

Problems Associated with Crop Rotation for Management of *Pratylenchus penetrans* on Easter Lily¹

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Abstract: In Humboldt and Del Norte counties of California and Curry County, Oregon, Easter lilies (*Lilium longiflorum*) are grown commercially in a 3- to 6-year rotation with pasture for cattle and sheep. Bulbs are sold to greenhouse operations to produce flowering plants. The lesion nematode, *Pratylenchus penetrans*, is a serious detriment to Easter lily production. Both soil and planting stock are often infested; typically, a dual nematicide application is used consisting of a preplant soil fumigation followed by an at-planting application of an organophosphate or carbamate. Nematicide usage has resulted in ground-water contamination. Several factors that could lead to an improved crop rotation program were examined in five field trials in Oregon. Examining the relative nematode host status of crops for feeding cattle and sheep indicated differences in host suitability among clovers and fescues that could prove useful in development of pasture mixes. Populations of *P. penetrans* under continuous fallow and pasture were monitored for 4 years following harvest of Easter lilies. Populations fluctuated in both situations but generally increased on pasture plants and decreased under fallow. Nematodes were still detectable at the end of 4 years of weed-free fallow. Populations of *P. penetrans* on Easter lilies were followed over two successive crops. Numbers in soil peaked in July and then decreased while numbers within roots continued to increase until harvest in October.

Key words: crop rotation, Easter lily, lesion nematode, *Lilium longiflorum*, nematode, *Pratylenchus penetrans*.

Easter lily bulbs (*Lilium longiflorum* Thunb.) have been the most important crop in Humboldt and Del Norte counties of California and Curry County, Oregon, since the early 1940s. This is the only area of the United States in which Easter lily bulbs are grown commercially. Approximately 250 ha of lilies are grown each year in a 3- to 6-year rotation with pasture for cattle and sheep, so that approximately 2,400 ha are part of the cropping system. The industry is the region's largest employer, with a yearly farm gate value of approximately \$5 million. Bulbs are sold to greenhouse operations to produce flowering plants (Hawkins, 1991).

Bulbs are grown for 2 to 4 years before they are large enough for sale. Quality is judged visually, with white bulbs with plentiful roots bringing the highest price. Typically, land is prepared in May, fumigated in

July, planted from August through October, and bulbs are harvested the following August through October. In the first year, bulblets (small, thumbnail-size bulbs that arise from stems of the previous crop) are planted at the rate of 256,000-385,000/ha. After one growing season, yearlings are replanted at the rate of 160,000/ha. At the end of the second season, yearlings that have reached 20 cm in circumference are sold. If they are smaller, they are replanted for a third or even a fourth season (Hawkins, 1991; L. Riddle, personal communication).

The lesion nematode, *Pratylenchus penetrans* (Cobb, 1917) Sher & Allen, 1953 is a serious detriment to Easter lily production (Koepsell and Pscheidt, 1991). This nematode has a broad host range of at least 400 plants (Jensen, 1953; Mai et al., 1977). Because of its wide host range, nonchemical control measures such as crop rotation and use of resistant cultivars generally have not been feasible methods of control. The nematode is found statewide in California and many other regions (Siddiqui et al., 1973) and is economically important on ornamentals, apple, cherry, strawberry, and other crops (McKenry and Roberts, 1985). *Pratylenchus penetrans* was found in Easter lily fields as early as 1946 (Butterfield, 1947).

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Damage symptoms are general devitalization of the plant: retarded top growth, chlorotic foliage, and restricted root growth (Overman, 1961). Shoots may not be able to emerge from bulbs. In less serious cases, the symptoms are not evident until late in the growing season.

A dual nematicide application, usually consisting of a preplant fumigant followed by an at-planting application of an organophosphate or carbamate, is used for Easter lilies because both the soil and the planting stock are infested by nematodes. The finding in 1982 that groundwater had been polluted by 1,2-dichloropropane and aldicarb has had significant adverse impacts on both the water consumers of these counties and on the bulb industry (Hawkins, 1991; Warner et al., 1989). The industry began using fenamiphos (Nemacur) instead of aldicarb and 1,3-dichloropropene (1,3-D, Telone II) instead of mixture of 1,2-D and 1,3-D (DD mixture) to reduce lesion nematode populations. Studies conducted by the California Department of Food and Agriculture (CDFA) in 1986 in Del Norte County indicated that fenamiphos had moved below the rooting depth of the crop and its use on lilies was withdrawn by the manufacturer (Hawkins, 1991). The use of 1,3-D in California was suspended from April 1990 until early 1996, and growers turned to metam-sodium or methyl bromide plus an at-planting application of an organophosphate phorate (Rampart).

