cavity spot rating (20VL) it received in the 1991 cultivar elevation at the Muck Research Station (McDonald et al. 1991). It was as resistant as Six Pak when grown in the non-irrigated plot but was more susceptible when grown under irrigated conditions. Cultivar SR-481 was included as a very susceptible cultivar in 1991 and 1992 based on the results from trials conducted by Sun Seeds, Brooks, OR (Roger Freeman, personal communication) but SR-481 was found to be less susceptible than Red Core Chantenay. Thus, cavity spot ratings based on AUDPC appear to be more reliable than assessments on a single harvest date. Unfortunately, the time involved in collecting the information for disease progress curves makes it very difficult to assess large numbers of cultivars using this method.

Cultivar in relation to fungicide and PGPR efficacy

Fungicides

The choice of cultivar had a significant effect on the efficacy of the fungicide treatments in 1988 and 1992. In 1988, the metalaxyl plus mancozeb drench significantly reduced the AUDPC on Six Pak and Chanton. The most resistant and most susceptible cultivars in the trial, respectively. In 1992 both metalaxyl plus mancozeb and fosetyl-Al were more effective on the susceptible cultivars than on resistant Six Pak. Metalaxyl plus mancozeb treatment reduced the AUDPC on all of the susceptible cultivars in the trial, while fosetyl-Al was ineffective except on Huron in the non-irrigated plot and Red Core Chantenay in the irrigated plot. Huron and Red Core Chantenay were the most susceptible cultivars in the respective trials, based on the AUDPC values of the untreated checks.

The results of this study are in agreement with those of Sweet et al.

(1989), who evaluated cavity spot severity in relation to cultivar resistance and treatment with metalaxyl plus thiram. They found that resistant varieties overall had less cavity spot and fungicide responses were greater in the more susceptible varieties.

The 1992 data indicate that there may be no advantage to applying selective fungicides to cultivars with relatively high levels of resistance, such as Six Pak. However, in 1988, when conditions were more conducive to disease development (AUDPC for Six Pak of 3599 and 1485 in 1988 and 1992, respectively) the metalaxyl plus mancozeb drench significantly reduced the AUDPC. Thus, if carrots are to be grown in a field with a history of severe cavity spot, the best approach may be to seed a resistant cultivar and apply metalaxyl.

In both 1988 and 1992, the application of metalaxyl plus mancozeb to susceptible cultivars reduced the cavity spot incidence to that of untreated Six Pak. This supports the suggestion by Fry (1975) and Bruin and Edgington (1983) that horizontal resistance can replace the bulk of fungicide use. Fry (1975) was able to quantify the reduction in rate of mancozeb in relation to the level of horizontal (polygenic) resistance to Phytophthora infestans (Mont.) de Bary in potatoes.

It was not possible to quantify the levels of cavity spot resistance in carrots based on rates of metalaxyl or metalaxyl plus mancozeb. No strong dose: response relationships were found in the present trial when metalaxyl was applied as a granular furrow treatment (0.2 to 4.0 kg ai/ha) or when metalaxyl plus mancozeb was applied as a foliar spray (1.2 or 3.6 kg ai/ha). Similarly, Gladders and McPherson (1986) and Sweet et al. (1989) found no differences in cavity spot severity at rates of 0.6 to 1.2 kg ai metalaxyl/ha, and White (1991) reported no differences in cavity spot incidence in response to a granular formulation of metalaxyl applied at rates of 0.43 to 4.28 kg ai/ha. The potato late blight and cavity spot of carrot disease systems are quite different and consequently differences in the relationship between cultivar resistance and fungicide rate are not

surprising. Fry (1975) was dealing with a protectant fungicide applied several times during the season and a polycyclic foliar disease, whereas metalaxyl is a systemic fungicide and is only applied once per season to control cavity spot. Vanderplank (1968) observed that the periodic application of a protectant fungicide acts in a similar manner to horizontal resistance in reducing the apparent infection rate. Conversely, the effect of a systemic fungicide may be similar to that of vertical resistance, in that it reduces the amount of effective initial inoculum.

Metalaxyl has been reported to stimulate the host defense systems, or more possibly to interfere with a pathogen's ability to suppress host defenses (Ward 1984). Metalaxyl may be less effective on Six Pak because the host's resistance mechanisms are already working more efficiently than those of more susceptible cultivars.

Plant growth-promoting rhizobacteria

There was a significant interaction between PGPR efficacy and cultivar susceptibility in the 1988 trial. Two of the isolates, Sp-102 and Pp-2 effectively reduced the AUDPC on Chanton, but none of the PGPR's was effective on the other, more resistant, cultivars. The efficacy of these PGPR's did not appear to be related to the degree of colonization of the seedling carrot roots of different cultivars. Recovery rates from Six Pak and Red Core Chantenay were higher than from Chanton. However, isolate Pp-2 was most effective on Chanton and was recovered from seedling roots of Chanton carrots at a higher rate than the other two isolates. There were insufficient data to reach a firm conclusion about efficacy and recovery rates. Colonization was estimated by determining the rate of recovery of rifampicin-resistant isolates from the roots. It is generally assumed that root colonization by introduced bacteria is essential for biocontrol of root pathogens and increasing the population of an

introduced bacterium on the root should enhance disease control (Weller 1988). The recovery of all three isolates from carrot roots was low (0.22-2.02 $X10^3$ cfu/cm root). Sher et al. (1984) defined root colonizers as those bacteria which attain a density of greater than $5X10^3$ cfu/g root. Whether the PGPR isolates in the present trial reached that density cannot be determined because the seedling roots were not weighed. Weller (1988) defines root colonizers as those bacteria which when introduced, become distributed along the root in natural soil, propagate, and survive for several weeks in the presence of competition from indigenous rhizosphere microflora. The PGPR isolates in the present study were applied to the carrot seed and recovered from roots three weeks after seeding. Thus, they meet the criteria of root colonizers.

There have been no other studies on the effects of PGPR seed treatment on the suppression of cavity spot or other carrot diseases. Therefore, it is not known whether the cultivar effect on the efficacy of the PGPR's is a widespread phenomenon or if Chanton is somehow unique.

Characterization of resistance to cavity spot

According to Vanderplank (1982) there are two types of resistance to plant disease, horizontal and vertical. Both types can exist in the same plant, but vertical resistance can mask horizontal resistance. Horizontal resistance reduces the rate of disease progress, while vertical resistance delays the start of the epidemic, although there are exceptions to both cases. The components of horizontal resistance are: 1) lower infection efficiency on resistant plants, 2) sporulation is less abundant, 3) the latent period is longer, and/or 4) infected tissue ceases to be infectious sooner (Vanderplank 1963).

In the present study, three epidemic parameters were analyzed and compared to determine whether the resistance of carrots to cavity spot was primarily horizontal or vertical. The parameters were: 1) the start of the epidemic, 2) the slope and 3) elevation of the disease progress

curves. The slope of the disease progress curve represents the apparent rate of the epidemic while the elevation indicates the infection efficiency of the inoculum. The disease progress curves were also compared to detect differences in the incubation period, as an estimate of the duration of the latent period.

None of the cultivars in the present trial had complete resistance to cavity spot; the resistance was only partial resistance, since some lesions did develop. Partial resistance can be either vertical or horizontal (Vanderplank 1982) but the resistance of Six Pak carrots to cavity spot has several of the components of horizontal resistance. Cultivar resistance did not significantly affect the start of the epidemic during any of the years of this trial with the possible exception of 1986. A delay in the start of the epidemic is the major effect of vertical resistance. There is also evidence that Pythium propagules have lowered infection efficiency on Six Pak. Six Pak consistently had a lower incidence of disease, regardless of the plant age when the sample was taken. The only exceptions were found early in the season when the levels of cavity spot were low and variable and there were no significant differences found among the cultivars. Also, the disease progress curves for Six Pak had lower elevations than those of the susceptible cultivars, indicating that fewer carrots became infected despite similar inoculum levels and similar environmental conditions.

