

AN ABSTRACT OF THE DISSERTATION OF

Nicholas L. David for the degree of Doctor of Philosophy in Botany and Plant Pathology presented on March 2, 2007.

Title: Biology and Management of *Meloidogyne chitwoodi* with Oxamyl on Potato in the Western United States.

Abstract approved:

Russell E. Ingham

Field trials were conducted during 2001 to 2003 to investigate soil population dynamics of *Meloidogyne chitwoodi*, tuber symptom suppression using oxamyl, and post-harvest tuber symptom development on short-season potato varieties Russet Norkotah and Russet Nugget (San Luis Valley only). The experiments were located in the San Luis Valley in Colorado, Klamath Basin in Oregon, and southern Columbia Basin in Oregon to represent, cool, warm, and hot growing regions, respectively. *M. chitwoodi* soil population dynamics were multi-modal in all three regions representing distinct periods of egg hatch and root and tuber infection. *M. chitwoodi* completed two generations in the cooler production areas of the Klamath Basin and San Luis Valley, and three generations in the hot region of the Columbia Basin. When left uncontrolled, *M. chitwoodi* infected and caused tuber symptoms in all three regions, but tuber symptoms were significantly reduced with the use of a bi-weekly oxamyl program that began at the hatch of the second generation. Furthermore, augmenting with in-furrow at-planting and crop emergence applications provided better protection. The level of reduction in symptoms using the application schedules outlined in this research was substantially better than that previously observed with this nematicide. Oxamyl did not control *M. chitwoodi* densities

in the soil. For that reason, internal and external symptoms increased when harvest was delayed by three weeks in the Columbia Basin regardless of whether or not oxamyl had been applied. Following harvest in the Columbia Basin and Klamath Basin there is potential for internal symptom development if tubers are stored warm. The percentage of tubers with internal symptoms increased when stored at 21-24°C and more than 740 post-harvest DD_{5C} were accumulated, regardless of whether or not oxamyl was used. However internal symptoms did not increase during long-term cold storage (3-5°C) when no more than 480 – 610 post-harvest DD_{5C} were accumulated. Unlike internal symptoms, there was no increase in external symptoms following harvest even when as many as 1,000 post-harvest DD_{5C} were accumulated. Oxamyl is currently the only chemical that growers can apply during the growing season to suppress tuber damage from *M. chitwoodi* and reduces symptoms on short-season potato cultivars in both cool and hot growing regions in the western United States.

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Biology and Management of *Meloidogyne chitwoodi* using Oxamyl on
Potato in the Western United States

by
Nicholas L. David

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APPROVED:

Major Professor, representing Botany and Plant Pathology

Chair of the Department of Botany and Plant Pathology

Dean of the Graduate School

I understand that my dissertation will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my dissertation to any reader upon request.

Nicholas L. David, Author

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CONTRIBUTION OF AUTHORS

Nadine Wade, Kathy Merrifield, and Brian Charlton were involved with data collection.

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DEDICATION

I dedicate this dissertation to my wife and children. I thank you all for your patience and support as we have done this together.

To my wife, Tara:

I am truly blessed by your selflessness to be a full-time mother and wife. I look forward to every day that I have been given the honor and responsibility to be your covering.

To my children, Kenny, Nathan, Caleb, Joshua, and those yet to be born:

I pray that as God draws you close to him you will accept the free gift of salvation offered to you by Lamb of God, our Lord and Savior, Jesus Christ, and that you will allow him to work his perfect will through your lives.

Biology and Management of *Meloidogyne chitwoodi* using Oxamyl on Potato in the Western United States

INTRODUCTION

Potato production in the United States (U.S.) consisted of 20.8 million metric tons in 2003, fourth most among world potato producing countries. Within the U.S.A., 170,000 hectares of potatoes were planted in states containing *Meloidogyne chitwoodi* Golden et al., commonly referred to as the Columbia root-knot nematode. Potato production in states where *M. chitwoodi* occurs represented 56% of the total acres planted and 61% of total production (www.ers.usda.gov/briefing/potatoes). Since its initial discovery in 1977 from an infected potato in Idaho, *M. chitwoodi* has been reported in California and Nevada (Nyczepir et al., 1982), Colorado (Pinkerton and McIntyre, 1987), New Mexico (Thomas et al, 2001), Oregon and Washington (Santo et al., 1980), Texas (Szalanski et al., 2001), and Utah (Griffin and Thompson, 1986).

M. chitwoodi is a sedentary endoparasite which invades roots, stolons, and tuber portions of potato. Tuber infection can result in both internal (brown spots in the cortex or pith) and external (galls on the periderm) symptoms which are commonly believed to increase following harvest. While *M. chitwoodi* reduces the quality of potato tubers, yield losses on potato have not been observed. *M. chitwoodi* is well adapted to the cool climatic conditions present during potato planting in the western United States (Charchar, 1987), which allow it to complete multiple generations, increasing the number of second-stage juveniles (J2) available to infect tubers and cause symptoms. As a result, the treatment threshold for on potato in the Columbia Basin of Oregon and Washington is one J2 per 250-g dry soil prior to planting (Ingham, unpublished data; Santo, unpublished data).

Chemical control is currently the most common method of managing *M. chitwoodi*. An estimated 2.1 million kg of metam sodium, 1.2 million kg of 1,3-dichloropropene, 6,000 kg of aldicarb, 16,000 kg of ethoprop, and 52,000 kg of oxamyl are used to control *M. chitwoodi* on the 12,000 hectares of potato grown in the Umatilla Basin of Oregon on an annual basis (Jack Jensen, J.R. Simplot Co., pers. com.). A common chemical practice in the Pacific Northwest is to fumigate in the fall prior to planting potatoes with 141 liters/hectare of 1,3-dichloropropene and 281 liters/hectare of metam sodium. This practice controls *M. chitwoodi* as well as *Verticillium dahliae*, a soil-borne fungus that reduces yield in many potato cultivars, but it costs approximately \$668 per hectare. While fumigation may be required for high densities, it would be an advantage to growers if a more economical management program could be developed for low to moderate populations. Other options to suppress *M. chitwoodi* damage in potato include non-fumigant chemicals, such as aldicarb (Temik[®]), ethoprop (Mocap[®]) or oxamyl (Vydate C-LV[®]). Aldicarb and ethoprop can be applied only at, or before planting, respectively, and have not provided season-long *M. chitwoodi* control in the Pacific Northwest. However, oxamyl can be applied before, at, or after planting until one week prior to harvest, and has the potential for extended protection during the growing season. Previous research on population dynamics of *M. chitwoodi* on potato in relation to degree-day accumulation indicated that a soil degree-day model might be used to time in-season nematicide applications (Pinkerton et al., 1991).

In order for in-season applications of oxamyl to be effective for suppression of tuber damage from *M. chitwoodi* throughout the western United States, further information on the biology of the nematode and the efficacy of oxamyl must be obtained.

If degree-day accumulation is to be used as a predictor of population development for timing nematicide applications, then population development in relation to degree-days would need to be similar among different potato cultivars and among different climatic regions. However, this relationship has only been described for one cultivar (Russet Burbank) from one growing region (southern Columbia Basin). Similarly, little information is available on the effects of oxamyl on *M. chitwoodi* populations or on tuber damage in the different growing regions. Cooler growing regions may produce fewer nematode generations and may require fewer applications than areas with warmer or longer seasons. In addition, an effective oxamyl treatment program would need to suppress tuber symptom development even if tubers remain in the field after applications have ceased and during long-term storage conditions.

The purpose of this research is to address the issues outlined above by studying 1) the dynamics of *M. chitwoodi* in the soil in relation to degree-days, 2) tuber symptom development after harvest, and 3) suppression of populations and tuber symptoms of *M. chitwoodi* with oxamyl on short-season table-stock potatoes grown in three different climatic regions of the western United States.

A Review of the Biology and Chemical Management of *Meloidogyne chitwoodi* on Potato

ABSTRACT

Meloidogyne chitwoodi is widespread throughout the potato (*Solanum tuberosum*) growing regions of the western United States. Internal and external symptoms produced when this nematode infects tubers are considered quality defects and crops with excessive symptoms are commercially unacceptable. Since *M. chitwoodi* is capable of infecting roots at low temperatures (5°C), the population cycle begins early in the season and as many as four generations may be produced by harvest. This rapid increase in population density represents a high probability of tuber infection and makes control difficult. Although resistance exists in some wild tuber-bearing species of *Solanum*, there is no resistance in commercially available cultivars. Several fumigant and non-fumigant nematicides have been tested but only 1,3-dichloropropene consistently provides acceptable control and only when injected deep (34cm) in the soil profile. Better understanding of the biology of *M. chitwoodi* and symptom development in tubers may provide information to improve applications of non-fumigant chemicals, such as oxamyl, and improve their control of *M. chitwoodi*.

INTRODUCTION

Potatoes (*Solanum tuberosum*) are grown world-wide and are parasitized by numerous species of soil-borne nematodes, including *Meloidogyne* spp. *M. incognita*, *M. arenaria*, and *M. javanica* (Jatala and Bridge, 1990; Vovlas et al., 2005) are the most important species in tropical potato production, while *M. hapla*, *M. chitwoodi*, and *M. fallax* (Griffin and Jorgenson 1969; Golden et al., 1980; Karssen 1996) are most common in temperate climates.

M. chitwoodi was first described from a tuber sample taken in 1974 from Aberdeen, Idaho (Golden et al., 1980). Subsequent surveys between 1977 and 1980 confirmed the presence of *M. chitwoodi* in western Washington, the lower, middle, and upper regions of the Columbia River Basin in Oregon and Washington, as well as the lower, middle, and upper regions of the Snake River Basin of Idaho (Santo et al., 1980). Further work between 1980 and 1981 detected *M. chitwoodi* in the Klamath Basin of Oregon and California as well as northern Nevada (Nyczepir, A.P. et al., 1982). Subsequently, *M. chitwoodi* has since been officially reported in Virginia (Eisenback et al., 1985), Colorado (Pinkerton and McIntyre 1987), Utah (Griffin and Thomson 1988), New Mexico (Thomas et al., 2001), and Texas (Szalanski et al., 2001). *M. chitwoodi* has also been reported outside the United States, in Mexico (Cuevas, 1995 MS Thesis), South Africa (Kleynhans 1991; Fourie et al., 2001), Argentina (Esbenshade and Triantaphyllou 1985), Belgium (Waeyenberge and Moens 2001), Germany (Heinicke, 1993; Müller et al., 1996), France, Portugal, and Spain (Mugniery, personal communication).

GENERAL BIOLOGY

Lifecycle: The biology of *Meloidogyne chitwoodi* is similar to that of other *Meloidogyne* species and is described as a sedentary endoparasite. These nematodes invade host tissue, develop a highly specific relationship with their host, and remain in the host until their life-cycle is complete. Root-knot nematodes have six distinct life-stages including: egg, first stage juvenile (J1), second stage juvenile (J2), third stage juvenile (J3), fourth stage juvenile (J4), and an adult stage. Beginning with the J1, the cuticle is replaced between each stage in a process referred to as molting (Dropkin 1989). J1 molt within the egg and when eggs hatch, J2 are released.

Parasitism: With the exception of adult males, J2 of *Meloidogyne spp.* are the only life-stage found in the soil, and are the only infective stage. Linford (1939) and Wyss (1992) observed the attractiveness of the area just behind the root cap in the elongation zone to *Meloidogyne sp.* infection, while Bird (1960) and Finley (1981) reported invasion around the area of lateral root juncture as well as in areas previously damaged by nematodes or soil-borne fungi. Once inside the roots, J2 generally migrate inter-cellularly (Wyss et al., 1992) towards the stele. Finley (1981) observed nematodes arranged radially around the stele of the root with the anterior portion of the nematode precisely situated in the phloem tissue. After migration to the primary or secondary phloem tissues, successful parasitism by root-knot nematodes is dependent upon the formation of specialized feeding cells referred to as giant cells. Giant cells are multi-nucleated and are formed when repeated mitotic cell divisions occur without subsequent cytokinesis (Huang et al., 1969). Almeida-Engler et al. (1999) demonstrated the

importance of mitosis in giant cell formation, while Goellner et al. (2001) recently identified five cell-wall modifying enzymes associated with giant cells development. Interestingly, their data suggest the enzymes are of plant origin rather than nematode origin.

Reproduction: Following infection and giant cell formation, J2 molt into J3, J4, and finally into adults. Adult females are sedentary for the rest of their life, while males, if present, migrate out of the root to fertilize females. As female adults mature in roots they become gravid and erumpent, and root cells increase in size and number causing the characteristic root gall (Finley, 1981). Prior to laying eggs, the adult female excretes a gelatinous matrix from six rectal glands (Maggenti et al., 1960) in two phases, the first consists of a transparent clear material, while the second is a yellowish brown material, into which most of the eggs are laid (Golden et al., 1980; Orion et al., 1994). The gelatinous matrix protects eggs from dehydration (Wallace 1968; Bird et al., 1972), microbial degradation (Orion et al., 1991), organophosphate nematicides (Mojtahedi et al., 1991a) and alters host cells for egg release into the environment (Orion et al., 1987; Orion and Frank, 1990). Once embryogenesis is completed and environmental conditions are favorable, a second generation of J2 will hatch from the eggs and invade susceptible plant material. Root-knot nematodes are capable of completing numerous generations within cropping systems, resulting in high populations of nematodes in the soil and a high risk of crop damage.