The climate in Curry, Del Norte, and Humboldt counties is characterized by cool summers with coastal fog, mild winters, and an average annual rainfall of 190 cm (primarily November through March). Cool soil temperatures, high water tables, and acidic soils contribute to the potential for groundwater contamination by pesticides in the area (Warner, 1985).

The objectives of this study were to i) determine the host status of pasture crops for *P. penetrans*, ii) examine population cycling of *P. penetrans* on Easter lilies, and iii) monitor population decline of *P. penetrans* under weed-free fallow.

MATERIALS AND METHODS

Field trials were conducted at the Easter Lily Research Foundation Station in Brookings, Oregon, in a site infested with *P. penetrans*. Prior to the trials, the area had been alternately cropped to a mixture of Potomoc orchard grass, Fawn tall fescue, Tetraploid ryegrass, New Zealand clover, Mt. Barker subterranean clover, and Kenland red clover (3 consecutive years) and Easter lily (1 year) since the 1970s. The soil type was a Knappa heavy clay loam with a pH of 5.3, a stable organic matter content of 7%, and a C.E.C. of 23 (Riddle, 1993). The experimental areas were managed according to standard commercial practices. For Easter lilies, land preparation in April and May consisted of mowing, disking, plowing, and redisking following the application of 5,000 kg/ha of agricultural lime and 1,000 kg/ha of gypsum. In early July, the soil was deep-ripped and subsoiled. At planting, 1,000 kg/ha of 6-20-20 fertilizer was applied. An additional 240 kg/ha of calcium nitrate was top-dressed in February and April. Herbicides used were glyphosate (Monsanto, St. Louis, MO) prior to bulb emergence, napropamide (ICI Americas, Richmond, CA) plus diuron (Griffin, Valdosta, GA) at emergence, and diuron following bulb emergence. From January through May, a foliar fungicide (copper hydroxide, Griffin, Valdosta, GA) was applied every 10 days throughout the growing season. Additionally, iprodione (Rhone-Poulenc, Research Triangle Park, NC) and chlorothalonil (ISK Biotech, Mentor, OH) were applied every 30 days. From June through October, copper hydroxide was applied every 30 days.

A field trial with four replicates of 23 crops (Table 1) used for feeding cattle and sheep was planted in a randomized complete-block design in October 1991 in an area from which Easter lilies had been harvested in September. Each replicate was 3 m × 3 m. A plug containing soil and roots was taken with a shovel from each replicate in April and October 1992. Nematodes were extracted from 50 ml of roots and soil placed in an intermittent misting chamber

TABLE 1. *Pratylenchus penetrans* per 50 cm³ soil and roots of selected pasture plants.

Common name	Scientific name	April	October
Oat	<i>Avena sativa</i>	8.8 a ^a	12 abcd
Potomoc orchardgrass	<i>Dactylis glomerata</i>	2.3 a	88 abcd
Fawn tall fescue	<i>Festuca arundinacea</i>	0.3 a	2 a
Annual ryegrass	<i>Lolium multiflorum</i>	1.4 a	111 d
Tetraploid ryegrass	<i>Lolium perenne</i>	0.1 a	74 abc
Ariki ryegrass	<i>Lolium</i> sp.	0.3 a	38 bcd
Birdsfoot trefoil	<i>Lotus corniculatus</i>	—	—
Loh's alfalfa	<i>Medicago sativa</i>	11.5 ab	602 cd
Timothy	<i>Phleum pratense</i>	0.3 a	—
Berseem clover	<i>Trifolium alexandrinum</i>	5.0 a	854 bcd
Salina clover	<i>Trifolium fragiferum</i>	7.0 a	133 d
Crimson clover	<i>Trifolium incarnatum</i>	5.3 a	—
Kenland red clover	<i>Trifolium pratense</i>	3.2 a	1,754 d
New Zealand clover	<i>Trifolium repens</i>	1.0 a	463 d
Ladino clover	<i>Trifolium repens</i>	0.2 a	357 d
Fancy White Dutch subterranean clover	<i>Trifolium repens</i>	4.9 a	255 d
Mt. Barker subterranean clover	<i>Trifolium subterraneum</i>	1.4 a	—
Bell bean	<i>Vicia faba</i>	24.5 bc	—
Common vetch	<i>Vicia sativa</i>	27.5 c	—
Cahaba white vetch	<i>Vicia sativa</i>	6.6 a	—
Irwin's PNW6-9-1 mix ^b		0.4 a	7 ab
Irwin's PNW4-9-1 mix ^c		0.2 a	167 bcd
Irwin's PNWIA mix ^d		1.0 a	21 abcd