A lag in the appearance of cavity spot lesions was observed on Six Pak carrots in 1986 and during portions of the epidemic in 1988 and 1992. This would suggest that the incubation period is longer on resistant Six Pak than on susceptible cultivars, under some conditions. Carrots were harvested at weekly intervals during part of the 1986 growing season but were harvested at two to three week intervals in 1988 and 1992. The longer harvest intervals may have obscured the lag in the disease progress curves if the differences in length of the incubation period were relatively short (i.e. one week) or if overlapping infections occurred.

A longer incubation period probably means that the latent period on Six Pak is longer as well. However, the duration of the latent period for cavity spot is unknown. It has not been established whether propagules are released during the growing season or in the following season after carrots are left in the ground to decay. Phelps et al. (1991) suggested that initial infections of carrot roots during the growing season result in subsequent reinfection of the same root, possibly by mycelial growth, and that the rate of the reproductive process is dependent on cultivar. Reinfection of the same root was not measured in the present study, but a cultivar dependent reproductive rate implies that horizontal resistance is involved. There were no differences among the slopes of the disease progress curves for the different cultivars in any year. That is, cultivar resistance did not affect the rate of disease progress. This would indicate that there were no differences in the levels of horizontal resistance among the cultivars. One possible explanation for this discrepancy is that the linear regressions did not adequately represent the disease progress curves and, thus, real differences in the slopes of the actual curves could not be detected. To determine conclusively whether the resistance is vertical or horizontal, cultivars with different levels of resistance must be challenged with different races of a pathogenic Pythium spp (Vanderplank 1968). No races of Pythium spp. have been identified. Six Pak appears to have many of the components of horizontal resistance, but the resistance could be partial vertical resistance similar to slow rusting of wheat (Vanderplank 1984).

Is the cavity spot epidemic monocyclic or polycyclic?

Cavity spot is probably a monocyclic disease, although it is difficult to determine the shape of a typical disease progress curve from those obtained from field trials and presented above. Gilligan (1983) cautioned against the misapplication of simple interest and compound interest disease models and Morall and Verma (1981) questioned the

inverted logic of making inferences about the disease cycle on the basis of goodness of fit tests to these growth models. Even Vanderplank (1982) warned that the logistic model should not be used as a model for disease increase because it fails to account for the incubation period.

Disease progress curves in the present study were usually best described by simple linear regression. In other instances, the logistic, logarithmic and Gompertz transformations resulted in the best fit. Only three of the sixty-eight curves were best described by the monomolecular model. Campbell et al. (1980) found that the simple interest disease model was not appropriate for describing epidemics of snapbean hypocotyl rot. They also found that linear regression adequately described some of the epidemics but did not discuss a possible biological basis for this pattern of disease progress. They did suggest that secondary infections of adjacent roots could take place across intertwined roots.

Phelps et al. (1991) studied the distribution of cavity spot and suggested that initial infections subsequently reinfect the same root. This type of secondary infection would not have been recorded in the present trial.

The results presented above and in other reports indicate that the Pythium spp. which cause cavity spot infect the carrot root within the first four to six weeks after seeding and possibly throughout the growth of the carrot (Gladders and McPherson 1986, White 1988). Lesions develop after infection takes place, but the duration of the incubation period is unknown. Oospores have been observed among the cells of infected carrots (Benard and Punja 1992). In addition to infecting the main tap root, the Pythium spp. also infect the lateral roots (White 1986). Most Pythium spp. that cause cavity spot do not produce zoospores (White 1988). Thus, oospores and sporangia which germinate directly would be the main propagules. These would be released into the soil when the carrot tissue decays. This would normally occur in the year following the initial infection. Thus, cavity spot would be a typical monocyclic disease.

However, there is a possibility that infected lateral roots could deteriorate within the same season they were infected, and release Pythium propagules that could infect neighbouring plants. Lyons and White (1992) found no evidence of the secondary infection of adjacent plants.

The linear disease progress curves for several epidemics, and the poor fit of some of the other transformations were probably caused by effects of environment on infection and/or symptom expression. Gilligan (1983) indicates that when assessing disease progress curves of soilborne plant pathogens, "Variation in infection rates due to variation in environmental conditions are probable and can cause poor fit". Disease progress curves for cavity spot often have several peaks and valleys probably as a direct response to changes in the environment. Because of these changes, linear regression would provide the best fit because it "averages" the peaks and valley.

Uneven distribution of inoculum, which is common for soilborne diseases, can also affect disease progress. If there are no secondary cycles of infection, the final level of disease may be lower if the inoculum is highly clustered than if it is less aggregated or randomly dispersed (Campbell 1982). Also, aggregation of inoculum may increase the variance for disease severity levels. Significant block effects for the analysis of variance for the cavity spot incidence were found in 1988 and 1990, which indicates that the inoculum was not randomly distributed in the field plots, or that other soil factors have an influence on infection. Aggregation of the inoculum may have also affected the shape of the disease progress curves. Since it is not possible to isolate Pythium violae from soil, it was not possible to determine inoculum densities for this fungus in the field plots.

Plant age

There were no indications that older carrots were more susceptible to cavity spot than younger carrots when carrots were seeded on different

dates in the same plot. No significant differences were found among the AUDPC values of individual cultivars seeded on different dates in 1990 or 1991. Cellobunch was the only exception, where carrots seeded on 9 July 1990 had a higher AUDPC than those seeded a month earlier. Younger carrots of this cultivar were more susceptible to cavity spot.

One example of older plant susceptibility was found on SR-481 carrots on the 19 September, 1991 sample date. Cavity spot increased dramatically on carrots seeded on 9 and 30 May, but not on those seeded 21 June or 12 July. These carrots had been seeded 19, 16, 13 and 10 weeks prior to the sample date. However, at subsequent sample dates there were no significant differences in cavity spot incidence among the carrots, regardless of seeding date.

Several researchers (Maynard et al. 1963, Montford and Rouxel 1988, Vivoda et al. 1991) observed that the severity of cavity spot increased during the growing season. However, this does not indicate that carrots become more susceptible as they age, only that cavity spot continues to develop during the season. Perry and Harrison (1979b) and Vivoda et al. (1991) did report that older carrots were more susceptible to cavity spot than younger carrots. Perry and Harrison (1979b) found an increase in the incidence of cavity spot while Vivoda et al. (1991) reported that incidence did not increase but the number of lesions per carrot increased with plant age from three to five months. However, neither study was conducted under field conditions. It is possible that changes in susceptibility to cavity spot occur as the carrot grows and matures. Indeed, Vanderplank (1984) insists that the age of a plant affects all components of its resistance to disease, except possibly resistance to infection.

If changes in susceptibility do occur in carrots, they do not have an effect on the final level of cavity spot at harvest. The increases and decreases in cavity spot during the growing season appear to be more closely related to environmental factors than to plant age. Varying the

seeding date cannot be used as a method to avoid or reduce cavity spot at harvest.

Disease assessment

Several epidemic parameters are commonly used to compare the effects of control measures on the development of epidemics (Berger 1988). These include the rate at which the epidemic proceeds, the duration of the epidemic, the area under the disease progress curve (AUDPC) maximum amount of disease, time to reach 50% disease, and the amount of disease at a given time or crop stage. The present study utilized the AUDPC, the amount of disease at harvest, apparent infection rate (slope of the linearized disease progress) and elevation of the linearized curve. Of these parameters, the AUDPC was the most useful indicator of differences among treatments, but comparisons of the slopes and elevations of the disease progress curves also provided useful information.