HOST RANGE

M. chitwoodi is polyphagous and able to parasitize both monocotyledonous and dicotyledonous plants. Some common hosts for *M. chitwoodi* are potato, field-corn, wheat, barley, oats, tomato (Santo et al., 1980), sweet-corn (O'Bannon et al, 1982), popcorn (Cardwell and Ingham 1997), alfalfa (Pinkerton et al., 1987), carrot (Santo et al., 1988), certain rangeland grasses (Griffin et al., 1984), beans, peas (Santo and Ponti, 1985), sunflower (Ferris et al., 1993), onion (Westerdahl et al., 1993), common vetch, yellow clover, red clover, white clover, birdsfoot trefoil, milk vetch (Griffin and Rumbaugh 1996), and numerous flower bulbs (Den Nijs et al., 2004). According to O'Bannon et al. (1982), some common weeds associated with potato production in the western United States are not good hosts for *M. chitwoodi*. For example, black nightshade (*Solanum nigrum*), common lambsquarters (*Chenopodium album*) and pigweed (*Amaranthus retroflexus*) were determined to be poor, very poor and non-hosts, respectively. Recently, R. Boydston (USDA, pers. com.) observed *M. chitwoodi* reproducing on hairy nightshade (*Solanum physalisfolium*). Host susceptibility to *M. chitwoodi* for many plant species is cultivar dependent and general statements about crop species susceptibility or resistance may be misleading. For example, Ferris et al. (1993) reported the host status within white lupine (*Lupinus albus*) and barley (*Hordeum vulgare*) ranged from good to poor and from moderate to poor, respectively, depending on the cultivar. Cardwell and Ingham (1997) reported similar results between popcorn cultivars and Mojtahedi et al. (1993) observed some cultivars of sudangrass were non-hosts while others supported reproduction.

RACE STRUCTURE

There are currently three races of *M. chitwoodi*. The wild-type (race 1) reproduces on carrot but not on alfalfa, while race 2 (Santo and Pinkerton 1985) reproduces on alfalfa but not on carrot (Santo et al. 1988). Furthermore, Mojtahedi et al. (1994) discovered a third race of *M. chitwoodi* in California (race 3) that reproduces on potato clonal selection PI275187.10 of *Solanum bulbocastanum*, a wild species that has resistance to *M. chitwoodi* races 1 and 2. Mojtahedi et al. (1988a) observed no difference in penetration of alfalfa roots between race 1 and 2 of *M. chitwoodi* but a significantly higher percentage of second-stage juveniles of race 1 egressed from alfalfa roots compared to race 2 and giant cell formation was uncommon within race 1. A differential host test to distinguish race 1 and race 2 was proposed by (Mojtahedi et al., 1988b) and included alfalfa cv. Thor and carrot cv. Red Cored Chantenay. A survey by Pinkerton et al. (1987) in the western United States determined both races were widespread. Charchar (1987) determined race 1 had a wider optimum temperature for root penetration, but both races caused serious damage to potato.

DEVELOPMENTAL THRESHOLD AND EPIDEMIOLOGY ON POTATO

Parasitism of roots: Charchar (1987) reported that the lowest temperature at which J2 of *M. chitwoodi* were able to invade potato roots was between 3 and 6°C. Griffin (1985) reported root invasion at about 5°C, while Inserra et al. (1983) reported less than 1% egg hatch at 4°C. Inserra et al. (1985) also reported wheat roots became infected at 4°C. As a result of the above work, 5°C (41°F) has been used as the lower developmental threshold for *M. chitwoodi*.

Population dynamics of *M. chitwoodi* on potato cv. Russet Burbank in relation to soil degree-days (DD_{5C}) were described by Pinkerton et al. (1991) in the Columbia Basin of Washington state. This is one of the few studies describing soil population dynamics of a plant-parasitic nematode in relation to soil degree-days. In micro-plot studies, they reported that second-stage juvenile soil densities immediately declined after planting and did not increase until 943 and 1,033 DD_{5C} after planting in 1984 and 1985, respectively. The initial increase in J2 from potato roots was defined as the second generation. After the initial increase, they reported subsequent increases after 1,736 DD_{5C} in 1984 and after 1,714 DD_{5C}, 2,047 DD_{5C}, and 2,393 DD_{5C} in 1985. The second and third increases in J2 densities from potato roots were defined as the third and fourth generations, respectively. In field studies, they reported that soil densities increased slightly after planting and then decreased until 1,115 and 1,104 DD_{5C} after planting in 1984 and 1985, respectively, when the first increase was recorded. The next increases occurred after 1,877 DD_{5C} and 1,639 DD_{5C} after planting during 1984 and 1985, respectively. They concluded that J2 penetrated roots shortly after potato planting and produced eggs between 600 DD_{5C} and 800 DD_{5C} after planting. Furthermore, they determined that second, third, and fourth generations of *M. chitwoodi* began at 950-1,100 DD_{5C}, at 1,500-1,600 DD_{5C}, and after 2,150 DD_{5C}, respectively.

Parasitism of tubers: Finley (1981) reported that second-stage juveniles penetrated roots, stolons, and tubers of potato plants. He noted that penetration often occurred near the juncture of lateral roots, as well as around the eyes of tubers. Successful tuber infection resulted in irregular enlargements on the surface of the tuber and brown lesions in the cortex and sometimes in the pith. He speculated that the brown lesion was a result

of the oxidation of phenolic compounds associated with the gelatinous matrix surrounding the egg mass and the surface enlargements were due to cortical cell hypertrophy. Pinkerton et al. (1991) concluded that over-wintering second-stage juveniles did not infect tubers, but second-generation second-stage juveniles were the first to infect tubers at 1,000 DD_{5C} after planting.

HOST RESISTANCE

Wild tuber-bearing relatives of *Solanum tuberosum* have demonstrated resistance to *M. chitwoodi*. *Solanum bulbocastanum* and *Solanum hougassi* (Brown et al., 1989 and 1991) have both demonstrated resistance to *M. chitwoodi* race 1 and 2, while *Solanum fendleri* (Brown et al., 2004) is resistant to race 1 only. Somatic hybridization was used to transfer resistance from *S. bulbocastanum* into the cultivated genome (Austin et al., 1993) and Mojtahedi et al. (1995) reported that both roots and tubers of the hybrid, CBP-223, were resistant to *M. chitwoodi*. Information about tuber resistance from *S. hougassi* and *S. fendleri* has not been reported. Although resistance may play an important role in future management of *M. chitwoodi* in potato, no commercially acceptable varieties are currently available so other strategies must be implemented.

CONTROL WITH PLANT-DERIVED CHEMICALS

Glucosinolates: Certain plants within the Brassicaceae family, such as rapeseed (*Brassica campestris* and *B. napus*), white mustard (*Sinapsis alba*), oriental mustard (*Brassica juncea*), black mustard (*Brassica nigra*), crambe (*Crambe abyssinica*), and the cole crops (*Brassica oleracea*) contain glucosinolates within roots, shoots, and leaves.

Glucosinolates themselves are not nematocidal (Lazzeri et al., 1993; Donkin et al., 1995), but are hydrolyzed enzymatically by myrosinase to isothiocyanates, nitriles, cyanoepithioalkanes, or thiocyanates (Bones and Rossiter, 1996) depending upon pH, presence of Fe^{2+} , and the parent glucosinolate (Borek et al., 1994). Under acidic conditions, glucosinolates are hydrolyzed into organic cyanides, while isothiocyanates are produced when conditions are near or above neutral. Mojtahedi et al. (1991c) reported that incorporating green plant material from rapeseed (*Brassica napus*) cultivars Jupiter and Bridger reduced the number of J2 of *M. chitwoodi* in the soil. Furthermore, fall planted rapeseed incorporated the following spring reduced tuber damage by *M. chitwoodi* (Mojtahedi et al., 1993a).

Cynogenic glycosides: Certain plants within the Poaceae family such as sorghum (*Sorghum bicolor*), sudangrass (*Sorghum sudanese*), sudangrass hybrids (*S. sudanese* x *S. sudanese*), and sorghum-sudangrass hybrids (*S. bicolor* x *S. sudanese*) produce the cyanogenic glycoside, dhurrin, which is found primarily in the epidermal cells of leaves. Epidermal and mesophyll cells also contain the enzyme β -glucosidase, which catalyzes the hydrolysis of dhurrin and liberates hydrogen cyanide. Incorporating sudangrass, sudangrass hybrids, and sorghum-sudangrass hybrids has been demonstrated to reduce *M. chitwoodi* populations. Mojtahedi et al. (1993) reported that nematode suppression was limited to the zone of incorporation but persisted for at least six weeks. They also reported that leaf and stem tissues suppressed *M. chitwoodi* more than root tissue, and that J2 appeared to be more susceptible than egg masses. Even though green manure cover crops, containing various phytochemicals, have demonstrated nematocidal

properties, reduction of tuber damage by *M. chitwoodi* has been inconsistent (Santo et al., 1992; Ingham et al., 1993; Ingham et al., 1995; and Santo et al., 1999).

CONTROL WITH FUMIGANT CHEMICALS

1,3-dichloropropene (Telone II®): Because of low industry tolerances for tuber damage, *M. chitwoodi* is primarily controlled with the fumigants, 1,3-dichloropropene (1,3-D) and metam sodium (sodium *N*-methyldithiocarbamate). 1,3-D (Telone II®, Dow Agrosiences) is injected into the soil as a liquid and is immediately converted to a gas that diffuses through the soil profile. Early research on 1,3-D in the Columbia Basin by Pinkerton et al. (1986) demonstrated that spring applications of 226 and 306 kg/ha of 1,3-D (190 and 256 l/ha of Telone II® respectively) injected 20 cm below the surface on shanks centered 22.5 cm apart did not significantly reduce tuber damage from *M. chitwoodi*. Subsequently, Griffin (1985) reported that deeper placement of 1,3-D in the soil increased control of *M. chitwoodi*. Spring applications near Blackfoot, Idaho, from 1978-1982 determined that rates ranging from 100 – 224 kg/ha of 1,3-D (86 – 190 l/ha of Telone II®) injected 30 cm deep and on 30 cm centers near, significantly reduced galled tubers. During both 1981 and 1982, 100 kg/ha of 1,3-D reduced galled tubers to 0% compared to 13% and 18% in the untreated controls, respectively. Similarly, near Logan, Utah, galled tubers from plots treated with 168 kg/ha 1,3-D (114 l/ha of Telone II®) injected at 30 cm over the course of three growing seasons were 2%, 2%, and 4%, respectively, compared to 39%, 59%, and 94% in the untreated controls (Griffin 1989). However, Santo and Wilson (1990) observed that while spring application of 218 kg/ha of 1,3-D (183 l/ha of Telone II®) using sweep shanks 30 cm deep on 23 cm centers,

significantly reduced the percentage of potatoes culled by *M. chitwoodi*, the level of damage remaining was still unacceptable. More recent work by Ingham et al. (2000) in the southern Columbia Basin of Oregon indicated that spring applications of 282 kg/ha of 1,3-D (238 l/ha of Telone II[®]), 45 cm deep on 38 cm centers provided excellent control. The above studies illustrate the importance of proper placement of fumigant nematicides for control of *M. chitwoodi*.

Metam sodium: Metam sodium is currently marketed in the U.S. by AMVAC Chemical Corp. as Vapam HL[®] and by Tessenderlo Kerley, Inc. as Sectagon 42[®]. After application, metam sodium breaks down in the soil to form methyl isothiocyanate, which is active against soil-borne nematodes, soil-borne fungi, and certain weed seeds. Methyl isothiocyanate has a relatively low volatility compared to other fumigant nematicides (Mitarai et al., 1997). As a result, metam sodium, can be applied by direct mechanical incorporation into soil from shank or tilling implements or via irrigation water (chemigation).

Control of *M. chitwoodi* in the Pacific Northwest with metam sodium has been investigated for some time. Santo and Qualls (1984) reported fall application of 179 kg/ha of metam sodium (356 l/ha of Vapam HL[®] or Sectagon 42[®]) applied in 2.5 cm of water directly to wheat stubble significantly reduced tuber infection from 82% in the untreated controls to 1.5%. Pinkerton et al. (1986) also demonstrated that fall or spring applications of 182 or 220 kg/ha of metam sodium (361 and 431 l/ha Vapam HL[®] or Sectagon 42[®]) in irrigation water significantly reduced the percentage of tubers culled from damage by *M. chitwoodi*, but none of the treatments were commercially acceptable. During a field trial in 1993, Ingham et al. (2000) observed that 200 kg/ha of metam

sodium (392 l/ha Vapam HL[®] or Sectagon 42[®]) applied in 1.9 cm water using a portable sprinkler applicator did not significantly reduce culled tubers compared to the untreated control. However, when metam sodium was applied through the center-pivot sprinkler in 1994, culled tubers were significantly lower than the untreated controls, although still commercially unacceptable.

While metam sodium is an effective nematicide, successful control of *M. chitwoodi* on potato seems to be dependent upon the depth of penetration of the chemical. For instance, in the early work of Santo and Qualls (1984), metam sodium controlled J2 to a depth of 91 cm and only minor tuber infection occurred at the end of the season. However, when J2 were not controlled to a depth of 60 cm, unacceptable tuber damage occurred (Ingham et al. 2000). Delivering metam sodium directly into the soil via chisels and/or sweeps may reduce tuber damage in potato compared to chemigation, by directly placing the chemical in the soil rather than relying on water incorporation. Ingham et al. (2001) found that 182 kg/ha of metam sodium (361 l/ha of Vapam HL[®] or Sectagon 42[®]) applied 15 and 30 cm below the surface as well as 285 and 356 kg/ha (560 and 700 l/ha of Vapam HL[®] or Sectagon 42[®]) applied 15, 30, and 45 cm below the surface significantly reduced midseason levels of *M. chitwoodi* in the soil. All three treatments significantly reduced the percentage of culled tubers, but only the two higher rates, injected at three depths, were close to being commercially acceptable. Riga and Wilson (2003) also found that injecting metam sodium on shanks at 182 kg/ha (361 l/ha of Vapam HL[®] or Sectagon 42[®]) reduced mid-season and harvest levels of *M. chitwoodi* in the soil while 143 kg/ha (285 l/ha of Vapam HL[®] or Sectagon 42[®]) did not. Furthermore,

the higher rate (361 l/ha) significantly reduced the percentage of culled tubers, while the lower rate (285 l/ha) did not.