Data are means of four replicates. Data are not reported for crops with poor emergence or survival.

^a Means followed by the same letter within columns are not different according to an LSD test ($P = 0.05$). Counts were transformed by $\log_{10}(x + 1)$ prior to analysis. Numbers in table are untransformed means.

^b Composition: 39% Potomoc orchardgrass, 34% Ariki perennial ryegrass, 15% New Zealand white clover, 10% Tama annual tetraploid ryegrass.

^c Composition: 39% Ariki perennial ryegrass, 20% Potomoc orchardgrass, 20% Fawn tall fescue, 9% Tama annual tetraploid ryegrass, 10% Mt. Barker subterranean clover, 10% New Zealand white clover.

^d Composition not available.

for 72 hours (Ayoub, 1977). Extracted nematodes were identified and then counted with a stereoscopic microscopic at $\times 45$.

Following the harvest of Easter lilies in

September 1994, a second field trial was initiated consisting of additional cultivars of fescue (Table 2), which had been the poorest host in the first trial, one cultivar of clover representing the best hosts, and fallow

TABLE 2. *Pratylenchus penetrans* per 50 cm³ soil and roots in selected fescues vs. clover.

Common name	Scientific name	1995		
		July	September	July-96
Fawn tall fescue	<i>Festuca arundinacea</i>	0 a ^a	80 ab	50 ^b
Zorro fescue	<i>Festuca megalura</i>	220 b	60 a	175
Creeping red fescue	<i>Festuca rubra</i>	60 a	20 a	38
Bonsai dwarf fescue	<i>Festuca</i> sp.	0 a	20 a	25
Richmond fescue	<i>Festuca</i> sp.	20 a	60 a	25
Kenland red clover	<i>Trifolium pratense</i>	20 a	200 b	138
Triple crown blend ^c		20 a	120 ab	25
Fallow		40 a	40 a	38

Data are means of four replicates. All fescues were free of endophytic fungi except Bonsai dwarf fescue, which was 73% infected (Harmony Farm Supply, pers. comm)

^a Means followed by the same letter within columns are not different according to Duncan's New Multiple Range Test ($P = 0.05$).

^b When all fescues except Zorro were grouped, they were different from clover at $P = 0.05$. When clover and Zorro were grouped and compared to the other fescues, they were different at $P = 0.005$.

^c Composed of 34% Arid, 33% Bonanza, and 33% Wrangler fescue.

maintained by periodic applications of glyphosate. Each plot was 1 row (0.92 m) wide by 6 m long, arranged in four randomized complete blocks. A 20-cm buffer was established surrounding each plot and maintained periodically with a glyphosate spray. In July and September 1995 and July 1996, extraction and analysis were conducted as described above.

Following harvest of Easter lilies in September 1992, a field trial consisting of four replicates of fallow and pasture (clover-grass mixture) plots in a randomized complete-block design was initiated. Each plot was 6 m \times 6 m. Fallow plots were maintained by periodic spraying of glyphosate. Over a 4-year period, sampling of each plot, followed by extraction and analysis, was conducted periodically as previously described.