Few significant cultivar by treatment interactions were found when carrots were assessed on single harvest dates throughout the growing season. Analysis of AUDPC provided a more reliable comparison of the effects of cultivar resistance, fungicide and PGPR treatment on the level of cavity spot. While cavity spot incidence can vary greatly from one sample date to the next, the AUDPC represents the amount of disease throughout the entire season. In practice, a grower would primarily be concerned about the cavity spot levels at the time of harvest but without an effective forecasting system, it is not possible to predict the incidence of cavity spot. However, choosing a cultivar or treatment that has the lowest AUDPC does not guarantee that these carrots will have the lowest levels of cavity spot on any one date, but increases the probability that they will.

It appears that the AUDPC is the better parameter than incidence to determine cultivar resistance and the efficacy of control measures even though, it is fast and easy to assess incidence. Assessment of AUDPC

requires more time and plot space since several samples must be taken during the season. Aust and Kranz (1988) suggest that five samples are the minimum needed to define a disease progress curve. However, analysis of AUDPC, provides the most information for the assessment of cavity spot. Fry (1978) also concluded that AUDPC was more reliable than the apparent infection rate or final disease rating for the quantification of effects of fungicide and resistance on late blight of potatoes. Similarly, Shaner and Finney (1977) found that the AUDPC was a better measurement of slow-mildewing of wheat than was the logit transformation.

Comparisons of slopes and elevations of disease progress curves provided information that was useful in determining the type of resistance to cavity spot in carrot. However, it was not possible to determine any effects of treatment with metalaxyl plus mancozeb by this method. There are a number of limitations to this method of disease assessment for cavity spot. The analysis of covariance only compares two regressions at a time, limiting multiple comparisons. Also, the regression lines that are compared are linear regressions. In 1991 and 1992, r^2 values were less than 0.5 for many regressions, indicating that neither simple linear regression nor the monomolecular, logarithmic Gompertz or logit growth curve transformations adequately described variation in disease incidence in relation to days after seeding. Many disease progress curves for the cultivars in the 1991 and 1992 trials had one or two peaks prior to the final harvest date. This is not a pattern that is described by the growth models commonly used in epidemiology. These peaks and valleys in the progress of cavity spot were probably a response to environmental factors that favoured infection or symptom expression. Thus, the comparison of slopes and elevations of linearized disease progress curves was not as useful for comparing measures to suppress cavity spot as was AUDPC or disease level at harvest.

Cavity spot development in storage

The present study confirmed observations that the severity of cavity spot increased while carrots were in cold storage. The mean number of lesions per carrot was found to decrease during the 1990/91 storage period but the number of large lesions/carrot increased. During the 1992/93 storage season, the number of lesions per carrot increased but the number of large lesions/carrot remained constant. Either of these changes would increase the severity of cavity spot.

The total number of lesions and large lesions per carrot were higher at the beginning of the storage period in 1990 than in 1992. The storage conditions were similar during both trials although the carrots did appear to lose more moisture during the 1990/91 storage period, which may have had an affect on disease development.

There have been no other studies examining cavity spot on carrots in storage, so it is not possible to compare the present study to other reports. However, there have been a number of studies on other diseases of carrot in storage (Heale et al. 1977, Davies and Lewis 1980, Lewis and Garrod 1983), which provide some information on the development of fungal diseases on carrots in cold storage.

Lesions caused by Mycocentrospora acarina (Hartig) Deighton and Botrytis cinera Pers. ex Fr. on carrot remain localized early in the storage period, but become progressive after four to six months at 2°C (Lewis and Garrod, 1983). The change from localized to progressive infection by B. cinerea has been attributed to a decline in ability of carrot tissue to accumulate 6-methoxymellein (Goodliffe and Heale 1978). An increase in the susceptibility of carrots to B. cinerea in storage has also been associated with water loss of more than five percent (Tronsmo 1989). This increase in susceptibility was also correlated with a decrease in the potential to accumulate 6-methoxymellein (Heale et al. 1977). Lewis and Garrod (1983) suggested that the changes in a carrot root which make it more susceptible to progressive infection by pathogens

coincide with the phase in the biennial cycle of the plant when growth of new shoots develops and might be considered an indication of root senescence.

An increase in the number or size of cavity spot lesions on carrots after several months of storage may be the result of the same physiological changes that govern the shift of B. cinerea and M. acarina infections from localized to progressive. Duration in storage appears to have the greatest effect on lesion number, with a decrease in the number of lesions occurring after two months. The increase in total number of lesions per carrot by the end of the 1992/93 storage period suggests that there were latent or asymptomatic Pythium infections in the carrot tissue when the carrots were harvested.

It is difficult to explain why the total number of lesions decreased during the 1990/91 storage period while the number of large lesions increased. Perhaps the levels of antifungal compounds were high enough to kill the hyphae in some, but not all of the lesions. The hyphae that remained functional were kept localized until the concentrations of 6-methoxymellein and other compounds decreased and then became progressive. Alternatively, secondary invaders may be responsible for the increase in lesion size, again in response to a reduction in the effectiveness of resistance mechanisms in the roots. It is also possible that the dehydration and shrinkage of the carrots concealed some of the smaller lesions.

It is important to note that, in general, levels of cavity spot in relation to cultivar resistance and treatment with metalaxyl plus mancozeb remained constant throughout the storage period. Neither cultivar resistance nor the effects of metalaxyl appeared to "break down" completely in storage. Thus, carrots with low levels of cavity spot going into storage will have relatively low levels of the disease at the end of the storage period.

The decrease in ability to accumulate antifungal compounds that

occurs in carrot roots after long periods of cold storage does not account for the decrease in the number of visible lesions after two months in storage. Wound healing, which can take place during storage, may effectively heal some of the lesions such that they are no longer visible or recognizable as cavity spot lesions. A reduction in the number of visible lesions on carrots during the later part of the growing season was observed in the present study, and may also be the result of wound healing.

Even though the metabolism of the root slows down, carrot root tissues remain capable of wound repair for a period of several months under conditions of high humidity and temperatures just above the 0°C, (Lewis and Garrod 1983). Wound repair can be stimulated by exposure to high temperatures (25°C) for $\geq$ 12 hours (Garrod et al. 1982). This treatment promotes lignification, suberization and sometimes callus development in carrot roots (Lewis and Garrod 1983). However, current recommendations for the commercial storage of carrots stress the importance of cooling the roots as quickly as possible to temperatures of 0-1°C (Ontario Ministry of Agriculture and Food 1992b). Low storage temperatures reduce the rate of wound healing and suberization in carrot (Garrod et al. 1982).

In the present study, the increase in lesion numbers during 1992/93 and large lesions during the 1990/91 storage period are probably the result of a reduction in the level of antifungal compounds that occur after prolonged storage and when carrot roots lose moisture. A reduction in the total number of lesions per carrot after a short period in storage may be the result of active wound healing. However, the results of this study may differ from the changes that occur in carrots under commercial storage conditions. During the time that the carrots were washed and assessed for cavity spot, they were exposed to temperatures of approximately 20°C for several hours. During assessment, the carrots were inadvertently subjected to a treatment that could stimulate wound healing

and thereby reduce the number of visible cavities per carrot. Further studies on the development of cavity spot in storage are required to determine how long carrots can be stored before lesion numbers or size begins to increase and to determine if a short pre-storage exposure to high temperatures might reduce or reverse the development of cavity spot in storage.

CONCLUSIONS

Several methods of suppressing cavity spot were evaluated to develop a comprehensive approach to manage the disease. Assessment of incidence or severity on a single harvest date gave variable results because cavity spot levels rose and fell through the growing season. Disease progress curves were examined to determine the efficacy of control measures. Area under the disease incidence curve was found to be the most reliable indicator of differences among the treatments.