While metam sodium alone has been inconsistent for control of *M. chitwoodi*, it has consistently increased potato yields by reducing levels of *Verticillium dahliae* in the soil (Hamm et al, 2003). As a result, it is commonly used in combination with 1,3-D which provides both soil-borne nematode and fungal control. This treatment has provided excellent control of tuber damage from *M. chitwoodi*, even when rates of 1,3-D and metam sodium are reduced (Ingham et al. 2000).

CONTROL WITH NON-FUMIGANT CHEMICALS

Several chemicals within the organophosphate and carbamate classes of insecticides are also active against soil-borne plant-parasitic nematodes (Pree et al., 1987). These chemicals generally have very low volatility and are considered non-fumigants. Unlike the fumigant chemicals, non-fumigant chemicals are not phytotoxic to plants at concentrations used to control nematodes and therefore can be applied prior-to, at, or after planting, depending on label use restrictions. Currently, non-fumigant nematicides registered for root-knot nematode suppression in potato in the U.S. include aldicarb (Temik[®]), ethoprop (Mocap[®]), and oxamyl (Vydate C-LV[®]).

Aldicarb: Aldicarb ([(2-methyl-2-methylsulfonyl-propylidene) amino] N-methylcarbamate) is a contact and systemic carbamate marketed by Bayer CropScience as Temik[®]. Aldicarb is commonly used in potato production for early season green peach aphid (Holbrook 1977; Powell 1980; Woodford et al., 1988) and Colorado potato beetle control (Lacey et al., 1999).

Early aldicarb research on *M. chitwoodi* control in potato by Griffin (1985) demonstrated that 5.5 g/ha of aldicarb applied at planting 15 cm deep on each side of the potato row significantly reduced galled tubers to 41% compared to 86% in the untreated control, but did not provide commercially acceptable control. Pinkerton et al. (1986) observed little effect of aldicarb on (92% culls) when used alone. Later research by Griffin (1989) utilized soil degree-day accumulation from planting to schedule aldicarb applications. Pre-plant applications of 5.5 kg/ha of aldicarb applied in a 30 cm band directly over the row and rototilled to a depth of 15 cm resulted in 25%, 36%, and 66% infected and galled tubers during growing seasons accumulating 1,344, 1,684, and 2,028 DD_{5C}, respectively. Additional applications of aldicarb between 500 and 1,200 DD_{5C} after planting further reduced infected and galled tubers to 18% and 49% during the years that accumulated 1,684 and 2,028 DD_{5C}, respectively. Interestingly, the best treatments during the last two years of the study were two post-plant applications of aldicarb made between 500-600 DD_{5C} and 1,000-1,300 DD_{5C} after planting resulting in 6% and 34% infected and galled tubers, respectively.

Ethoprop: Ethoprop (O-ethyl S, S-dipropylphosphorodithioate) is a contact organophosphate nematicide currently marketed by Bayer CropScience as Mocap[®]. Once incorporated into the soil, ethoprop is hydrolyzed to O-ethyl-S-propyl-phosphorothioic acid and has a half-life of approximately 6 weeks in sandy loam soils with low organic matter (1%) of the Columbia Basin of Washington. Repeated applications of ethoprop to the same field resulted in increased biodegradation (Mojtahedi et al., 1991a; Karpouzas et al., 1999) which may compromise efficacy. As a result, a two-year interval between successive ethoprop applications is recommended to reduce biodegradation (Mojtahedi et

al., 1991a). Ethoprop has a relatively low water solubility of 843 grams per 100 grams of water and therefore limited mobility in the soil. While Mojtahedi et al. (1991a) were able to move ethoprop nearly 20 cm below the root zone with 7.5 cm of water, Smelt (1977) was unable to move ethoprop 10 cm below the application depth with nearly 35 cm of water between May and October. Carlson et al. (1990) found that physically incorporating ethoprop to a depth of 20 cm reduced the percentage of tubers blemished by *M. chitwoodi* to 12% compared to 48% when the ethoprop was only incorporated to a depth of 5 cm. Ingham et al. (1991) observed that pre-plant mechanical incorporation of ethoprop by rototilling or disking significantly reduced tubers culled by *M. hapla*, but post-plant water incorporation did not.

While ethoprop alone may provide adequate control of the *M. hapla* on potato, ethoprop has been relatively ineffective against *M. chitwood*, generally providing reduced tuber damage, but not to commercially acceptable standards. Early research by Griffin (1985) indicated that applying 5.5 kg/ha of ethoprop at planting using chisels 15 cm deep on either side of the potato row significantly reduced galled tubers from 86% to 61%. When Santo and Wilson (1990) surface broadcast 6.6, 9.9, and 13.2 kg/ha of ethoprop followed by physical incorporated to a depth of 15 cm, 88%, 92%, and 98% of the tubers were culled respectively, and harvest numbers of *M. chitwoodi* were no lower than in the untreated control. Ingham et al., (2000) also reported that 13.2 kg/ha of ethoprop surface applied and physically incorporated to 15 cm failed to reduce harvest levels of *M. chitwoodi* in the soil, but significantly reduced culls to 24%.

Oxamyl: Oxamyl (Methyl N'N'-dimethyl-N-[(methyl carbamoyl)oxy]-1-thiooxamimidate) is a contact and systemic carbamate chemical currently marketed by

E.I. du Pont de Nemours as Vydate C-LV[®]. Once inside the plant (Harvey et al., 1978a) or in soil-solution (Harvey and Chan 1978b), oxamyl is hydrolyzed into a non-nematicidal oxime compound. The half-life of oxamyl in soil is relatively short, reported to be approximately two weeks in fallow soil (Bromilow 1973), and influenced by pH (Harvey and Chan 1978b), moisture, and temperature (Gerstl 1984).

Early work using oxamyl to control *M. chitwoodi* indicated that in-furrow at planting applications of 0.6, 1.1, and 2.2 kg/ha of oxamyl at-planting did not reduce culled tubers (Santo et al., 1981). Furthermore, 114 l/ha of 1,3-D (Telone II[®]) followed by 1.1 kg/ha of oxamyl in-furrow at planting (20% culls) was no better than 114 l/ha of 1,3-D alone (23% culls). However, 114 l/ha of 1,3-D gpa followed by 2.2 kg/ha of oxamyl in-furrow at planting significantly reduced culls (4%) to acceptable levels. Reducing the rate of 1,3-D to 95 l/ha followed by 2.2 kg/ha oxamyl in-furrow at planting (34% culls) was no better than 142 l/ha of 1,3-D alone (Santo et al., 1982). Low volume foliar applications of oxamyl applied post plant to the potato crop have been ineffective in providing commercially acceptable *M. chitwoodi* control in potato (Ingham et al., 1993; Santo et al., 1998; Ingham et al., 2000).

SUMMARY

While parasitism of *M. chitwoodi* on a long-season potato variety has been studied in one growing region in the western United States, no information on the behavior of *M. chitwoodi* on short-season varieties or in other growing regions is currently available. Furthermore, tuber symptom development following harvest has not been investigated. Since the majority of the potato crop grown in the western U.S. is

stored on average for more than six months before it is marketed, the risk of further tuber symptom development during storage would provide useful information to growers.

Management of soil-borne nematodes with non-fumigant nematicides that may require multiple applications, such as oxamyl, requires an understanding of the growth of the host; the biology of the pathogen; and the influence of different environmental conditions associated with different production areas. Possible deviations of behavior in the host or pathogen in different climatic conditions may render successful management strategies in one region to be ineffective in another. Additional research is needed to determine proper applications of non-fumigant nematicides for successful control of *M. chitwoodi* in varied growing regions throughout the western United States.

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Population Dynamics of *Meloidogyne chitwoodi* on Potato in Three Production Areas in the Western United States

ABSTRACT

Research plots were established in 2001, 2002, and 2003 in the southern Columbia Basin near Hermiston, Oregon in the Klamath Basin near Klamath Falls, Oregon and in the San Luis Valley near Blanca, Colorado to determine the effect of, and the interaction between accumulated soil-degree days base 5°C (DD_{5C}) and oxamyl use on soil population dynamics of *Meloidogyne chitwoodi*. Population dynamics of *M. chitwoodi* on potato (*Solanum tuberosum*) were multi-modal in all three regions, representing distinct periods of egg hatch and root and tuber infection. *M. chitwoodi* completed two generations in Klamath Falls and Blanca, and three generations in Hermiston. Second generation eggs began to hatch in Klamath Falls, Hermiston, and Blanca between 740 – 835 DD_{5C}, 920 – 1,070 DD_{5C}, and 980 – 1,055 DD_{5C} after planting, respectively, regardless of oxamyl program. Oxamyl applications (1.1 kg/ha) in-furrow at-planting and at crop emergence, followed by bi-weekly chemigation applications in 3.2 cm/ha water beginning between 890 and 1,000 DD_{5C} reduced soil densities of second-stage juveniles (J2) between the hatch of the second generation and harvest in Klamath Falls and Hermiston, but not in Blanca. Oxamyl applications did not reduce numbers of J2 at harvest compared to those at planting. This study provides the first population dynamics information on short-season potato cultivars in the Columbia Basin, and on any variety in the Klamath Basin and San Luis Valley. Results indicate in-season nematicide applications targeting the hatch of the second generation should be made prior to 740, 920, and 980 DD_{5C} after planting in the Klamath Basin, Columbia Basin, and San Luis Valley, respectively.

INTRODUCTION

The Columbia root-knot nematode (*Meloidogyne chitwoodi* Golden et al.) is a soil-borne sedentary endoparasite first reported in eastern Idaho in 1974 (Golden et al., 1980). Since then it has been reported in Oregon and Washington (Santo et al., 1980), California and Nevada (Nyczepir et al., 1982), Virginia (Eisenback et al., 1986), Colorado (Pinkerton and McIntyre 1987), Utah (Griffin and Thomson 1988), New Mexico (Thomas et al., 2001), and Texas (Szalanski et al., 2001). *M. chitwoodi* has also been reported outside the United States in Argentina and Holland (Esbenshade and Triataphyllou, 1985), South Africa (Kleynhans 1991; Fourie et al., 2001), Germany (Heinicke, 1993; Muller et al., 1996), Mexico (Cuevas, 1997), Belgium (Waeyenberge and Moens 2001), and France, Portugal, and Spain (Mugniery, INGA, pers. com.).

Although *M. chitwoodi* has a wide host range it is most important as a pathogen of potato (*Solanum tuberosum*). There is no report that this nematode reduces yield, but successful tuber invasion by second-stage juveniles (J2) followed by egg production reduces tuber market value by causing external galls and internal discoloration (Finley, 1981). Tuber symptoms are considered damage by the United States Department of Agriculture and no more than 5% damage or 5% serious damage is allowed in U.S. No. 1 table-stock or U.S. No. 1 processing potatoes, respectively (www.ams.usda.gov/standards/vppot.pdf).

Since nematodes can not regulate their temperature, physiological development is dependent upon external heat accumulation above and below a minimum and maximum temperature. As a result, developmental events in a nematode's life-cycle may be more accurately predicted based on physiological time rather than calendar date. The lower

developmental threshold for *M. chitwoodi* has been determined to be 5°C (Inserra et al. 1983; Griffin 1985; Inserra et al. 1985; Charchar 1987), making it well adapted to the cool spring temperatures present during potato planting in the western United States. Pinkerton et al. (1991) studied population dynamics of *M. chitwoodi* on potato cv. Russet Burbank in the southern Columbia Basin and developed a phenology model based on accumulated soil degree-days after planting. They determined that since potato roots are not immediately present after planting, 1,000 DD_{5C} (1,000 accumulated soil degree-days above 5°C) were required to complete the first generation, at which time, second generation eggs hatched and J2 were released into the soil. Subsequent generations were completed in only 500 to 600 DD_{5C} because J2 could immediately infect roots and begin another life-cycle. Perhaps most importantly, they concluded that first generation J2 did not infect potato tubers and that initial tuber infection coincided with the release of second generation J2 into the soil. Because of its low temperature threshold, as many as four generations have been reported when growing long-season potato varieties in the Columbia Basin of Washington (Pinkerton et al., 1991) resulting in high densities of J2 late in the growing season. Ingham et al. (2000) reported that when left uncontrolled, *M. chitwoodi* populations were nine times higher at harvest than at planting and 77% of the tubers were infected.

While the effect of degree-day accumulation on *M. chitwoodi* population dynamics has been studied on potato cv. Russet Burbank in the southern Columbia Basin, no information is available from other cultivars or geographical regions.

Control of *M. chitwoodi* is typically achieved by the use of pre-plant fumigant and non-fumigant nematicides. The most commonly used fumigant is 1,3-dichloropropene,

which is very effective but can only be applied before planting (Ingham et al., 2000). The non-fumigant nematicides ethoprop and aldicarb can be applied before or at planting, respectively, but do not provide adequate control when used alone (Ingham et al., 2000). No post-plant nematicide was available on potatoes until E.I. du Pont de Nemours and Company received registration for the systemic nematicide oxamyl. Based on the work by Pinkerton et al. (1991), the labeled recommendation for *M. chitwoodi* suppression was bi-weekly chemigation applications that began at 950 DD_{5C} after planting and continued until seven days prior to harvest. Pinkerton et al. (1991) suggested that in-season non-fumigant nematicide applications at the hatch of the second generation (950 DD_{5C}) would reduce third generation inoculum, and consequently tuber infection, but this hypothesis has not been tested. In order for this approach to be successful, the physiological timing of the second generation hatch would need to be uniform among varieties and different growing regions.