Following 3 years in pasture (clover/grass mixture), experiments to follow nematode populations on Easter lilies (four replicates) were initiated in October 1992 and 1993. In each experiment, plots were 1 row (0.92 m) wide by 6 m long. Nellie White bulblets for planting stock were hand-picked from stems of the previous year's crop and weighed ca. 7 g each. Each plot was planted with 160 bulblets placed in two lines with a spacing of 4 cm between bulblets. Bulblets were planted 10 cm deep in October and harvested in September 1993 and October 1994. Prior to planting, bulblets were dipped for 1 hour at 12 °C in a freshly made solution of 0.72 kg a.i. pentachloronitrobenzene (PCNB, Terrachlor 400, Uniroyal, Middlebury, CT), 0.95 kg a.i. tetramethylthiuram disulfide (42-S Thiram, Gustafson, Plano, TX), and 0.81 kg a.i. carboxin (Vita-vax-34, Gustafson, Plano, TX) in 379 liters of water and planted within 24 hours of treatment. Both trials were sprinkler-irrigated as needed. In 1993, the trial was sampled in April, May, June, July, and September. In 1994, the trial was sampled in March, April, July, and October. Samples were taken with a shovel and consisted of five bulbs with surrounding soil per plot. Nematodes were extracted from a 400-cm³ soil subsample with a modified semiautomatic elutriator and sucrose centrifugation technique (Byrd et al.,

1976). Nematodes were extracted from roots removed from the base of bulbs and on some dates from stem roots. Roots were weighed and placed in an intermittent mist chamber for 72 hours (Ayoub, 1977). Extracted nematodes were identified and counted at $\times 45$. Data from the 2 years were pooled for analysis.

Soil temperatures were monitored at a 15-cm depth with a continuously recording thermograph (T603 three-point thermograph, Weather Measure, Sacramento, CA) located adjacent to the plots. Rainfall was monitored with an Easy Read Jumbo Rain Gauge (Easy Read, Lincoln, NE).

Results were subjected to analysis of variance followed by Least Significant Difference (LSD) testing, Duncan's New Multiple Range Test, or orthogonal comparison of means (Abacus Concepts, Berkeley, CA), regression, and correlation analysis (SAS Institute Inc., Cary, NC). To stabilize variances in some trials, $\log_{10}(x + 1)$ transformations were used for nematode counts prior to analysis of variance.

RESULTS

In April 1992, seven months after initiation of the first crop rotation trial, bell bean and common vetch had higher ($P = 0.05$) populations of *P. penetrans* than the other crops (Table 1). Bell bean, crimson clover, timothy, Mt. Barker subterranean clover, birdsfoot trefoil, common vetch, and Cahaba white vetch did not survive to the second sampling in October 1992. On the surviving crops, nematode populations ranged from a low of 2/50 ml soil and roots on Fawn tall fescue to a high of 1,754 on Kenland red clover (Table 1). Crops that supported lower ($P = 0.05$) nematode reproduction than Kenland red clover were Fawn tall fescue, tetraploid rye, and Irwin's PNW6-9-1 pasture mix. Among the clovers, Salina and Fancy White Dutch supported low populations, although they were not statistically different from Kenland red clover.

In the second crop rotation trial, when first sampled in July 1995, Zorro fescue had a higher ($P = 0.05$) nematode population

than the other crops (Table 2). In September 1995, Kenland red clover had a higher ($P = 0.05$) number of nematodes than fallow and several of the fescues. In July 1996, differences were evident when the fescues were grouped and compared to Kenland red clover ($P = 0.05$) or to Kenland red clover and Zorro fescue grouped ($P = 0.005$).

In the trial comparing populations of *P. penetrans* in pasture and fallow, pasture populations fluctuated throughout the 4 years of the trial (Table 3). The variability in the data made it difficult to elucidate seasonal trends. Populations under fallow conditions fluctuated in a manner similar to that observed under pasture for the first 19 months of the trial and then fell to low but detectable levels. Nematodes extracted in Baermann funnels after 4 years of fallow were still mobile (Table 3).

Populations of *P. penetrans* in soil surrounding Easter lily, in stem roots, and in the bulb roots remained at low levels for 7 months after planting, until May (Table 4). Soil populations were highest ($P = 0.05$) in

TABLE 3. Population changes of *Pratylenchus penetrans* under conditions of fallow and pasture over a 4-year period.

Assay dates		<i>Pratylenchus penetrans</i> / 50 cm ³ soil and roots	
Year	Month	Fallow	Pasture
1992	October	863 c ^a	288 bc
1993	March	100 abc	100 abc
	April	13 ab	5 ab
	May	29 ab	30 abc
	June	75 ab	—
	July	138 abc	—
	September	300 abc	0 a
1994	November	80 ab	80 abc
	March	440 bc	160 abc
	April	300 abc	2,100 bc
	July	0 a	880 bc
1995	October	20 ab	100 abc
	April	0 a	260 abc
	September	0 a	100 abc
1996	April	40 ab	180 abc
	July	0 a	900 bc
	September	20 ab	840 c

Data are means of four replicates.