The most effective method of suppressing cavity spot was the use of resistant cultivars. The cumulative incidence of cavity spot on resistant Six Pak was 20 to 50 percent that of susceptible cultivars such as Chanton and Huron. Six Pak consistently had a lower incidence of cavity spot.

The selective fungicide, metalaxyl, effectively suppressed cavity spot when applied in a granular formulation in the seed furrow or as a drench in combination with metalaxyl. Metalaxyl application within six weeks of seeding provided the best control while foliar applications of metalaxyl or fosetyl-Al later in the growing season were less effective. A drench application of 4.0 kg ai/ha fosetyl-Al at seeding suppressed cavity spot only on the susceptible cultivars Huron and Red Core Chantenay.

Metalaxyl plus mancozeb treatment was less effective on resistant Six Pak than on more susceptible cultivars. Under conditions of low to moderate disease pressure, cultivar resistance could substitute for fungicide use. When disease pressure was high, as in 1988, very

susceptible cultivars should be avoided since treatment with metalaxyl plus mancozeb only reduced cavity spot levels to that of untreated Six Pak. Under these conditions the use of metalaxyl plus mancozeb in conjunction with a resistant cultivar is recommended to achieve maximum disease control.

The biological control of cavity spot with plant growth-promoting rhizobacteria warrants further study, especially application of Pseudomonas putida isolate GR12-2(Pp-2) and Serratia proteamaculans isolates 1-102 (Sp-102). The efficacy of the PGPR's varied with cultivar; they were only effective on the susceptible cultivar Chanton.

Changing the seeding date of carrots was not an effective method for avoiding or reducing cavity spot. There was no evidence that older carrots were more susceptible to the disease. In some cases the youngest carrots appeared more susceptible, but the results were not conclusive.

Vanderplank (1963), Bruin and Edgington (1983) and others have asserted that fungicide research should be combined with plant breeding and that breeding for horizontal resistance will have the best long term results. Six Pak exhibited several features that are characteristic of horizontal resistance: when exposed to a certain density of inoculum, fewer carrots became infected, and lesions took longer to appear, suggesting a reduction in infection efficiency and a longer latent period. Also, there were no differences in the start of the epidemic among cultivars of varying resistance. However, cultivar resistance did not significantly reduce the rate of disease development, which is an important characteristic of horizontal resistance. The discovery of races of a Pythium spp. with differential virulence on carrots is required to conclusively determine the type of resistance that these carrots exhibit.

The severity of cavity spot increased after several months in storage. The increase in disease may be associated with dehydration of the roots or physiological age. Rankings of cavity spot severity remained constant during the storage period, thus it is important to store only

those carrots with low levels of cavity spot.

Comparisons and analysis of the cavity spot progress curves was complicated by the peaks and valleys that occurred in the curves, apparently as a result of changing environmental conditions. Reductions in the incidence of cavity spot occurred during and near the end of the season, especially on metalaxyl-treated carrots. This study has identified several management practices that can be used to suppress cavity spot on carrots grown in organic soil. These management practices can be used in conjunction with a disease forecasting system to provide the basis for an effective disease management program for cavity spot of carrot.

CHAPTER 6

GENERAL DISCUSSION

The present study was the first to investigate the effects of cultivar resistance, fungicide application and plant-growth rhizobacteria (PGPR) on the development of cavity spot in the field. This was also the first study to document disease progress in relation to rainfall and soil temperature.

This study was undertaken as the initial step in developing a disease management system for cavity spot, involving the use of cultivar resistance and the judicious use of selective fungicides or other control agents in conjunction with a disease forecasting system. A predictive system for cavity spot may allow better timing of fungicide applications and indicate the optimal time to harvest.

Cavity spot was originally described in 1961 and identified as a physiological disorder (Guba et al. 1961). Several other hypotheses were put forward as to the cause of cavity spot but there have been reports that cavity spot was caused by one or more species of Pythium (Groom and Perry, 1985, White 1986, Montfort and Rouxel 1988, Vivoda et al. 1991). Therefore, it was necessary to confirm that cavity spot in Ontario was also caused by Pythium infection. Pythium spp. were recovered from carrots in the trial plots in 1988, 1991 and 1992.

The frequency of recovery from cavity spot lesions was significantly higher than from asymptomatic portions of the carrot root. Isolates of P. violae, P. ultimum and P. irregulare recovered from cavities in 1992 caused typical cavity spot lesions on carrots grown in artificially-infested soilless growing media and were reisolated from the lesions; this fulfilled Koch's postulates. The association of Pythium spp. with cavity spot, comparisons of the symptoms with published photographs and descriptions, and the ability of the selective fungicide metalaxyl to

control the disease, led to the conclusion that cavity spot of carrots (also known as horizontal lesions) in Ontario was the same as the disease known as cavity spot in Britain (White 1986) and California (Vivoda et al. 1991) and as brown blotted carrots in Japan (Nagai et al. 1986).

The management practices which effectively suppressed the incidence and severity of cavity spot as identified by this study were:

a) the use of resistant cultivars, specifically Six Pak,

b) metalaxyl applied as a granular formulation (0.5 kg ai/ha) at seeding or as a drench (1.0-2.0 kg ai/ha) within six weeks of seeding,

The PGPR isolates GR12-2 of Pseudomonas putida, and 1-102 of Serratia proteamaculans applied to a highly susceptible cultivar suppressed the cavity spot index as effectively as metalaxyl plus mancozeb but further study is necessary to determine their general effectiveness. Delaying the seeding date to avoid the disease was not an effective management practice.

Resistant cultivars, selective fungicides and PGPR's reduced the incidence of cavity spot, but to different degrees. Cavity spot levels were consistently lower on resistant Six Pak than on more susceptible cultivars, although there was not complete control of the disease. Resistant cultivars should be used whenever possible. These cultivars are commercially available (Ontario Ministry of Agriculture and Food 1992b, National Institute of Agricultural Botany, 1991) and are the most economical management practice, since no additional cost is involved. However, during some years, unacceptable levels of cavity spot developed on resistant Six Pak (40 and 48% in 1986 and 1988, respectively). Also, the available resistant cultivars may not have the desired horticultural characteristics, such as the shape and quality required for processing (Ontario Ministry of Agriculture and Food 1992b). In these instances, additional control measures would be required.

Carrot cultivars are assigned a rating to indicate resistance to

cavity spot in Ontario (McDonald et al. 1991), British Columbia (Odermatt and Snow 1991) and Britain (National Institute of Agricultural Botany 1991). Carrots are usually assessed on a single harvest date, but the results of the present study have shown that this may not be the most accurate method of assessment. Cultivar Eagle was included in the 1992 trial as a resistant cultivar, based on cavity spot assessments at the Muck Research Station (McDonald et al. 1991) but had a significantly higher AUDPC than Six Pak in the irrigated plot in 1992 and thus was sometimes more susceptible than Six Pak.

The incidence of cavity spot can vary throughout the season. The resistance rating may depend on the time of harvest as much as the resistance or susceptibility of the cultivar. Maintaining standard cultivars in the trials, to act as benchmarks, may improve the system, but irregular assessments could still be obtained. For instance, if Six Pak and Red Core Chantenay were harvested from the non-irrigated plot on 27 October 1992, Red Core Chantenay would be assessed as susceptible with a significantly higher disease incidence than Six Pak, (73 vs. 15%, respectively, Tables, 24b, a). However, if the assessment were done three weeks later, on 17 November, Red Core Chantenay would appear less susceptible and the incidence would not be significantly different from Six Pak (28 vs. 18%, respectively). A more accurate method of comparing resistance is to calculate the AUDPC for both cultivars. However, the time and additional plot space required to make the assessment of AUDPC is difficult to manage when a large number of cultivars have to be assessed. Sweet et al. (1989) alluded to the problem of changeable susceptibility ratings when carrots were harvested at different times. Cavity spot ratings of cultivars conformed to the NIAB ratings on carrots from one farm but not another, and levels of cavity spot increased four-fold on some cultivars harvested in January, as compared to October.