The objective of this study was to determine the effect of degree-day accumulation and the effect of the non-fumigant nematicide, oxamyl, on *M. chitwoodi* soil densities on potato cv. Russet Norkotah grown in the Columbia Basin (CB) and Klamath Basin (KB) of Oregon and on Russet Norkotah and Russet Nugget grown in the San Luis Valley (SLV) of Colorado. Each area was specifically chosen to represent different climatic conditions associated with potato production in the western United States. The CB is a long, hot growing region similar to western Idaho and central California. The KB is a warm growing area representative of central Idaho and north-western Washington, while the SLV has a short, cool growing season similar to eastern Idaho.

MATERIALS AND METHODS

Study areas: The trials were located at the Hermiston Agricultural Research and Extension Center near Hermiston, Oregon, in the CB; the Klamath Experiment Station near Klamath Falls, Oregon, in the KB; and grower fields in Alamosa and Costilla counties in the SLV of Colorado. The soil types were Atkins fine loamy-sand (pH 7.6), Poe fine loamy-sand (pH 6.5 – 7.0), and Gunbarrel loamy-sand (pH 8.0 – 8.5), in the CB, KB, and SLV, respectively. All sites had a history of damage from *M. chitwoodi* on potato and the previous crop during all years was a small grain. Prior to potato planting, sites were ripped (45 cm), tandem disked (20 cm), and roller-harrowed (10 cm).

Certified Russet Norkotah potato seed was planted using a two-row assist feed planter on 26 April 2001 and 17 April 2002 in the CB and on 21 May 2002 and 22 May 2003 in the KB. Certified Russet Nugget and Russet Norkotah potato seed was planted by grower cooperators on 1 May 2002 and 7 May 2003, respectively, in the SLV. Cultural practices, including: irrigation, weed, insect, and disease control were consistent with those of each growing region.

Plot design and oxamyl application: Four-row potato plots (3.5 m x 9.1 m), (3.3 m x 6.1 m), and (3.5 m x 6.1 m) were established as experimental units in the CB, KB, and SLV, respectively. Two oxamyl programs, a standard program beginning at 950 DD_{5C}, and a full-season program (in-furrow at planting + crop emergence + standard program), were used to determine if oxamyl applied during the growing season would reduce J2 inoculum. The standard program was chosen to test the hypothesis that initial in-season applications at the hatch of the second generation would reduce J2 inoculum for the remainder of the growing season. The full-season program was chosen to

determine if oxamyl applications targeting the first generation improved the efficacy of the standard oxamyl program. The rationale for the full-season program was early season applications may reduce first generation root penetration, thus, reducing second generation inoculum. The target physiological time for the initial application in the standard program was 950 DD_{5C} after planting but actual timings varied slightly (Table 1). Oxamyl programs were assigned in a randomized complete block design with five replications. The 2001 CB experiment was spatially blocked. All experiments in 2002 and 2003 used pre-plant nematode densities as the blocking factor.

Oxamyl was applied at a rate of 1.1 kg/ha and injection solutions were always buffered to a pH less than 7 (Table 1). The in-furrow, at-planting applications were made as a 15 cm wide band directly in the bottom of the furrow behind the planter shoe in 140 liters/ha spray solution. Applications at crop emergence were made as a 15 cm wide band directly over the potato rosette in 234 liters/ha spray solution. All other applications were chemigated in 3.2 cm/ha water. Chemigation was simulated in the CB using a side mount boom with flood jet nozzles moving at 0.07 m/second, while applications in the KB and SLV were made through solid-set and center-pivot irrigation systems, respectively. Non-treated plots in the KB and SLV were covered during the application with a poly tarp (118 g/m² – 900 Denier – 10x10 Weave Count) supported by polyvinyl chloride (PVC) hoop frames.

Degree-day monitoring: Watchdog model 125 data loggers (Spectrum Technologies, Inc. Plainsfield, IL) were installed at each site to record soil temperature at seed-piece depth (22 cm) every 30 minutes. The averaging (rectangle) method (Arnold 1960) was used to calculate soil degree-days. By this method, beginning at potato

planting, *M. chitwoodi* developmental degree-days were calculated from the average daily soil temperature minus the minimum temperature of 5°C and cumulative degree-days were determined by summing daily values through the season.

Sampling and extraction of nematodes: Soil samples were collected from the middle six meters of a center row from each four-row plot every seven days from planting until potato harvest in the CB, and every 14 days from planting until 700 DD_{5C} after planting, then every seven days until harvest in the KB and SLV. A sample consisted of 10 soil cores taken to a depth of 30 cm using a 2.5 cm-diam. probe. Samples were sieved and mixed, and nematodes were extracted from a 250-g subsample by density centrifugation (Jenkins 1964) as modified by Ingham (1994). *M. chitwoodi* J2 were counted using a dissecting microscope and reported per 250-g dry soil.

Statistical analysis: Nematode densities were transformed to $\log_{10}(x+1)$ prior to analysis of variance (ANOVA). The effects of degree-day accumulation and oxamyl program on *M. chitwoodi* soil J2 densities were determined by repeated measures ANOVA with between-subjects factors using PROC MIXED in SAS version 9.1.3. Degree-day accumulation was the within-subjects factor and oxamyl program the between-subjects factor. Following ANOVA, estimates of means and 95% confidence intervals were back-transformed and reported with *P* values.

RESULTS

There was no evidence ($P > 0.05$) of an interaction between soil degree-day accumulation and oxamyl program on densities of *M. chitwoodi* J2 in the CB, KB, or SLV during 2001, 2002, or 2003, so only the main effects are reported.

Degree-day accumulation: Average soil degree-day accumulation (5°C) was highest in the Columbia Basin (2,020), while accumulation was 17% less (1,680) in the Klamath Basin and 20% less (1,626) in the San Luis Valley.

Effect of degree-day accumulation on soil densities of Meloidogyne chitwoodi: Degree-day accumulation had a significant effect ($P \leq 0.0001$) on densities of J2 at all sites and years. Three periods of increases ($P \leq 0.05$) in numbers of J2 were observed in the CB, while only two were observed in the KB and SLV (Table 2). Averaged over two growing seasons, the first increase occurred at 1,050 DD_{5C}, 835 DD_{5C}, and 1,070 DD_{5C} after planting in the CB, KB, and SLV, respectively (Table 2). The second increase began on average 1,410 DD_{5C}, 1,280 DD_{5C}, and 1,520 DD_{5C} after planting in the CB, KB, and SLV, respectively, while the third increase occurred on average 1,840 DD_{5C} after planting in the CB. Representative J2 population dynamics on potato in relation to accumulated degree-days are illustrated in Figure 1 (CB), Figure 2 (KB), and Figure 3 (SLV).

Harvest densities of J2 were no different than those at planting in the CB during 2001 or 2002 (Table 3). However, densities of J2 were 122 and 26 times higher in the KB and 5 and 26 times higher in the SLV at harvest than at planting in 2002 and 2003, respectively.

Effect of oxamyl on soil densities of Meloidogyne chitwoodi: Oxamyl significantly reduced densities of J2 during the period from the second generation hatch (first increase in soil J2 densities) until potato harvest in the CB (2001) and KB (2002), but not during other years in these two areas (Table 4). The CB full-season oxamyl program reduced ($P = 0.07$) J2 by 66% (126 to 43 J2) compared to the untreated control in 2001, but oxamyl had no affect in 2002. The KB standard and full-season oxamyl programs reduced ($P = 0.05$) J2 by 79% (627 to 133) and 70% (627 to 189) compared to the untreated control in 2002, but the full-season program did not further reduce J2 numbers compared to the standard program. The KB full-season program did not reduce J2 in 2003. Although the SLV standard and full-season programs lowered J2 by 28% and 63%, respectively, these reductions were not significant.

DISCUSSION

This study provides the first information on population dynamics of *M. chitwoodi* in relation to accumulated soil degree-days on short-season table stock potato varieties in the CB, KB, and SLV. Soil degree-day accumulation was equal in the cooler growing regions of the KB and SLV but less than the warmer CB.

Degree-day accumulation had a significant effect on soil densities of *M. chitwoodi* on potato. When growing the short-season cultivar Russet Norkotah in the CB, KB, and SLV and Russet Nugget in the SLV, *M. chitwoodi* produced two generations in the SLV and KB and three generations in the hot climate of the CB. Others have reported four generations when a long-season cultivar, Russet Burbank, was studied in the CB (Pinkerton et al., 1991). The number of generations observed in the current study has not been previously reported for a short-season cultivar in the CB or for any cultivar grown in the SLV or KB.

Populations of *M. chitwoodi* significantly increased between planting and harvest in the KB and SLV, regardless of oxamyl program, demonstrating high reproductive potential on short-season cultivars in these two areas, information that has been previously unknown. Unlike the KB and SLV, *M. chitwoodi* soil densities at harvest were not different than at planting, which is contrary to previous reports on the long-season cultivar, Russet Burbank (Pinkerton et al., 1991; Ingham et al., 2000). One hypothesis is that harvest samples were taken between generations during the period when J2 had infected roots and tubers and the hatch of eggs from the next generation had just begun. Another possible explanation is that potato roots and tubers were more heavily infected in the CB than in the KB and SLV, so that lower densities were present in the soil at

harvest. A third hypothesis is that the potato crop was heat stressed from the extreme temperatures in the CB and unable to support the high levels of *M. chitwoodi* observed in the KB and SLV.

Following planting, soil densities declined as first generation J2 invaded roots, initiating the endoparasitic portion of the first generation. This initial decrease was observed in the CB and the SLV but not in the KB, likely due to low nematode densities at planting. Upon completion of the first generation, second generation eggs began to hatch on average between 970 (2002) and 1,130 DD_{5C} (2001) in the CB, confirming the work by Pinkerton et al. (1991). Similar numbers of degree-days, between 1,030 (2003) and 1,110 DD_{5C} (2002), were required to complete the first generation in the SLV. However, the second generation in the KB began to hatch between 790 (2003) and 880 DD_{5C} (2002) which was earlier than observed in the CB and SLV.

One hypothesis for the earlier hatch in the KB is related to the host's ability to produce a greater root mass earlier at higher temperatures (Timlin et al., 2006). Potato roots may have emerged and grown more rapidly in the KB since the average soil temperature at planting was 15°C, compared to 13.5°C and 10.5°C in the CB and SLV, respectively. As a result there may have been less of a delay between planting and root invasion, resulting in fewer degree-days accumulated from planting until the second generation hatch. This would likely not be a management issue within the SLV or KB, where all potato fields are planted within one month of each other, but could be a concern in the CB where planting occurs in March, April, and May. According to the Agrimet weather station at the Hermiston Agricultural Research and Extension Center, the average soil temperature at 10 cm since 1998 has been 7°C and 21°C on 1 March and 31 May,

respectively. Based on this hypothesis, second generation *M. chitwoodi* would require fewer degree-days from planting-to-hatch in a potato crop that was planted at the end of May compared to a potato crop that was planted at the beginning of March.

A second hypothesis for the earlier hatch in the KB is that the isolate of *M. chitwoodi* penetrated roots sooner after planting because of intraspecific variation in the pathogen. This hypothesis is supported by Charchar (1987), who determined that the Klamath Falls isolate of *M. chitwoodi* more readily infected roots at 12°C than the Patterson, WA (CB) isolate. While the data collected in the current study do not provide the necessary information to determine if the Klamath Basin isolate should be classified as a different biotype or pathotype (Van der Beek et al., 1999), fewer degree-days required to complete the first generation suggest that the KB isolate may be more aggressive than the CB or SLV isolate in terms of a higher percentage of J2 penetrating roots at lower temperatures.

The degree-day intervals between the first and second increases in J2 suggest that the physiological time for the second generation to produce the third generation was 360 DD_{5C}, 535 DD_{5C}, and 465 DD_{5C} in the CB, KB, and SLV, respectively, and 485 DD_{5C} for the third generation to produce the fourth generation in the CB. With the exception of the second generation in the CB, these physiological times are similar to previous research which suggested between 500 and 600 DD_{5C} were required from J2 to J2 (Charchar 1987; Pinkerton et al., 1991).

The results from this study also demonstrate that the effect of degree-day accumulation on *M. chitwoodi* soil densities was not influenced by the oxamyl programs tested. Consequently, early season applications in-furrow at planting and at crop

emergence did not delay the hatch of the second generation. Furthermore, adding an application in-furrow at-planting and at crop emergence to a standard program did not reduce the fecundity of the first and second generations compared to the standard program alone in the KB and SLV during 2002. This may be a result of the high reproductive potential (Al-Rehiayani, et al., 1999) of *M. chitwoodi* on potato. These results suggest that adding an in-furrow application at planting and a banded application at crop emergence to a standard program may not reduce tuber infection compared to the standard program alone, but this hypothesis needs to be tested. Although the full-season program was no better than the standard program, the full-season program reduced densities of *M. chitwoodi* in the CB and KB compared to the untreated control during 2001 and 2002, respectively.