^a Means followed by the same letter within columns are not different according to Duncan's New Multiple Range Test ($P = 0.05$). Nematode counts were transformed by $\log_{10}(x + 1)$ prior to analysis.

TABLE 4. Populations of *Pratylenchus penetrans* on Easter lily during one growing season.

Month	Per liter of soil	Per gram of	
		Bulb	Stem
March	25 a ^a	2 a	— ^b
April	75 a	18 a	6 a
May	25 a	50 ab	15 a
June	389 ab	40 ab	57 a
July	663 b	237 c	306 b
September	263 ab	200 bc	—
October	100 a	466 d	—

Data are means of four replicates.

^a Means followed by the same letter within columns are not different according to Duncan's New Multiple Range Test ($P = 0.05$).

^b No data.

July and then decreased toward harvest in October. Populations in bulb roots increased more gradually and were highest ($P = 0.05$) at harvest.

During the growing season, soil temperatures and rainfall followed expected seasonal trends. Soil temperature decreased from planting in September, reached a low in December or January, increased in spring and summer, and began to fall again before harvest (Table 5). Nematode counts were related to 20-year averages for soil temperature and rainfall (Table 6).

DISCUSSION

Both field and laboratory trials have indicated that populations of *P. penetrans* exhibit geographical variability with respect to host range (France and Brodie, 1996; Olthof, 1968). MacDonald and Mal (1963) concluded from pot experiments that Sudan grass (*Sorghum vulgare* cv. Sudanense) was a poor host for *P. penetrans*. Bird (1968), in a similar study, found that both Sudan grass and perennial rye grass (*Lolium perenne*) were poor hosts for this nematode. In contrast, Marks et al. (1973) and Marks and Townshend (1973) found Sudan grass to be a good host for *P. penetrans* in both field and pot studies. In a pot test, Marks and Townshend (1973) found perennial rye grass and creeping red fescue (*Festuca rubra*) to be poorer hosts for *P. penetrans* in Ontario than Sudan grass, buckwheat (*Fagopyrum esculen-*

TABLE 5. Average monthly soil temperature (°C) and total monthly rainfall (cm) at field test site during Easter lily growing seasons.

Month	Temperature						Rainfall		
	1991-92	1992-93	1993-94	1994-95	1995-96	20-year average ^a	1991-92	1992-93	20-year average ^b
October	16.7	15.6	16.1	15.1	13.8	15.2	6.6	10.7	12.9
November	9.9	10.0	10.4	7.2	10.3	10.3	15.0	15.2	26.3
December	6.9	6.4	7.2	6.6	8.1	7.6	15.7	29.5	27.2
January	7.2	5.4	8.4	7.9	6.3	7.4	22.4	28.4	22.1
February	10.0	7.6	7.2	10.1	8.2	8.4	17.0	19.3	25.3
March	12.8	10.4	11.6	10.4	10.6	10.3	9.9	27.9	22.9
April	15.1	11.9	13.5	13.3	12.3	12.8	27.9	39.9	13.5
May	21.6	15.1	17.3	17.7	16.6	17.0	0.0	23.6	8.3
June	24.1	20.3	20.6	19.9	21.2	19.9	11.2	6.4	5.1
July	23.2	23.1	22.8	24.1	22.4	21.8	1.8	0.5	1.3
August	21.3	22.3	23.7	23.1	22.1	20.7	5.1	0.0	2.9
September	18.7	19.1	20.0	20.3	18.3	18.4	0.0	5.1	5.0

^a From 1974-1995.^b From 1971-1992.

tum), Italian rye grass (*Lolium multiflorum*), and rye (*Secale cereale*). Florini and Loria (1990), in pot experiments, found populations increased more on potato, oat, and corn than on rye, wheat, and sorgho-sudangrass. There were no differences in host suitability among four rye cultivars or between two oat cultivars. Thies et al. (1995) found that 29 northeastern and north-central U.S. forage grasses and legumes were hosts for *P. penetrans* in greenhouse, growth chamber, and field experiments but varied widely in their suitabilities. As in our trial, tall fescue was among the poorer hosts.