The selective fungicide, metalaxyl, suppressed cavity spot when applied as a granular formulation or drench in combination with mancozeb.

Seed dressings provided inconsistent control while foliar sprays of metalaxyl plus mancozeb suppressed cavity spot but not as effectively as a drench application. Fosetyl-Al, another fungicide that is selective for oomycetous fungi, suppressed cavity spot when applied as a foliar spray, but at higher rates than metalaxyl. A drench application of fosetyl-Al was effective only on the highly susceptible cultivar Huron, but higher rates of application later in the season might improve the efficacy of fosetyl-Al. An interaction between cultivar resistance and fungicide efficacy was demonstrated and affected the management recommendations. The metalaxyl plus mancozeb drench suppressed cavity spot on the susceptible cultivars but not on resistant Six Pak, except in 1988 when disease levels were high. Treatment of a susceptible cultivar with metalaxyl plus mancozeb suppressed the incidence and AUDPC to a level equivalent to untreated Six Pak. Sweet et al. (1989) reported on the control of cavity spot with metalaxyl plus thiram and noted that the fungicide response was greater on susceptible carrots. However, no statistical analyses were presented to indicate any significant interaction.

Vanderplank (1963) suggested that horizontal resistance could substitute for the bulk of fungicide use. Fry (1978) was able to quantify the resistance to late blight in potatoes in terms of incremental reductions in the rate of fungicide used. The present study also demonstrated that the resistance in Six Pak could substitute for fungicide use, especially in a year when cavity spot was not severe. However, no clear dose/response relationship has been found for metalaxyl and cavity spot. The response was all or nothing.

A single application of metalaxyl applied early in the growing season has been shown to significantly suppress cavity spot in a number of trails (Sweet et al. 1989, Walker 1990). In the present trial, a single application of metalaxyl or metalaxyl plus mancozeb also suppressed cavity spot. However, in 1988 when incidence of cavity spot was high (80% on

Chanton), the reduction in cavity spot, though significant, was not enough to be considered good control. Fifty percent of Chanton carrots had cavity spot lesions, despite the application of granular metalaxyl. If disease forecasting could predict a major increase in cavity spot, a second fungicide spray or drench could be applied at the appropriate time to further suppress cavity spot development.

Bacterization of seed with plant growth-promoting rhizobacteria Pp-2 and Sp-102 suppressed cavity spot on Chanton, the most susceptible cultivar. Analysis of the main effects on AUCSIC indicated that Pp-2 was as effective as metalaxyl plus mancozeb in reducing the AUSCIC on all cultivars. Root colonization by all three PGPR's tested was low, but the isolates could be detected on roots three weeks after seeding, despite hot, dry soil conditions. Isolates Sp-102 and especially Pp-2 appeared to have some biological control activity for cavity spot, and more research in this area is warranted. It is interesting to note that both metalaxyl and the PGPR's were more effective on susceptible cultivars.

The incidence and severity of cavity spot generally increased with increasing plant age but examination of the disease progress curves revealed a number of increases and decreases throughout the growing season. In both 1991 and 1992, maximum disease incidence was recorded before the final harvest date. These changes often occurred at the same time on different cultivars and sometimes followed within nine to thirty five days of rainfall events. Treatment with metalaxyl plus mancozeb appeared to lengthen the incubation period in several instances. A minimum of nine to ten days was required for symptom development following a rainfall event, but sampling interval and soil temperature would both affect the apparent incubation period.

Total rainfall during a growing season was not a good indicator of maximum disease incidence because lower incidence was associated with the highest levels of rainfall (720 mm) than with other levels (550 mm). There was an indication that very low levels of rainfall (200-400 mm) were

related to low levels of cavity spot. Total rainfall only accounted for some of the variability in final cavity spot levels.

The success of early-season applications of metalaxyl in suppressing cavity spot suggested that an important amount of infection occurred during the early weeks of plant growth. Recovery of Pythium spp. from seedling carrot roots confirmed that Pythium infection did occur at this time. However, examination of rainfall during the four, six, eight and four to eight weeks after seeding failed to find any relationship with maximum disease incidence or AUDPC. There was a consistent relationship between low soil temperatures during the six and eight weeks after seeding and high levels of cavity spot, but the r^2 values were generally low (0.20-0.43) indicating that other factors also affected cavity spot development. The inoculum density in the plots was probably different from year to year and this would confound the analyses of cavity spot over several years.

The present study demonstrated that Pythium spp. infected seedling carrot roots and could also be recovered from expanding and mature tap roots. It is likely that Pythium infections occurred throughout most of the growing season, but the relative contributions of early or later infections to symptom development is not known, nor whether asymptomatic infections can become progressive and cause lesions in response to changes in the carrot or the surrounding environment.

Measurements of the soil moisture content (percent by weight) in the plots indicated that cavity spot increased in 1991 when the soil moisture content increased but did not approach saturation, while in 1992 the incidence of cavity spot decreased during a period when the soil was saturated. Lifshitz and Hancock (1981) found that populations of P. ultimum did not increase when the soil was saturated. Few, if any of the Pythium spp. that initiate cavity spot produce zoospores (Van der Plaats-Niterink 1981, Lyons and White 1992) thus saturated soil would not be required to stimulate zoospore release and allow for their movement.

If soil saturation is not required to stimulate the germination and

release of Pythium propagules, rainfall may initiate an increase in Pythium infections by increasing soil moisture to a level more favourable for germination and growth of Pythium (approximately -0.3 bars (Stanghellini 1974)), if even for a short period of time. The most likely effect of the rainfall is to increase the exudation and diffusion of nutrients from roots. Sporangia are exogenously dormant in field soil (Stanghellini 1974) and a number of reports have identified the central role of plant exudates in the infection of seeds and plants by Pythium spp. (Stanghellini and Burr 1973, Nelson 1987). Indeed, reduced colonization of seed by P. ultimum has been attributed to decreased exudation (Osburn and Schroth 1988). While exudation from roots may increase under saturated soil conditions, an increase in the area of soil into which the exudates diffused would only increase infection within the distance that the Pythium hyphae could extend to the root. The reduction in infection during a prolonged period of high soil moisture may reflect exhaustion of the propagules within the immediate vicinity of the roots.

There have been no reports in the literature describing the nature of resistance to cavity spot. White (1991) suggested that carrots had different levels of horizontal resistance to cavity spot but he did not provide any data to substantiate this observation. In the present trial, Six Pak was consistently more resistant to cavity spot than the other cultivars. Fewer carrots in a sample became infected. Examination of the disease progress curves showed that the apparent incubation period on Six Pak carrots was often longer than on more susceptible cultivars. On some sampling dates, fewer Pythium colony-forming units were recovered from Six Pak than from other cultivars. However, cavity spot epidemics began on Six Pak carrots at the same time as on other cultivars.

Six Pak appears to have horizontal resistance to cavity spot. However, comparison of the slopes of the disease progress curves found no significant reduction in slope for Six Pak carrots indicating no reduction in the rate of disease progress, the main criterion of horizontal

resistance. Six Pak was definitely more resistant to cavity spot than the other cultivars and the resistance is most likely horizontal resistance. Cavity spot is probably a simple interest disease and inoculum density can have a greater effect on disease levels than the rate of disease development (Vanderplank 1982). Variations in inoculum density in plots may have increased the variability of the data such that changes in the rate of disease development were obscured or were too small to be detected by statistical analysis.