This study clearly demonstrates that the oxamyl programs tested did not eliminate *M. chitwoodi* in the soil at harvest. The inability of repeated oxamyl applications to eliminate the nematode from the soil may be due to the fact that oxamyl behaves as a nematostat above 1 ppm (Bunt 1979). As a nematostat, oxamyl restricts locomotion and prevents root and tuber penetration, but does not directly kill the nematode. This would explain why populations of *M. chitwoodi* always increased between planting and harvest in the KB and SLV when oxamyl was applied. Using a nematostat such as oxamyl may protect tubers from infection (David et al, unpublished) but may maintain a population of J2 in the soil that regain infectivity when the oxamyl concentration decreases below 1 ppm. In order to reduce densities of J2 between planting and harvest, oxamyl may have to be applied at shorter intervals or at higher rates than used in the current study.

The original labeled recommendation for suppression of *M. chitwoodi* was to begin oxamyl applications between 950 and 1,000 DD_{5C} after planting, regardless of growing region. This study indicates the original recommendation may be adequate for the SLV since the earliest increase in numbers of J2 occurred between 980 and 1,080 DD_{5C}, but may be too late for the CB or KB since J2 were present in the soil prior to 950 DD_{5C}. Based on this study, initial oxamyl applications targeting the second generation should be made prior to 740, 920, and 980 DD_{5C} in the KB, CB, and SLV, respectively, in order for oxamyl to be in soil-solution prior to the second generation hatch. Furthermore, this application should not be delayed if an in-furrow or a crop emergence application is made since neither application had an affect on the timing of the second generation hatch. Initial applications made after 740, 920, and 980 DD_{5C} in the KB, CB, and SLV, respectively, may allow enough tuber infection to cause economic damage to the crop. Beginning applications earlier in the CB and the KB than previously recommended may increase the efficacy of the oxamyl program by reducing tuber infection, but this hypothesis also needs to be confirmed.

The inability of oxamyl to eliminate or reduce densities of *M. chitwoodi* between planting and harvest should be carefully considered when deciding how to manage populations of *M. chitwoodi* in potatoes. Oxamyl may not be a good choice for markets that require a harvest soil sample before a phytosanitary certificate will be issued. Certified seed and export table-stock markets both require phytosanitary certificates that state the potatoes are free of *M. chitwoodi*. In addition, the sole use of oxamyl over several potato crops may allow soil populations of *M. chitwoodi* to increase to high

levels. Thus, the nematode may not be adequately controlled the next time potatoes are grown or may result in economic damage to susceptible rotational crops.

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Table 1. Description of oxamyl programs tested

Oxamyl Program ^a	Description ^b
2002 KB Standard	(940) ^c followed by 14 days (1,100) and 28 days (1,330)
2002 SLV Standard	(890) followed by 14 days (1,110) and 28 days (1,280)
2003 SLV Standard	(890) followed by 14 days (1,050)
2001 CB Full Season	In-furrow at-planting (0), crop emergence (340) and then (1,000) followed by 14 days (1,180), 28 days (1,380), and 42 days (1,630)
2002 CB Full Season	In-furrow at-planting (0), crop emergence (470) and then (960) followed by 14 days (1,200), 28 days (1,450), and 42 days (1,680)
2002 KB Full Season	In-furrow at-planting (0), crop emergence (430) and then (940) followed by 14 days (1,100) and 28 days (1,330)
2003 KB Full Season	In-furrow at-planting (0), crop emergence (500) and then (870)
2002 SLV Full Season	In-furrow at-planting (0), crop emergence (380) and then (890) followed by 14 days (1,100) and 28 days (1,280)
2003 SLV Full Season	In-furrow at-planting (0) and then (890) followed by 14 days (1,050)

^aKB = Klamath Basin; CB = Columbia Basin; SLV = San Luis Valley

^bIn-furrow at-planting applications were 15 cm wide in the bottom of the furrow in 140 liters/ha spray solution.

^bCrop emergence applications were made at 100% plant emergence in a 15 cm wide band directly over the potato rosette in 234 liters/ha spray solution.

^bAll applications made after crop emergence were chemigated in 1.3 cm water.

^cNumbers in parenthesis are soil degree-days (5°C) after planting.

Table 2. Timing of increases in J2 of *Meloidogyne chitwoodi* in potato fields in relation to soil degree-day accumulation^a (5°C) after planting.

	<u>Columbia Basin</u>		<u>Klamath Basin</u>		<u>San Luis Valley</u>	
Increase in soil J2 ^b	2001 (n = 10)	2002 (n = 10)	2002 (n = 15)	2003 (n = 15)	2002 (n = 15)	2003 (n = 15)
1 st	1,070 – 1,185	920 – 1,020	825 – 940	740 – 840	980 – 1,080	1,055 – 1,160
	Avg. 1,050		Avg. 835		Avg. 1,070	
2 nd	1,385 – 1,480	1,340 – 1,445	1,040 – 1,110	1,410 – 1,550	1,560 – 1,630	1,420 – 1,470
	Avg. 1,410		Avg. 1,280		Avg. 1,520	
3 rd	1,730 – 2,100	1,700 – 1,830	--	--	--	--
	Avg. 1,840					

^aSoil degree-days were calculated using soil temperature at seed piece depth (20 cm).

^bIncreases in densities of *M. chitwoodi* from start to end of the degree-day intervals are significant at $P \leq 0.05$.

Table 3. Average densities of *Meloidogyne chitwoodi* (J2/250 g dry soil) at planting and at harvest.

	<u>Columbia Basin</u>		<u>Klamath Basin</u>		<u>San Luis Valley</u>	
	2001 (n = 10)	2002 (n = 10)	2002 (n = 15)	2003 (n = 15)	2002 (n = 15)	2003 (n = 15)
Planting	72 (33 – 158) ^a	2 (1 – 3)	8 (4 – 15)	16 (8 – 29)	269 (151 – 477)	13 (7 – 23)
Harvest	122 (56 – 266)	3 (2 – 4)	912 (450 – 1,851)	402 (219 – 739)	1,389 (782 – 2,468)	334 (182 – 610)
	$P = 0.32$	$P = 0.30$	$P \leq 0.0001$	$P \leq 0.0001$	$P \leq 0.0001$	$P \leq 0.0001$

^aNumbers in parenthesis are 95% confidence intervals.

Table 4. The effects of oxamyl program on average soil densities of *Meloidogyne chitwoodi* (J2/250 g dry soil) across all sample dates from the hatch of the second generation until harvest.

Treatment ^a	<u>Columbia Basin</u>		<u>Klamath Basin</u>		<u>San Luis Valley</u>	
	2001	2002	2002	2003	2002	2003
Control	126 ^b (52 – 304) ^c	3 (2 – 5)	627 (242 – 1,623)	227 (85 – 610)	969 (421 – 2,228)	35 (20 – 62)
Standard	--	--	133 (78 – 465)	--	698 (315 – 1,546)	45 (26 – 79)
Full Season	43 (18 – 103)	2 (1 – 4)	189 (52 – 335)	172 (65 – 450)	363 (160 – 824)	34 (19 – 60)
	$P = 0.07$	$P = 0.44$	$P = 0.05$	$P = 0.72$	$P = 0.22$	$P = 0.55$

^aSee text for full treatment description.

^bData are back-transformed means.

^cNumbers in parenthesis are 95% confidence intervals.

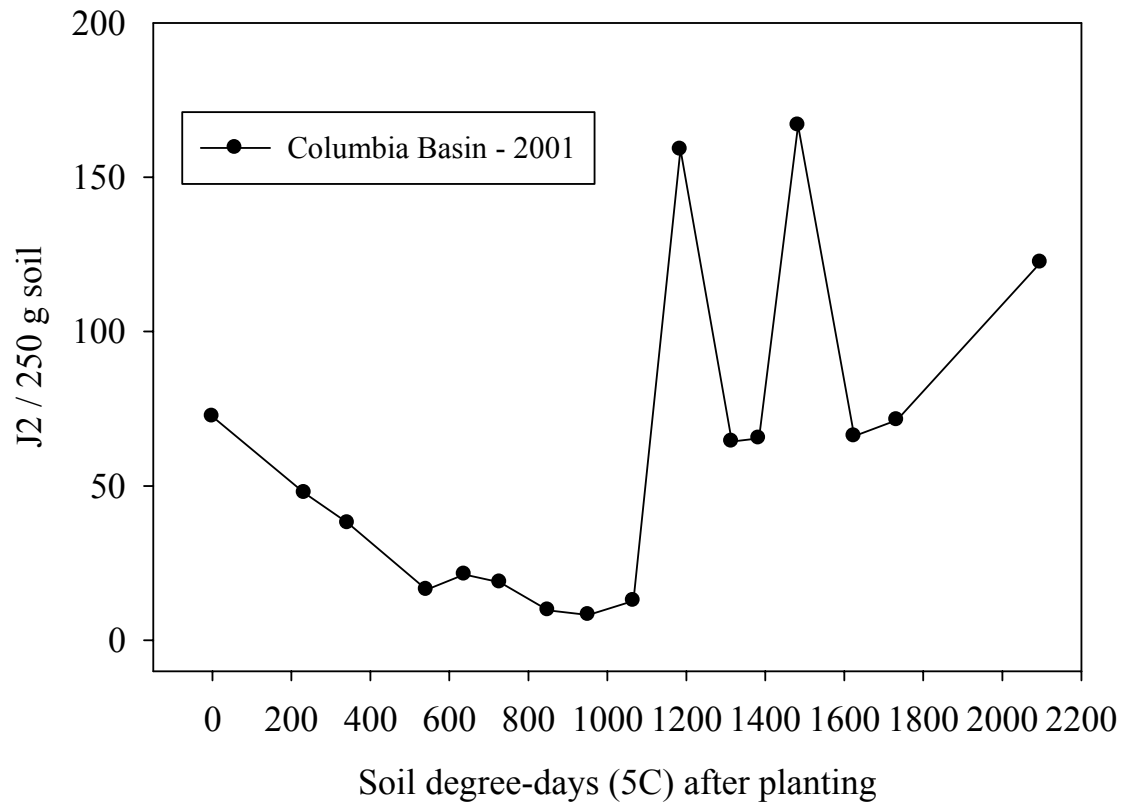


Figure 1. Population dynamics of *Meloidogyne chitwoodi* on potato cv. Russet Norkotah in relation to accumulated soil degree-days (5°C) after planting in the Columbia Basin.

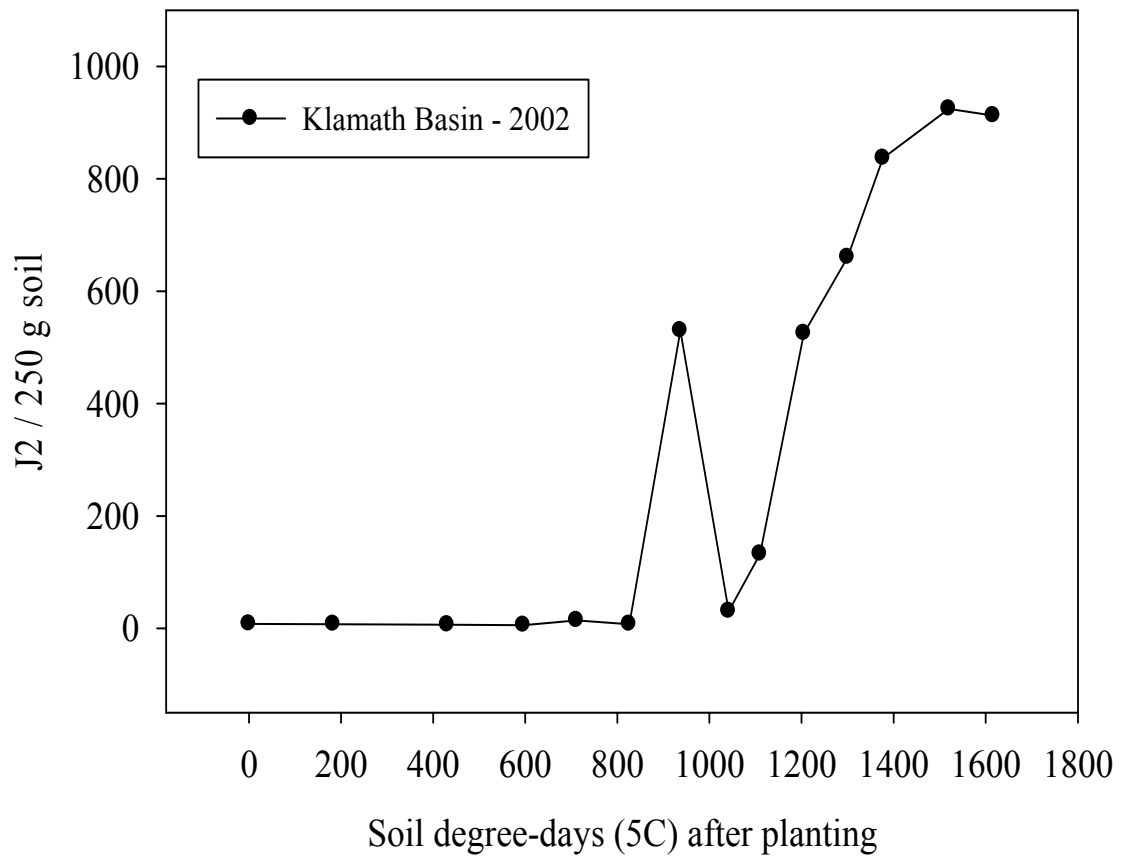


Figure 2. Population dynamics of *Meloidogyne chitwoodi* on potato cv. Russet Norkotah in relation to accumulated soil degree-days (5°C) after planting in the Klamath Basin.