No studies have been done to determine why Six Pak is more resistant to cavity spot but there are a number of resistance mechanisms in carrots that may be involved. Preformed antifungal compounds such as falcinardiol may play a role in reducing the numbers of infections and phytoalexins such as 6-methoxymellein could halt or limit infection. The rate at which suberin and lignin are deposited can affect lesion size and the effectiveness of wound repair but do not limit infection in the absence of 6-methoxymellein (Garrod et al. 1982). Another factor that may affect resistance and susceptibility is the amount of root exudates produced. Six Pak may exude fewer nutrients and thus stimulate the germination of fewer propagules, but this hypotheses has not been tested.

The effect of metalaxyl plus mancozeb on cavity spot development was similar to that of host resistance. Fewer carrots in a sample were infected and on several occasions the incubation period was longer. The cavity spot epidemic also began later in 1992 on several cultivars treated with a metalaxyl plus mancozeb drench at seeding. One interesting characteristic of the fungicide drench was that the effects appeared to be more pronounced late in the season, especially in 1988 where significant differences between treated and untreated carrots were not found until 19 October. Incidence on the untreated carrots remained constant in November and December while incidence on metalaxyl-treated Six Pak and Red Core Chantenay decreased, even though treatment occurred 26 weeks earlier.

Cultivar by fungicide interactions were identified in this study.

Metalaxyl is reported to have a direct effect on the resistance of the host (Cohen and Coffey 1986, Ward et al. 1980). Metalaxyl plus mancozeb treatment was less effective on resistant Six Pak, but did reduce incidence under conditions of high disease pressure. Metalaxyl has a direct effect on Pythium and related fungi (Fisher and Hayes 1982). Perhaps the observed effect of metalaxyl on Six Pak carrots was only the direct effect of reducing the inoculum in the soil. Stimulation of the plant's resistance would be redundant because the resistance mechanisms were operating as efficiently as possible. Effects of metalaxyl treatment on more susceptible cultivars could be viewed as a combination of reducing the inoculum and enhancing host resistance. This hypothesis concurs with that of Ward (1984) who suggested that metalaxyl operated entirely on the fungus by suppressing its ability to elicit a compatible reaction with the host and hence the host response was one of resistance. However, the decrease in cavity spot late in the season indicates that metalaxyl may also have some direct effects on the host, possibly stimulating the deposition of suberin and lignin which is involved in host resistance and wound repair.

There is still much to be learned about the epidemiology of cavity spot before an accurate predictive system can be established. The present study provides a framework for estimating the relative cavity spot levels that will develop during a season and for further research. Several host and environmental factors have been identified that can be incorporated into a predictive system for cavity spot.

These are:

a) cultivar resistance was the major factor determining the relative cavity spot incidence in any year.

b) incidence was high during seasons where there were several intermittent heavy rainfalls of 20 mm or more.

c) cavity spot incidence increased within nine to thirty nine days of heavy rainfall.

d) incidence was high when soil temperatures were low (16 to 17.5°C) during the six-eight weeks after seeding.

e) incidence was high when moderate to high (500 to 600 mm) rain fell during the season, and low when total rainfall during the season was low (200-400 mm).

f) cavity spot incidence decreased following periods of little (>5 mm each day) or no rainfall for thirteen or more days.

g) cavity spot incidence did not increase, and sometimes decreased during periods when soil moisture exceeded field capacity for several days or weeks.

h) there was no indication that rainfall (over 5 mm) in each of the four weeks preceding the sampling date increased the rate of infection of carrots by Pythium spp. or the incidence of cavity spot.

Several effective methods of managing cavity spot were identified in the present study. Some involved the use of metalaxyl. This fungicide is not registered for use on carrots in Ontario, but has been submitted for a Minor Use registration (C. Hunter, Ontario Ministry of Agriculture and Food Minor Use Coordinator, personal communication). Recommendations for the management of cavity spot, assuming the registration of metalaxyl, should include the following components:

a) Avoid fields with a known history of severe cavity spot.

b) Choose a resistant cultivar.

c) If a resistant cultivar with the desired horticultural characteristics is not available, apply metalaxyl as a granular formulation (Subdue 5G at 0.5 kg ai/ha) or as a drench with mancozeb (Ridomil MZ 72 WP at 2.0 kg ai/ha metalaxyl) within six weeks of seeding.

d) Use metalaxyl plus a resistant cultivar if seeding carrots in a field known to have a history of severe cavity spot.

e) Metalaxyl treatment may not be as effective on carrots that

are harvested by mid-September. Fungicide treatment is important on carrots that will not be harvested until November.

f) Seeding date does not affect cavity spot development on most cultivars. Seed in May or early June, if possible.

Crop rotation would not be included as a recommended management practice, while growing carrots on raised beds and inter-row cultivation to improve drainage would be recommended if these techniques fit into the general production practices. A review of the literature revealed that Pythium sulcatum, P. ultimum and P. sylvaticum have been isolated from asymptomatic lettuce roots, (Wisbey et al. 1977) while P. sulcatum has been isolated from roots of onions (Kalu et al. 1976) This may explain why crop rotation with onions and other crops failed to reduce the severity of cavity spot. Some or all of the Pythium spp. capable of causing cavity spot may increase on the roots of the onion or lettuce rotation crops.

Both Perry (1983) and Jacobsohn et al. (1984) reported a reduction in the severity of cavity spot when the soil was cultivated, or when carrots were grown on ridges. These recommendations can be incorporated into a management system for cavity spot, although unacceptably high levels of cavity spot have been found on carrots grown on raised beds in the Bradford area.

Other approaches to managing cavity spot were investigated in the present study and warrant further research. Plant growth-promoting rhizobacteria, especially Pseudomonas putida isolate GR12-2 suppressed cavity spot and should be tested further and developed for biological control of cavity spot. Esso Ag Biologicals has continued the research on these PGPR's, has improved the formulations, and is now ready to release them again for field trails (Dr. Reddy, Esso Ag Biologicals, personal communication).

Fosetyl-Al was less effective than metalaxyl plus mancozeb when applied as a drench at double the rate, but was equally effective as a foliar spray at 1.33 times the rate of metalaxyl. However, Lyshol et al. (1984) and Walker (1990) achieved some control of cavity spot with much higher rates of fosetyl-Al. Perhaps fosetyl-Al could provide an alternative chemical control at higher rates or with better timing of the applications. Alternatives to the continuous use of metalaxyl are important to delay the development of resistance in the target fungi.

Bruin and Edgington (1983) expressed concern about the rapid development of resistance in fungi to selective fungicides such as metalaxyl. They advocated the use of improved application techniques such as seed dressings, soil drenches and granules, to deliver the fungicide to the site where it was needed. Soil drenches and granular applications of metalaxyl were the most effective methods of applying the metalaxyl in the present trial. Bruin and Edgington (1983) also noted that the problem with fungicide resistance increased with fungicide use and encouraged the adoption of disease forecasting systems to allow for better-timed and consequently fewer, fungicide applications. Systemic fungicides allow a farmer to wait until infection has taken place and still effectively protect a crop. Acylalanine fungicides are effective eradicants if applied during the first half to two-thirds of the incubation period (Bruin and Edgington 1983).

It may be possible to reduce the use of metalaxyl by avoiding a preventative application of metalaxyl at seeding and only applying a drench six weeks after seeding if soil temperatures were cool, or by applying metalaxyl or fosetyl-Al within a few days of a heavy rainfall. If the minimum incubation period is nine to ten days and metalaxyl can eradicate cavity spot within the first half of the incubation period, then a spray within four to six days of the rainfall should be effective. This would allow time for the soil to dry enough for a sprayer to travel through the field. If environmental conditions are very conducive to

cavity spot development, or if inoculum levels in the field were suspected to be high, then a mid-season spray, in conjunction with metalaxyl applied at seeding, may improve the control of cavity spot. Davis et al. (1991) reported that split applications of metalaxyl were more effective on carrots grown on sandy soil. Better control may be achieved if the split applications were timed to follow within a few days of rainfall or irrigation.

More research needs to be done to verify and refine the disease forecasting system and to determine if cavity spot can be managed more efficiently with mid-season applications of fungicide. However, accurately forecasting cavity spot requires determining the factors that result in a reduction in the disease. Cavity spot incidence decreased on both untreated and metalaxyl-treated carrots during the growing season. If the factors that governed the decreases were known, it may be possible to reduce the application of metalaxyl. There would be no point in applying a spray after a rainfall if the incidence was going to decrease naturally. Another important use of this information would be in timing the harvest to coincide with a period when incidence was expected to be low.

A major factor limiting further development and implementation of a disease forecasting system is the inability to isolate Pythium violae from soil. Thus it is not possible to determine the effects of changes in environmental parameters on the Pythium populations which cause cavity spot, nor is it possible to determine whether a soil has an inoculum density high enough to cause severe cavity spot. Growers and researchers must estimate the potential for cavity spot development based on history of the field, and this is not a very efficient method. With such uncertainly, growers will likely err on the side of caution once metalaxyl is registered and apply an "insurance" metalaxyl treatment at seeding.

Etiology of Pythium-induced diseases of carrot - a hypothesis

The present study on the etiology of cavity spot, and a review of the literature, led to the hypothesis that the three Pythium-induced diseases of carrot are caused by the same Pythium species. The expression of the different diseases is dependent upon the growth stage of the carrot plant at the time of infection. Damping-off occurs when the germinating seed is infected, pythium root dieback results when Pythium spp. infect seedling roots from the time of emergence to approximately four weeks after seeding and cavity spot develops from infections that occur after the plants are four weeks old. Whether Pythium infects the seed, seedling or enlarged tap root depends on the presence of favourable environmental conditions. An increase in soil moisture is the main requirement, but soil temperatures may play a role.

This study and other research (White 1988, Vivoda et al. 1991) have shown that several species of Pythium were associated with cavity spot of carrot. Pythium sulcatum and P. violae (White 1988) and P. violae and P. ultimum, (Vivoda et al. 1991) were found to be the major causal agents. Several Pythium spp. were also associated with two other diseases of carrot, Pythium-induced damping-off and pythium root dieback (also known as rusty root). Both of these diseases have been observed on carrots grown in the Bradford area within the past five years.

Most of the Pythium spp. isolated from cavities and asymptomatic periderm of carrot roots were the same as those identified as causal agents of pythium root dieback. In Ontario, Kalu et al. (1976) found that Pythium sulcatum, and P. irregulare produced severe pythium root dieback, while Wisbey et al. (1977) reported that P. sulcatum was the major cause of the disease in British Columbia. Studies in Wisconsin (Mildenhall et al. 1971) indicated that P. sulcatum and P. irregulare caused symptoms of pythium root dieback, while P. sylvaticum and P. paroecandrum were less aggressive. Howard (1975), collected soils from across North America and determined that P. irregulare and P. sulcatum were the primary causal

agents of pythium root dieback, and Liddell et al. (1989) found that P. irregulare and P. ultimum were the cause of pythium root dieback in the San Joaquin Valley of California.

Pythium-induced damping-off is also caused by a similar group of Pythium species. Mildenhall et al. (1971) noted that P. sulcatum, P, irregulare and P. paroecandrum significantly reduced emergence of carrot seedlings. Howard (1975) also found that P. irregulare and P. sulcatum caused significant levels of damping-off and Liddell et al. (1989) reported that the isolates of P. ultimum and P. irregulare that caused pythium root dieback also caused high levels of damping-off. Thus, most Pythium spp. that cause pythium root dieback can also cause damping-off, and those species that cause cavity spot, with the possible exception of P. violae, also cause pythium root dieback.

Other researchers have observed a connection between various Pythium -induced diseases of carrot. McElroy et al. (1971) noted that "Pythium debaryanum attacks carrot seedlings causing damping-off; young plants causing stunting and root deformations; or mature carrot roots, causing a storage rot, rubbery slate rot". Pythium debaryanum was later found to be synonymous with P. ultimum (Van der Plaats-Niterink 1981). Montfort and Rouxel (1988) observed that P. violae produced symptoms similar to cavity spot or pythium root dieback on carrots grown in artificially-infested soil. They suggested that factors such as physiological stage of the carrot and climatic conditions would determine which symptoms would develop. They did not discuss what these factors were, but did indicate that the development of cavity spot symptoms on carrots in the field was favoured by high soil moisture aggravated by soil compaction and poor drainage.

The physiological stage of the carrot at the time of infection may be the primary factor in determining which symptoms develop. By definition, damping-off occurs on very young seedlings often before they emerge from the soil and infection usually occurs at the hypocotyl. Howard (1975)

found that excising the tap root tips of carrot seedlings that were one to two weeks of age produced significantly more forked roots than excising the root tips of carrots that were four weeks of age. Thus, infection of roots of carrots that are four weeks old or younger produces the symptoms of pythium root dieback, while infection of older roots results in cavity spot.

Whether Pythium infects the seedling or more mature carrot will depend on the presence of favourable environmental factors. An increase in soil moisture appears to be an important factor in determining the timing and severity of Pythium infections and may be the critical factor for carrots grown in temperate regions such as southern Ontario. Howard (1975) demonstrated that damping-off increased when soil, in which carrots were seeded, was saturated for over four days. In the same experiment, the severity of pythium root dieback increased with increasing duration of saturation, from zero to ten days. Liddell et al. (1989) found that P. ultimum killed virtually all the carrot seedlings grown in artificially-infested saturated soil. Several researchers (Perry and Harrison 1979b, Soroker et al. 1984 and Vivoda et al. 1991) have reported an increase in cavity spot lesions associated with saturated or flooded soil conditions.

An increase in soil moisture could increase the severity of these Pythium-induced diseases by increasing the exudation of nutrients from the seed or root, and allowing the exudates to diffuse further into the surrounding soil. The exudation of sugars and other nutrients from carrot roots increased significantly when carrot roots were held in water (Perry 1983, Soroker et al. 1984). Liddell et al. (1989) noted that the isolates of P. ultimum and P. irregulare in their trials did not produce zoospores and could infect carrots at soil matric potentials of -30 kPa. Thus saturated soil conditions would not be necessary to promote infection by these fungi, in contrast to those species of Pythium which produce zoospores. Pythium sulcatum has been reported to produce zoospores at 20°C, so saturated soil conditions may directly affect the dissemination

of this pathogenic Pythium species (Van der Plaats-Niterink 1981). However, Nagai et al. (1986) were unable to induce the formation of sporangia or zoospores in isolates of P. sulcatum from carrots and Lyons and White (1992) concluded that this fungus lacked an asexual reproductive stage.

An increase in nutrient exudation from carrot roots in response to increased soil moisture or flooding may explain the infection of mature expanding carrot tap roots by Pythium spp. Fungi in the genus Pythium usually infect juvenile tissues such as the tips of growing roots (Hendrix and Campbell 1973). It is unusual for Pythium spp. to directly infect a more mature root. An increase in the quantity of nutrients exuded from the roots would stimulate the germination of Pythium propagules in the root zone and subsequently the number of Pythium infections of the root.