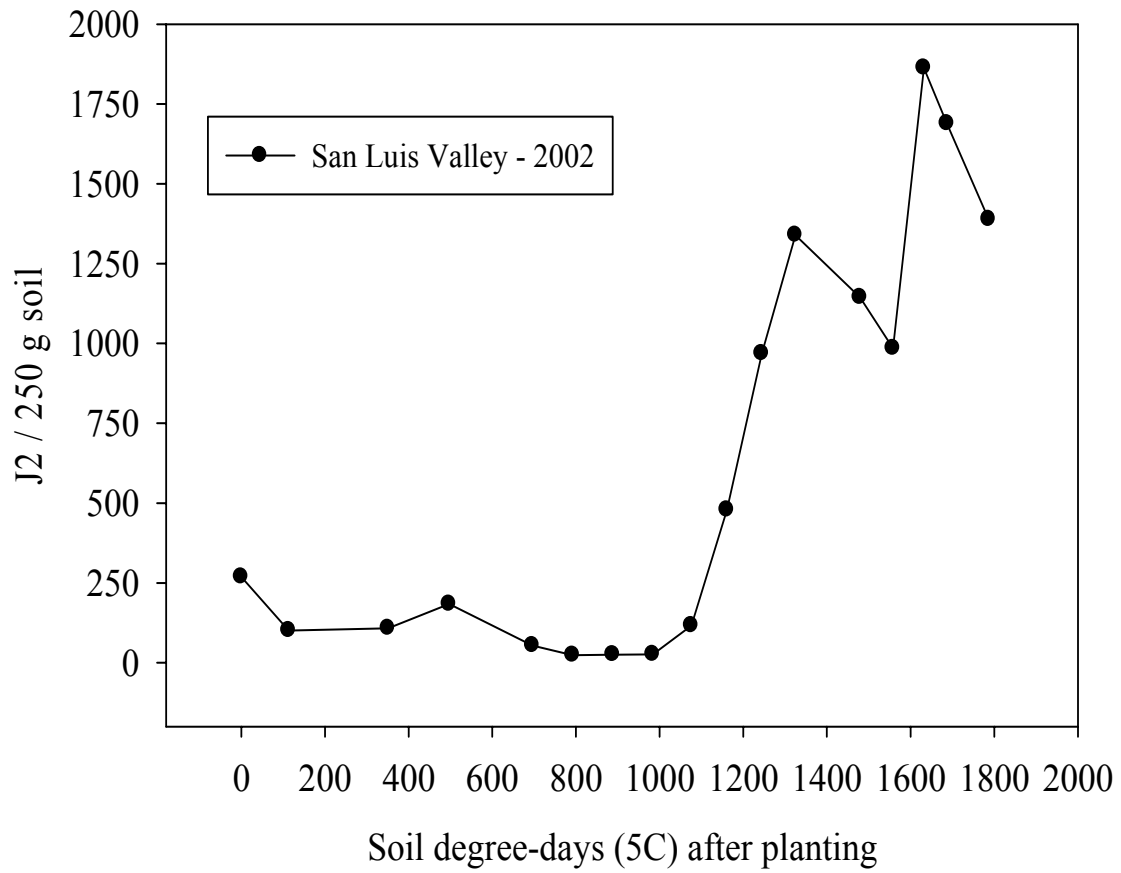


Figure 3. Population dynamics of *Meloidogyne chitwoodi* on potato cv. Russet Nugget in relation to accumulated soil degree-days (5°C) after planting in the San Luis Valley.

The Use of Oxamyl to Reduce Tuber Symptoms of *Meloidogyne chitwoodi* on Short-season Potato Cultivars in Three Growing Regions in the Western United States

ABSTRACT

Research plots were established in 2001, 2002, and 2003 at Hermiston and Klamath Falls, Oregon and Blanca, Colorado to determine the effects of, and the interaction between, oxamyl use, harvest date, and post-harvest degree-day accumulation on tuber symptoms of *Meloidogyne chitwoodi* on short-season table-stock potato (*Solanum tuberosum*) varieties. Three bi-weekly chemigation applications of oxamyl (1.1 kg/ha) in 3.2 cm/ha water beginning between 890 and 1,000 degree-days base 5°C (DD_{5C}) reduced internal symptoms in Klamath Falls and Blanca, but four applications were necessary in Hermiston. Augmenting this practice with in-furrow at-planting and crop emergence applications increased control of *M. chitwoodi*. Delaying harvest by three weeks in Hermiston increased internal (162%) and external (255%) symptoms and was not affected by oxamyl use. Comparing tuber symptoms of *M. chitwoodi* at harvest, following storage at 3 – 5°C, or at 21 - 24°C, found that oxamyl applied during the growing season did not affect post-harvest symptom development. Internal symptoms increased when tubers were stored between 21 and 24°C and accumulated more than 740 post-harvest DD_{5C}, but not when stored between 3 and 5°C and no more than 610 DD_{5C} were accumulated. External symptoms did not increase following harvest, regardless of storage temperature. This study provides the first information that chemigated oxamyl programs can be used to suppress *M. chitwoodi* tuber symptoms in three different growing regions on short-season table-stock varieties.

INTRODUCTION

The Columbia root-knot nematode, *Meloidogyne chitwoodi*, Golden et al., is a soil-borne sedentary endoparasite that was first reported in eastern Idaho in 1974 (Golden et al., 1980). Since then it has been reported from eight other states in the western United States (Santo et al., 1980; Nyczepir et al., 1982; Pinkerton and McIntyre 1987; Griffin and Thomson 1988; Thomas et al., 2001; Szalanski et al., 2001). *M. chitwoodi* overwinters primarily as eggs (Pinkerton et al., 1991), which hatch during the spring and release first-generation second-stage juveniles (J2) into the soil that can parasitize potato (*Solanum tuberosum*) as well as a wide range of monocotyledonous and dicotyledonous plants (Santo et al., 1980). First generation J2 penetrate roots as soon as the soil temperature is above 5°C (Inserra et al. 1983; Griffin 1985; Inserra et al. 1985; Charchar 1987), making it well adapted to the cool soil temperatures present during potato planting in the western U.S. As a result of the above studies, 5°C was established as the lower developmental threshold for *M. chitwoodi* and physiological time is expressed as soil degree-day accumulation base 5°C after planting (DD_{5C}). Pinkerton et al. (1991) determined the first generation was completed 950 DD_{5C} after planting, at which time eggs hatched, releasing second generation J2 that were able to infect roots, stolons, or tubers (Finley 1981). Pinkerton et al. (1991) reported that *M. chitwoodi* produced as many as four generations of J2 on the long-season potato variety Russet Burbank, when grown in the Columbia Basin of Washington state. The ability to complete multiple generations per growing season can result in high population densities and severe tuber damage when left untreated (Ingham et al., 2000). While there are no foliar symptoms or yield loss associated with *M. chitwoodi* parasitism on potato, successful tuber infection

can result in internal (brown spot in the cortex or pith) or external (gall on the periderm) symptoms which are considered quality defects by the United States Department of Agriculture (USDA). The brown spots inside the tubers become apparent when the adult female lays eggs and surrounds them with a gelatinous matrix (David et al., unpublished). Pinkerton et al. (1991) determined that eggs were laid 500 – 600 DD_{5C} after tuber infection. No information is available on how many degree-days are required after infection for internal or external symptoms to be apparent.

In order to regulate the overall quality of potato lots, grades have been established by the USDA for table-stock, process, and seed potatoes with strict tolerances for defects, including nematode damage. While there is an allowable tolerance for nematode damage in U.S. No. 1 table-stock and process potatoes, there is no tolerance in certified-seed potatoes. Even though there are several grades, U.S. No. 1 potatoes have the lowest tolerance for defects, and as a result, demand a premium price. If nematode damage is above the allowable tolerance, the grade is reduced or the lot is rejected, resulting in an economic loss to the grower.

According to the National Potato Council, over one-third of the potatoes produced in the U.S. are grown in the San Luis Valley (SLV) of Colorado, the Klamath Basin (KB) of Oregon and California, and the Columbia Basin (CB) of Oregon and Washington. Any issue that impacts production or quality could reduce supply of U.S. potatoes.

The SLV is located in south-central Colorado at 2,300 meters above sea level and has a cool, short growing season. Table-stock and certified-seed potatoes are raised from May – October and degree-day accumulation is similar to potato producing areas in eastern Idaho. The KB is located in north-central California and south-central Oregon at

an average elevation of 1,220 meters above sea level and also has a short growing season, but is warmer than the SLV. Table-stock, chip, and certified-seed potatoes are raised from May – October and degree-day accumulation is similar to potato regions in central Idaho and north-western Washington. The CB is a long-season agricultural region located in north-central Oregon and south-central Washington, 180 meters above sea level, where table-stock, chip, and process potatoes are raised from March – October. Degree-day accumulation is similar to other long-season potato producing areas such as western Idaho and central California.

Following the discovery of *M. chitwoodi* in these three potato production areas (Santo et al., 1980; Nyczepir et al., 1982; Pinkerton and McIntyre 1987), fumigant and non-fumigant nematicides were evaluated for control in the CB (Santo and Qualls 1984; Pinkerton et al., 1986; Santo and Wilson 1990; Ingham et al., 2000; Riga and Wilson, 2003) and in the KB (Carlson et al., 1990; Rykbost et al., 1991), but have not been tested in the SLV. While 1,3-dichloropropene, metam sodium, ethoprop, and aldicarb are all registered for use on potato in the Pacific Northwest, none of these chemicals can be applied after planting. As a result, growers had no way to manage *M. chitwoodi* during the growing season if the pre-plant nematicides did not provide adequate control.

The registration of oxamyl as Vydate C-LV[®] (E.I. du Pont de Nemours, Wilmington, DE) in 1993 provided potato growers an opportunity to apply a nematicide during the growing season. Oxamyl is a systemic carbamate that controls nematodes by contact and systemic activity (Bunt, 1979) and if soil concentrations remain above 1 ppm, root penetration is inhibited (Bunt, 1987). However, oxamyl has a short half-life of approximately 14 days (Bromilow 1973) so multiple applications were considered

necessary to protect tubers from infection by *M. chitwoodi*. Pinkerton et al. (1991) determined that Russet Burbank tubers grown in the CB were not infected until second generation J2 emerged (950 DD_{5C}) and hypothesized that nematicides applied at this time would reduce tuber infection. Consequently, the labeled recommendation was to make bi-weekly applications in 1.3 cm water from 950 DD_{5C} after planting until 7 days prior to harvest. However, no information is available on the effectiveness of this practice or how many applications are required for adequate suppression. Nor is there any information available on how potato variety or growing region influenced oxamyl's ability to reduce *M. chitwoodi* tuber infection on potato. Recent work by David et al. (unpublished) documented that second-generation J2 were present in soil earlier than 950 DD_{5C} after planting when the short-season cv. Russet Norkotah was grown in the CB and KB. This would suggest that early season applications made prior to 950 DD_{5C}, such as in-furrow at-planting or at crop emergence, may be necessary to provide adequate tuber protection.

David et al. (unpublished) also demonstrated that oxamyl does not eliminate *M. chitwoodi* in the soil even after multiple applications, but rather the population increases through the crop season. In contrast, 1,3-dichloropropene (Telone II[®]), which is widely used to control *M. chitwoodi*, effectively reduces nematode numbers throughout the crop season (Ingham et al., 2000). Given that *M. chitwoodi* may always remain in the soil when oxamyl is used, production practices in the CB may contribute to late-season tuber infection. While the threat of frost limits planting and harvest periods in both the SLV and KB, CB growers can harvest potatoes from July – October. Early in the harvest season, between July and August, CB growers often only dig the amount needed to fill daily orders, and as a result, it may take two to three weeks to harvest an entire 51 hectare

field. No information is available on how leaving potatoes in the field affects the risk of tuber symptom development.

Previous work by Pinkerton et al. (1991) and David et al. (unpublished) demonstrated that eggs must be laid before internal symptoms are observed. If late-season tuber infection occurs, symptoms may not be visible until 500 – 600 DD_{5C} later. Since oxamyl does not eliminate *M. chitwoodi* in soil (David et al., unpublished), tubers may be at risk to infection after applications have ceased and symptoms may occur after harvest. Table-stock and certified-seed potatoes are stored in high humidity (> 95% RH) facilities between 3 and 5°C until shipped to buyers over the next 12 months. When infected tubers are placed into storage and reach a holding temperature below 5°C, further symptom development of *M. chitwoodi* may not occur. However, no information on post-harvest symptom development in relation to oxamyl use is available.

The objectives of this study were: 1) compare multiple (standard) and single application programs that begin at 950 DD_{5C} with like programs which include early season applications prior to 950 DD_{5C}; 2) determine if delaying harvest increases the percentage of tubers with symptoms of *M. chitwoodi* in the CB; and 3) determine if the percentage of tubers with symptoms of *M. chitwoodi* increases during long-term cold storage below 5°C.

MATERIALS AND METHODS

Study areas: The trials were located at the Hermiston Agricultural Research and Extension Center near Hermiston, Oregon, in the CB; the Klamath Experiment Station near Klamath Falls, Oregon, in the KB; and grower fields in Alamosa and Costilla counties in the SLV of Colorado. The soil types were Atkins fine loamy-sand (pH 7.6), Poe fine loamy-sand (pH 6.5 – 7.0), and Gunbarrel loamy-sand (pH 8.0 – 8.5), in the CB, KB, and SLV, respectively. All sites had a history of damage from *M. chitwoodi* on potato and the previous crop was a small grain. Prior to potato planting, sites were ripped, tandem disced, and roller-harrowed to a depth of 45 cm, 20 cm, and 10 cm, respectively.

Certified Russet Norkotah potato seed was planted with a two-row assist feed planter on 26 April 2001, 17 April 2002, and 14 April 2003 in the CB, and on 21 May 2002 and 22 May 2003 in the KB. Certified Russet Nugget and Russet Norkotah potato seed was planted in the SLV by grower cooperators on 1 May 2002 and 7 May 2003. Cultural practices, including: irrigation, weed, insect, and disease control were consistent with those of each growing region. Individual plots in the CB were harvested with a two-row level bed digger on 23 August and 12 September 2001, 21 August and 5 September 2002, and 29 August and 16 September 2003. Plots in the KB were harvested with a single-row harvester on 17 September 2002 and 22 September 2003, while SLV plots were harvested with a single-row level bed digger on 1 October 2002 and 13 September 2003.

Plot design and oxamyl application: Four-row potato plots (3.5 m x 9.1 m), (3.3 m x 6.1 m), and (3.5 m x 6.1m) were established as experimental units in the CB, KB, and SLV, respectively. Bi-weekly applications beginning at 950 DD_{5C} (standard

program) and a program beginning with an application in-furrow at-planting and followed by the standard program (full-season program) were tested in the CB (2001 and 2002), KB (2002); and SLV (2002). The target physiological time for the initial application in the standard program was 950 DD_{5C} after planting (Pinkerton et al., 1991) but actual timings varied slightly (Table 5). During 2003, a single application of oxamyl (single program) at the hatch of the second generation and an in-furrow application followed by the single program were compared to an untreated control in the KB and SLV. Oxamyl programs were assigned in a randomized complete block design with five replications. The 2001 CB experiment was spatially blocked. All experiments in 2002 and 2003 used pre-plant nematode densities as the blocking factor.

Oxamyl was applied at a rate of 1.1 kg/ha and injection solutions were always buffered to a pH less than 7 (Table 5). The in-furrow, at-planting applications were made as a 15 cm wide band directly in the bottom of the furrow behind the planter shoe in 140 liters/ha spray solution. Applications at crop emergence applications were made as a 15 cm wide band directly over the potato rosette in 234 liters/ha spray solution. All other applications were chemigated in 1.3 cm water. Chemigation was simulated in the CB using a side mount boom with flood jet nozzles moving at 0.07 m/second, while applications in the KB and SLV were made through solid-set and center-pivot irrigation systems, respectively. Non-treated plots in the KB and SLV were covered during the application with a poly tarp (118 g/m² – 900 Denier – 10x10 Weave Count) supported by a polyvinyl chloride (PVC) hoop frame.

Degree-day monitoring: Watchdog model 125 data loggers (Spectrum Technologies, Inc. Plainsfield, IL) were installed at each site to record soil temperature at

seed piece depth (22 cm) every 30 minutes. Using the averaging (rectangle) method (Arnold 1960), beginning at potato planting, *M. chitwoodi* developmental degree-days were calculated from the average daily soil temperature minus the minimum temperature of 5°C and cumulative degree-days were determined by summing daily values through the season. These measurements were used to time oxamyl applications during the course of the experiment. Additional data-loggers were used to record temperatures following harvest to determine post-harvest degree-days.

Tuber sampling: Twenty-five tubers between 110 and 340 grams were randomly collected from the middle of each four-row plot at harvest for immediate nematode symptom evaluation. Two additional 25-tuber samples were collected from the same plot for nematode symptom evaluation after long-term commercial storage between 3 and 5°C (2003 CB, 2003 KB, 2002 SLV, and 2003 SLV) and following storage between 21 and 24°C (2002 and 2003 CB, KB, and SLV). The samples to be stored between 3 and 5°C were placed in commercial facilities representing storage conditions for each area, while the samples to be stored between 21 and 24°C were shipped to Corvallis, Oregon and then placed in a dark room and allowed to accumulate a minimum of 740 post-harvest DD_{5C}. The sample stored at 21 and 24°C provided enough DD_{5C} that J2 present in tubers could develop into adult females and produce symptoms (Pinkerton et al., 1991) and represented the maximum potential for post-harvest symptom development.

Evaluation of tuber symptoms: The percentage of tubers with internal and external nematode damage was determined for each tuber. External symptoms were evaluated by visually inspecting the periderm for the presence of the characteristic bump

associated with *M. chitwoodi* infection, while internal symptoms occurring in the cortex and pith were identified using a magnifying lamp after the tubers had been hand peeled.

Statistical analysis: Analysis of the residuals indicated that an arcsine square root transformation of the data did not improve the homogeneity of variance so the untransformed tuber symptom data were analyzed. The effects of oxamyl, harvest date, and long-term storage on *M. chitwoodi* tuber symptoms were determined by analysis of variance (ANOVA) using PROC MIXED in SAS version 9.1.3. Following ANOVA, estimates of means and 95% confidence intervals were reported with *P* values.

RESULTS

Post-harvest degree-day accumulation: Following harvest, samples stored between 3 and 5°C accumulated 610, 510, 457, and 490 DD_{5C} in the 2003 CB, 2003 KB, 2002 SLV, and 2003 SLV trials, respectively, while the samples stored between 21 and 24°C accumulated 850, 740, 1,000, 893, and 1,140 post-harvest DD_{5C} in the 2002 CB, 2002 KB, 2003 KB, 2002 SLV, and 2003 SLV experiments, respectively.

*Effect of a standard and full-season oxamyl program on tuber symptoms caused by *Meloidogyne chitwoodi*:* There was no interaction between oxamyl program, harvest date, and year on tuber symptoms caused by *M. chitwoodi* in the CB so data were combined and the main effects of oxamyl program are reported (Table 6). Additionally, there was no interaction between oxamyl program and evaluation period on tuber symptoms in the KB and SLV, so the main effects of oxamyl program in these two regions are reported (Table 6). Nematode pressure was moderate to heavy as 64%, 89%, and 77% of the untreated tubers expressed internal symptoms in the CB, KB, and SLV, respectively. Oxamyl reduced ($P \leq 0.0005$) internal symptoms in all three growing regions, but only reduced external symptoms in the KB ($P = 0.0008$) and SLV ($P = 0.01$). Compared to the standard program, the full-season program reduced internal symptoms in the CB ($P = 0.06$) and KB ($P = 0.0008$) but not in the SLV.

Effect of reduced oxamyl programs in the KB and SLV: There was no interaction between oxamyl program and evaluation period on tuber symptoms in the SLV or on external symptoms in the KB during 2003 so all evaluations were combined (Table 7). There was an interaction between oxamyl program and

evaluation period on internal symptoms in the KB, so the effect of oxamyl program is reported for each evaluation period. A single application at 900 DD_{5C} lowered internal symptoms in the KB when the samples were evaluated at harvest ($P \leq 0.0001$) and after storage at 3 – 5°C ($P \leq 0.0001$; Table 7), but not when stored at 21 – 24°C. The same program reduced internal symptoms in the SLV ($P = 0.002$) and external symptoms in the KB ($P = 0.009$) across all evaluation periods. Adding an in-furrow application to a single program in the SLV further reduced ($P = 0.10$) internal symptoms compared to the single program alone across all evaluation periods. This program also reduced ($P = 0.01$) internal symptoms in the KB when the tubers were evaluated after storage at 3 – 5°C.

Effect of harvest date on tuber symptoms in the CB: The incidence of both internal and external symptoms increased ($P \leq 0.05$) between the August and September harvest dates (Figure 4). The percentage of tubers with internal and external symptoms increased from 37 to 60% and from 9 to 23%, respectively.

Effect of storage on tuber symptoms: Compared to the harvest evaluation, internal symptoms did not increase during storage between 3 and 5°C in the CB, KB, or SLV whether or not oxamyl was applied (Table 5). However, internal symptoms increased when tubers were stored between 21 and 24°C in the CB ($P \leq 0.0001$) and KB ($P \leq 0.0001$), but not in the SLV. When tubers were stored at 21 - 24°C, the increase in internal symptoms was not dependent upon oxamyl program in the CB, but it was in the KB, where the increase was only observed in plots treated with oxamyl (Table 5).

External symptoms did not increase when stored between 3 and 5°C or between 21 and 24°C from any area (Table 5).

DISCUSSION

This study provides the first information on the risk of tuber infection by *M. chitwoodi* when short-season table-stock potato varieties are grown in three regions with different season lengths and soil heat accumulation. Tuber infection was a certainty in all three growing areas when the nematode was not controlled. In addition, given the diversity of the potato production areas used in this study, *M. chitwoodi* can be expected to cause tuber damage anywhere potatoes are grown in the western United States.

The work described here also provides the first information that chemigated oxamyl programs reduce, but do not eliminate internal or external tuber symptoms caused by *M. chitwoodi* on short-season potato cultivars. Beginning oxamyl applications as originally recommended by E.I. du Pont de Nemours and Company (standard program) reduced internal symptoms in all three production areas, supporting the hypothesis that applications made at the hatch of the second generation would reduce tuber symptoms (Pinkerton et al., 1991).

The standard program appeared to reduce internal symptoms in the SLV to a greater extent in the SLV than in the CB or KB. One possible explanation is that second generation J2 were present in the soil prior to the initial oxamyl application in the CB and KB (David et al., unpublished). This may have resulted in tuber infection before the initial application. Another explanation may be that the center-pivot irrigation systems in the SLV delivered oxamyl to the soil more uniformly than the solid-set hand lines used in the KB or the chemigation simulator used in the CB. Center-pivots can deliver oxamyl with water in a relatively fast, but highly uniform manner using moderate droplet sizes with low pressure nozzles, while solid-set hand lines operate at high pressure over a long

time period, increasing the probability that wind could potentially reduce uniformity. According to the Center for Irrigation Technology at California State University in Fresno, California, solid-set and center-pivot irrigation systems generally have water application efficiencies between 70 -80% and 75 – 90%, respectively. The chemigation simulator used in the CB applied water in a uniform manner but the application rate was much faster than a center-pivot or solid-set system. This may have caused excessive runoff, resulting in lower oxamyl concentrations around the roots and tubers. When using an irrigation system to deliver oxamyl, it is important that it is performing to appropriate standards.

We hypothesized that adding an in-furrow application at planting and another at crop emergence to a standard program in the KB and SLV would not reduce tuber infection since these additional applications did not further reduce the fecundity of the first and second generations (David et al., unpublished). This hypothesis was supported by results in the SLV but not in the KB. Tuber infection was further reduced when early season applications were added in the CB and KB, suggesting that tuber infection had already occurred when the initial standard program application was made in the CB (960 DD_{5C}) and the KB (940 DD_{5C}). Early season applications did not reduce infection in the SLV, indicating tuber infection occurred after 890 DD_{5C}.

Given the fact that average yields of Russet Norkotah in the CB, KB, and SLV during the 2006 western regional potato variety trial were 6.4, 4.3, and 4.0 metric tons/hectare, respectively, the gross economic return is greater in the CB. KB and SLV growers may be reluctant to make late-season oxamyl applications because of higher input costs. Eliminating the last oxamyl application in the KB and SLV (David et al.,

unpublished) did not result in increased tuber symptoms, suggesting that fewer applications may provide adequate control in the KB and SLV. While the current study indicates that two additional oxamyl applications after 950 DD_{5C} reduce tuber symptoms caused by *M. chitwoodi* in the KB and SLV, the number of applications required after 950 DD_{5C} may be dependent upon degree-day accumulation. Fewer applications may be adequate during years of normal degree-day accumulation, but may result in unacceptable damage during unusually warm years. Regional degree-day information would be required to properly predict the number of applications necessary. Further work needs to be done to confirm this hypothesis.

This study demonstrated that a single application of oxamyl at 900 DD_{5C} after planting may reduce *M. chitwoodi* symptoms in the KB and SLV. Since adding an in-furrow application increased the efficacy of the single program at both locations, tuber infection may have occurred prior to 900 DD_{5C}.

Growers in the CB who store Russet Norkotah potatoes in the ground increase the risk of tuber infection and greater symptom development due to additional degree-day accumulation. The percentage of tubers with internal and external symptoms was 1.6 and 2.5 times higher, respectively, when harvest was delayed by three weeks, regardless of oxamyl use. Oxamyl does not eliminate *M. chitwoodi* from the soil (David et al., unpublished) and leaving the crop in the ground increases the risk that the concentration of oxamyl will fall below 1 ppm, allowing J2 to infect tubers (Bunt 1987). As a result, increased rejections due to *M. chitwoodi* symptoms may rise in the CB if this practice continues.

The majority of the table-stock potato crop grown in the western United States is placed in long-term storage facilities below 5°C until marketed. Any defect that increases during storage is a serious concern because crop quality would be less than anticipated at harvest. Finley (1981) suggested that internal symptoms of *M. chitwoodi* are a result of the oxidation of phenolic compounds in the gelatinous matrix surrounding egg masses (Maggenti et al., 1960) and that external tuber symptoms are a result of the hypertrophy of cortical cells. The common belief is that infected tubers, which are non-symptomatic at harvest, develop internal and external symptoms from *M. chitwoodi* in storage (Ingham et al., 2000; Powers et al., 2005). This study found that the percentage of tubers with internal symptoms increases following storage at 21 - 24°C when at least 740 post-harvest DD_{5C}, which was enough time for *M. chitwoodi* to mature and lay eggs (Pinkerton et al., 1991; David et al., unpublished). However, the percentage of tubers with internal symptoms did not increase when potatoes were stored at 3 – 5°C, suggesting the risk of increased internal symptoms in stored table-stock potatoes is low. Symptoms may develop under warmer storage conditions such as those for process potatoes (7 - 10°C), which are above the lower developmental temperature of *M. chitwoodi*.