Soil temperature also appears to be a factor that influences Pythium infection. Liddell et al. (1989), working with Pythium isolates from California found that P. ultimum, P. irregulare and P. aphanidermatum killed more seedlings (i.e. caused more damping-off) at 35°C than at 25°C, and that P. ultimum caused more forking of carrots at 27°C than at 23°C. In another study, Vivoda et al. (1991), also working in California, reported that P. ultimum caused more cavity spot lesions on carrots grown at 15°C than on those grown at 20° or 25°C. The increase in damping-off at high temperatures is unusual. Pythium-induced damping-off is usually associated with low soil temperatures (Hendrix and Campbell, 1973). Perhaps there are biotypes of these species in California that are adapted to higher soil temperatures. Temperatures recorded in organic soil at the Muck Research Station during the growing season ranged from a high of 21 to 24°C in July to a low of 1 to 2°C in December. While low soil temperatures after seeding were associated with higher levels of cavity spot, changes in soil temperature were not associated with cavity spot increases or decreases in response to rain. During most of the growing season in Ontario, soil temperature would not be a limiting factor

governing infection.

With further research, disease forecasting and management systems for cavity spot could be broadened to include all three of these Pythium - induced diseases of carrot.

CHAPTER 7

GENERAL CONCLUSIONS

Cavity spot remains a major field disease of carrots in the Bradford and District marshes in Ontario. A large proportion of carrots can be affected, sometimes reducing the marketable yield to a point where the crop is disked under rather than harvested. Disease severity fluctuates from year to year, apparently in response to rainfall and other changes in the environment, but the influence of the environment on these changes is unknown. The only methods currently recommended in Ontario for the management of this disease are the use of resistant cultivars and avoidance of over-fertilizing the soil. No fungicides or biological controls are available to suppress cavity spot on carrots. Growers need an effective system to maintain the disease below economic levels with the most efficient use of resources.

There have been several conflicting reports on the cause of cavity spot since the disease was described in 1961. Therefore, it was important to confirm that the disease was caused by Pythium spp. and was the same as cavity spot described in other parts of the world.

The objectives of this research were to determine the cause of cavity spot and begin the development of a disease management system through the evaluation of control methods and a study of the epidemiology of the disease. A series of field trials was conducted over a six year period to address these objectives. Carrots were harvested at two to three week intervals throughout the growing season and cavity spot was assessed. Small portions of tissue from the root surface were plated onto a semi-selective medium to recover Pythium species and the pathogenicity of some isolates was confirmed.

Cavity spot of carrots grown on organic soils in Ontario was similar to that reported in Britain, France, and California and to brown-blotted carrots in Japan. Both slow and fast-growing Pythium spp. were recovered from lesions and from asymptomatic portions of the root,

but the frequency of recovery from lesions was higher. Fewer Pythium colonies were recovered from roots of Six Pak and from carrots treated with a metalaxyl plus mancozeb drench on some sample dates, which suggested that fewer infections occurred on resistant and fungicide-treated carrots. The results were not consistent enough to be used as a screening method for resistance or fungicide efficacy.

Examination of disease progress curves in relation to days after seeding, rainfall and soil temperature demonstrated that disease incidence and AUDPC increased with increasing days after seeding (r^2=0.14-0.82). Disease incidence reached a maximum between 4 August and 27 October (62 to 159 days after seeding) on 24 of 27 disease progress curves recorded over six years. On four of these 24 disease progress curves, incidence decreased in November or December. Cavity spot increases were often associated with increasing cumulative rainfall and decreasing soil temperatures but effects of these parameters could not be determined because they were closely related to days after seeding (r^2=0.74-0.99).

Increases in cavity spot incidence occurred nine to thirty nine days after a day or series of four days with rainfall totalling 20 mm or more when rainfall occurred before 15 October and soil moisture content was below field capacity (approximately 265% soil moisture by weight). Decreases in incidence followed at least 13 days of little (> 5 mm per day) or no rainfall, or periods where soil moisture was at or above field capacity for several days. The time period between rainfall and increase in incidence varied with cultivar and may have been affected by soil temperature. Sudden increases in soil moisture probably stimulated the germination of Pythium sporangia by increasing the quantity of root exudates and the distance of diffusion into the surrounding soil.

Cavity spot incidence was low during growing season where total rainfall was low (200-400 mm), higher in seasons with moderate to high rainfall (550 mm), and lower when rainfall was very high (720 mm).

The incidence of cavity spot increased with decreasing soil temperatures, but this effect was not consistent. Low soil temperatures (16-18°C) during the six to eight weeks after seeding were associated with high areas under the disease incidence curve, but were not the only factor that affected the levels of cavity spot (r^2=0.43 and 0.27 for susceptible and resistant cultivars, respectively).

The selective fungicide metalaxyl effectively suppressed cavity spot when applied as a granular formulation at seeding (0.5 kg ai/ha) or as a drench with mancozeb (2.0 kg/ai metalaxyl) within six weeks of seeding. Foliar sprays of metalaxyl plus mancozeb (1.2-3.6 kg/ai/ha metalaxyl) applied 12 or 17 weeks after seeding also suppressed cavity spot, but not as effectively as the drench applications. Seed dressings (1-5 g/100 g seed) provided inconsistent results. Fosetyl-Al and phosphorous acid, suppressed cavity spot as effectively as metalaxyl when applied as a foliar spray (1.6-4.8 kg ai/ha) but not when applied as a drench (4.0 kg ai/ha) at seeding.

The plant growth-promoting rhizobacteria (PGPR) Sp-102 and Pp-2 effectively suppressed cavity spot incidence on the susceptible cultivar Chanton. Isolate Pp-2 also reduced the cavity spot index on the three cultivars tested.

The fungicides and PGPR's were more effective on the susceptible cultivars than on Six Pak. Neither fungicide reduced cavity spot in Six Pak in 1992 when there were moderate levels (1485 incidence days) of cavity spot. Metalaxyl plus mancozeb treatment reduced cavity spot incidence on Six Pak when disease levels were high (3780 incidence days) in 1988.

Seeding date did not affect incidence or AUDPC except on Cellobunch carrots seeded on 9 July, 1990. These carrots had a higher AUDPC and incidence than carrots of the same cultivar seeded on 7 June. There was no indication that older plants were more susceptible to cavity spot.

The severity of cavity spot increased while carrots were in cold

storage. From 1990 to 1991, the number of large lesions per carrot increased while the total number of lesions per carrot decreased during the four month trial. When the trial was repeated from 1992 to 1993, both the number of lesions and large lesions per carrot decreased after two months in storage, then increased when assessed four and a half months later. Resistant and metalaxyl-treated carrots had fewer lesions at the beginning of the storage period and the relative ranking was maintained while the carrots were in storage.

Soil moisture content was higher in soil 15 cm below the surface than at 5 cm depth. The moisture content increased in conjunction with rainfall and decreased when there were seven or more days with no rain.

The present study provides the framework for a disease forecasting system for cavity spot but more information is needed to develop a reliable system. The specific conditions which lead to a reduction in incidence have to be determined, as do the incubation periods for different cultivars at various soil temperatures. Forecasting of cavity spot and research on this disease would be easier if populations of Pythium violae in the soil could be quantified. Currently there is no method for determining the potential for cavity spot development in the field, except by relying on the history of the disease. If P. violae could be detected in soil, more information could be obtained on the relationship between inoculum density and disease incidence. This relationship can presently be determined for individual isolates in pots, but competition among Pythium spp. in the soil may affect the incidence that develops in the field.

The management of cavity spot in Ontario will be enhanced by the registration of metalaxyl and the identification of more resistant cultivars. Improved control of cavity spot may be possible through disease forecasting and timing metalaxyl or fosetyl-Al treatments to coincide with increases in infection.

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