Unlike internal symptoms, external symptoms do not develop following harvest, regardless of storage temperature. This suggests that cell hypertrophy does not occur following harvest, but there is no information available on post-harvest hypertrophy in potato tubers. Furthermore, internal symptoms were more prevalent than external symptoms, indicating that external evaluations may underestimate the percentage of tubers infected with *M. chitwoodi* and therefore may not be the most accurate method to measure the incidence of infection. Growers who purchase seed grown in soil infested

with *M. chitwoodi* should not assume that it is free of nematodes if external symptoms are not observed.

The work here demonstrates that oxamyl reduces tuber symptoms caused by *M. chitwoodi* on short-season potato cultivars in the western United States. The most efficacious oxamyl program includes applications in-furrow at-planting and at crop emergence, followed by three, three, and four bi-weekly chemigation applications in the SLV, KB, and CB, respectively, beginning at the hatch of the second generation. David et al. (unpublished) reported that the second generation can occur as early as 920, 740, and 980 DD_{5C} after planting in the CB, KB, and SLV, respectively.

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Table 5. Description of oxamyl programs tested.

Oxamyl Program ^a	Description ^b
2001 CB Standard	(1,000) ^c followed by 14 days (1,180), 28 days (1,380), and 42 days (1,630)
2002 CB Standard	(960) followed by 14 days (1,200), 28 days (1,450), and 42 days (1,680)
2002 KB Standard	(940) followed by 14 days (1,100) and 28 days (1,330)
2002 SLV Standard	(890) followed by 14 days (1,110) and 28 days (1,280)
2001 CB Full Season	In-furrow at-planting (0), crop emergence (340) and then (1,000) followed by 14 days (1,180), 28 days (1,380), and 42 days (1,630)
2002 CB Full Season	In-furrow at-planting (0), crop emergence (470) and then (960) followed by 14 days (1,200), 28 days (1,450), and 42 days (1,680)
2002 KB Full Season	In-furrow at-planting (0), crop emergence (430) and then (940) followed by 14 days (1,100) and 28 days (1,330)
2002 SLV Full Season	In-furrow at-planting (0), crop emergence (380) and then (890) followed by 14 days (1,100) and 28 days (1,280)
2003 KB Single	(870)
2003 SLV Single	(890)
2003 KB In-furrow + Single	In-furrow at-planting (0) and then (870)
2003 SLV In-furrow + Single	In-furrow at-planting (0) and then (890)

^aKB = Klamath Basin; CB = Columbia Basin; SLV = San Luis Valley

^bIn-furrow at-planting application was a 15 cm wide in the bottom of the furrow in 140 liters/ha spray solution.

^bCrop emergence application was made at 100% plant emergence in a 15 cm wide band directly over the potato rosette in 234 liters/ha spray solution.

^bAll applications made after crop emergence were chemigated in 1.3 cm water.

^cNumbers in parenthesis are soil degree-days (5°C) after planting.

Table 6. The effects of standard and full-season oxamyl programs on the percentage of tubers with internal or external symptoms caused by *Meloidogyne chitwoodi* on Russet Norkotah in the Columbia Basin and Klamath Basin and on Russet Nugget in the San Luis Valley.

Oxamyl Program ^c	Columbia Basin ^a		Klamath Basin ^b		San Luis Valley ^b	
	Internal ^d	External ^e	Internal ^d	External ^e	Internal ^d	External ^e
Control	64 (51 - 76) ^f	24 (11 - 37)	89 (71 - 100)	55 (38 - 73)	77 (69 - 85)	37 (20 - 53)
Standard	48 [§] (35 - 60)	13 (1 - 26)	40 [§] (21 - 58)	15 [§] (0 - 32)	11 [§] (3 - 18)	< 1 [§] (0 - 16)
Full-Season	34 [†] (21 - 46)	11 (0 - 24)	4 [‡] (0 - 22)	3 (0 - 20)	5 (0 - 14)	< 1 (0 - 17)
	$P = 0.0005$	$P = 0.22$	$P = 0.0002$	$P = 0.0008$	$P \leq 0.0001$	$P = 0.01$

^aColumbia Basin data presented are both harvest dates combined from the 2001 and 2002 data because there were no two or three-way interactions.

^bKlamath Basin and San Luis Valley data are presented from 2002 and are the combinations of all evaluations because there was no interaction.

^cSee text for full treatment description.

^dPercent tubers with any internal symptoms.

^ePercent tubers with any external symptoms.

^fNumbers in parenthesis are 95% confidence intervals.

[§]Standard program is significantly ($P \leq 0.05$) different than the untreated control.

[†]Full-season program is significantly ($P = 0.06$) different than the standard program.

[‡]Full-season program is significantly ($P = 0.0008$) different than the standard program.

Table 7. The effects of reduced oxamyl programs on the percentage of tubers with internal or external symptoms caused by *Meloidogyne chitwoodi* on Russet Norkotah in the Klamath Basin and San Luis Valley.

Oxamyl Program ^c	Klamath Basin ^a		San Luis Valley ^b	
	Internal ^d	External ^e	Internal ^d	External ^e
Control	91 (79 - 100) ^f	59 (43 - 74)	37 (27 - 47)	1 (0 - 3)
Single	55 [§] (43 - 68)	25 [§] (9 - 40)	14 [§] (3 - 24)	2 (0 - 4)
In-furrow + Single	31 [†] (19 - 44)	28 (12 - 44)	3 [‡] (0 - 13)	1 (0 - 3)
	$P \leq 0.0001$	$P = 0.009$	$P = 0.002$	$P = 0.94$

^aInternal data are from the sample stored at 3 - 5°C. Other evaluation periods are reported in the text. Evaluation periods were combined for the external data.

^bInternal and external data are presented from the combined evaluations.

^cSee text for full treatment description.

^dPercent tubers with any internal symptoms.

^ePercent tubers with any external symptoms.

^fNumbers in parenthesis are 95% confidence intervals.

[§]Single program is lower ($P \leq 0.05$) than the untreated control

[†]In-furrow + single program is lower ($P = 0.01$) than the single program.

[‡]In-furrow + single program is lower ($P = 0.10$) than the single program.

Table 8. The effects of storage between 3 and 5°C or between 21 and 24°C on internal and external tuber symptoms caused by *Meloidogyne chitwoodi* in the Columbia Basin, Klamath Basin, and San Luis Valley.

Evaluation ^a	Columbia Basin	Klamath Basin ^b	San Luis Valley
<i>Internal symptoms^c</i>			
Harvest	66 (60 - 73) ^d	57 (45 - 70)	29 (22 - 36)
Storage (3 - 5°C)	60 (53 - 66)	55 (43 - 68)	29 (22 - 36)
Storage (21- 24°C)	79 (73 - 86)	91 (79 - 100)	35 (28 - 42)
	$P \leq 0.0001$	$P \leq 0.0001$	$P = 0.39$
<i>External symptoms^e</i>			
Harvest	57 (46- 68)	36 (28 - 44)	10 (< 1 - 20)
Storage (3 - 5°C)	36 (24 - 47)	--	14 (4 - 23)
Storage (21- 24°C)	53 (42 - 64)	30 (22 - 37)	14 (4 - 23)
	$P = 0.002$	$P = 0.007$	$P = 0.64$

^aHarvest samples were evaluated immediately after harvest; Storage samples were evaluated following storage (See text for DD_{5c} accumulation in each area)

^bKB internal symptom data are from the 2003 single oxamyl treatment because of an interaction. Other KB treatments are discussed in the text. KB external data are combined because there was no interaction.

^cPercent tubers with any internal symptoms.

^d95% confidence intervals.

^ePercent tubers with any external symptoms.

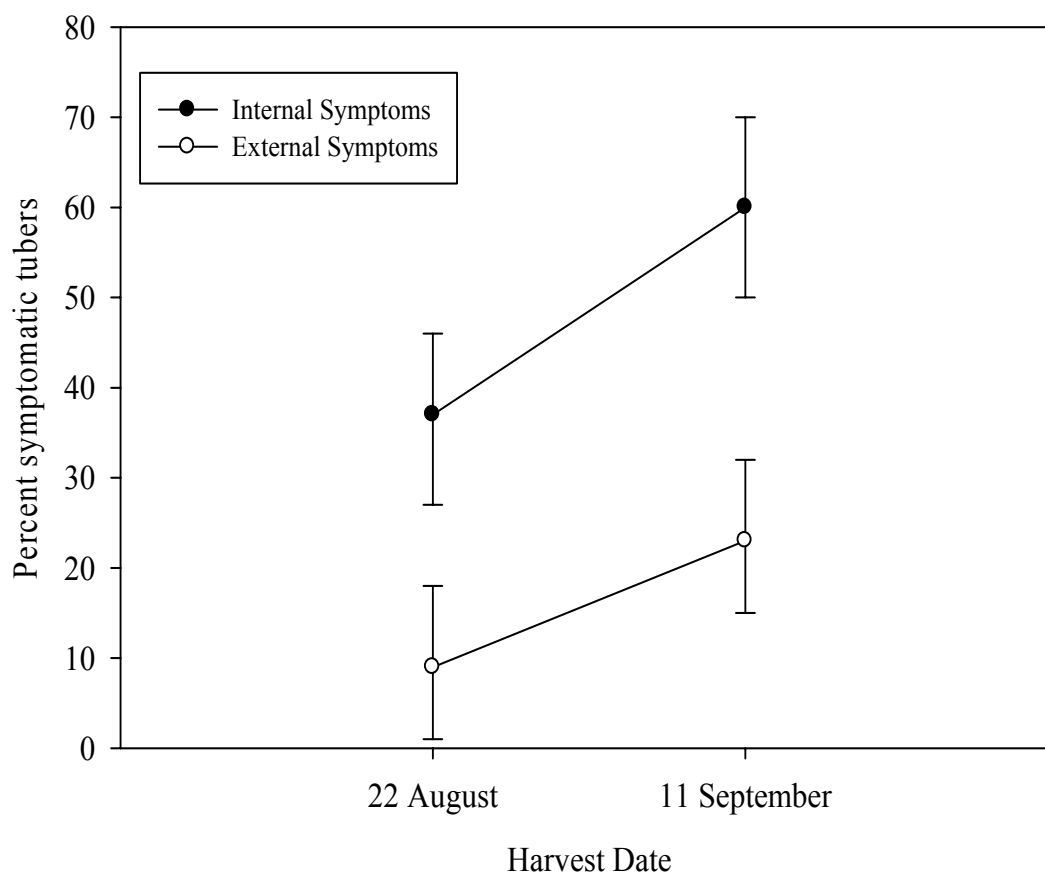


Figure 4. The effect of average harvest date on tuber symptoms caused by *Meloidogyne chitwoodi* on potato cv. Russet Norkotah in the Columbia Basin during 2001 and 2002. Bars represent 95% confidence intervals.

CONCLUSION

These studies provide the first soil population dynamics information for *Meloidogyne chitwoodi* on short-season potato cultivars in the Columbia Basin, Klamath Basin, and San Luis Valley. They reveal that population dynamics of *M. chitwoodi* can be reliably predicted using soil physiological time (degree-day accumulation) after planting. However, populations of *M. chitwoodi* should be studied and modeled for individual growing regions since this research demonstrated that second-stage juveniles (J2) of *M. chitwoodi* emerge from eggs earlier in the Klamath Basin than in the Columbia Basin or the San Luis Valley. However, within the Columbia Basin and San Luis Valley, the physiological time required for *M. chitwoodi* to complete generations on Russet Norkotah and Russet Nugget was similar to that described earlier for Russet Burbank. This suggests that the development of *M. chitwoodi* may not be dependent on potato cultivar. While other cultivars need to be studied, it indicates that management strategies based on nematode population development may be generally applicable within a region.

Using the population dynamics information, specific generations of *M. chitwoodi* can be reliably predicted and management strategies implemented. Based on these results, non-fumigant nematicides targeting the hatch of the second generation should be applied prior to 740, 920, and 980 DD_{5C} in the Klamath Basin, Columbia Basin, and San Luis Valley, respectively.

The non-fumigant nematicide, oxamyl, has the potential to reduce J2 soil densities of *M. chitwoodi* from the hatch of the second generation until harvest, but it does not alter when second-stage juveniles are released into the soil. Furthermore, oxamyl does not reduce the soil densities of *M. chitwoodi* at harvest compared to those at planting. This

may be due to the high reproductive capacity of *M. chitwoodi*, the short half-life of oxamyl or the low rates applied. A greater impact on population densities may be observed if oxamyl was applied at more frequent intervals, higher rates or both.

Tuber symptoms of *M. chitwoodi* were reduced in all three growing regions with the use of oxamyl and adding early applications before the standard program frequently improved control. Therefore, early applications, particularly in-furrow at planting, should be added to the recommended use. The level of reduction in tuber symptoms by using the oxamyl programs in these studies was superior to that previously described. However, oxamyl had no affect on symptom development when the tubers were stored in the ground to accommodate a delayed harvest or when stored long-term after harvest at 3-5°C or short-term at 21-24°C. The risk of increased tuber symptom development is high when the short-season potatoes are stored in the ground or at 21 – 24°C. Therefore, oxamyl should not be used as the sole management program if tubers are to be stored warm at the end of the season. However, tuber symptoms did not increase at 3 – 5°C and growers should be confident that tubers that are symptom-free at harvest would not express symptoms when removed from storage at these temperatures.

Since symptoms increased when tubers were stored at 21-24°C but not at 3-5°C it indicated that tubers were infected but symptom development was suppressed at 3-5°C. This may cause concern for markets with no tolerance for *M. chitwoodi*, such as seed or export, since it suggests that infected but asymptomatic tubers could be marketed inadvertently. Storing a representative sample of tubers at 21-24°C until 740 DD_{5C} or more have accumulated would increase the probability of detecting the presence of *M. chitwoodi* in these tubers.

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