Townshend (1984) examined anhydrobiotic survival of *P. penetrans* under laboratory conditions in two soil types and under several soil moisture regimes, and observed typical anhydrobiotic coiling (Demeure et al., 1979; Freckman, 1978). Survival was

greatest in soil allowed to dry slowly on a greenhouse bench. When the experiments were concluded after 776 days, 1% of the nematodes were still alive in one of the slowly dried soils. Given the high rainfall and high soil organic matter in our experimental area, nematodes may not have been in an anhydrobiotic state but did exhibit survival abilities similar to those observed by Townshend (1984).

Several studies have emphasized the importance of looking at total populations of *P. penetrans* in a given habitat rather than just the soil or root component (DiEdwardo, 1961; Merrifield and Ingham, 1996). The method used in our crop rotation and fallow-pasture trials, in which nematodes were extracted from a plug containing soil and roots, is consistent with this thinking, as is the method utilized in the Easter lily trial in

TABLE 6. Relationships of *Pratylenchus penetrans* counts on Easter lily in field tests, soil temperature (°C), and rainfall (cm).

Y variable ^a	X variable	Regression equation	r ²	P	Pairwise correlation	P
Log ₁₀ (Soil + 1)	Temperature	y = 1.9 - 0.06x	0.896	0.0001	-0.9	0.0001
Bulb roots	Temperature	y = 1158 - 172x + 6.6x ²	0.918	0.007	0.9	0.01
Log ₁₀ (Soil + 1)	Rainfall	y = 0.4 + 0.08x - 0.002x ²	0.797	0.002	0.7	0.02
Log ₁₀ (Bulb roots + 1)	Rainfall	y = 3.0 - 0.1x + 0.002x ²	0.954	0.002	-0.8	0.04
Log ₁₀ (Stem roots + 1)	Rainfall	y = 2.4 - 0.04x	0.498	0.08	-0.7	0.08
Rainfall	Temperature	y = 41.4 - 1.7x	0.586	0.004	-0.7	0.01

^a Soil = nematodes per liter; bulb roots and stem roots = nematodes per gram; temperature and rainfall = 20-year averages.

which nematodes were extracted from roots and from soil immediately surrounding the roots.

Merrifield and Ingham (1996) postulated that population fluctuations of *P. penetrans* observed on peppermint in western Oregon represented generations. In their study, times between population peaks during the growing season were 56 days (May to mid-July), 40 days (mid-July to late August), and 62 days (late August to mid-November). In a field of red clover in Prince Edward Island roots were invaded in mid-June 3 weeks after seeding, and Kimpinski (1975) observed population peaks in roots and soil in early August, mid-September, and early November corresponding to generations. Mamiya (1971) found that the length of the life cycle of *P. penetrans* on *Cryptomeria* seedlings decreased as temperature rose from 15 to 30 °C but that development was inhibited at 33 °C. A similar trend was found for this nematode on alfalfa (Mai et al., 1977). Based on this information, the generation times in the Merrifield and Ingham (1996) and Kimpinski (1975) studies are plausible. In our study, population peaks occurred in soil in April and June and in bulb roots in May, July, and October, which suggests the occurrence of three generations during the growing season.

Jensen (1966) followed populations of *P. penetrans* at bimonthly intervals on Ace and Croft Easter lilies. The nematode population in roots remained low during the cool winter months and increased during the warmer part of the spring. This trend continued until the population peaked during early summer and then fell in early fall. A similar trend occurred in the soil, although there was a tendency for the soil population to lag behind that of the roots. In our trial on Nellie White Easter lilies, soil populations followed a trend similar to that of roots in Jensen's study, with a tendency for root populations to lag behind those in soil.

Population fluctuations have been observed in other studies on *P. penetrans*. Spring and fall peaks have been reported on peppermint (Pinkerton and Jensen, 1983). On strawberry in New Jersey, soil popula-

tions of *P. penetrans* peaked in June while root populations peaked in July and again in September (DiEdwardo, 1961). On raspberry in northwestern Oregon (Lolas et al., 1992) and in Fraser Valley, British Columbia (Vrain et al., 1997), *P. penetrans* populations peaked in spring and(or) fall and were inconsistent between years. Populations under a rye-tobacco rotation in Delhi, Ontario, peaked in fall (Olthof, 1971). *Pratylenchus penetrans* fluctuations also have been observed on clover (Kimpinski, 1975) and potato (Bird, 1977).

In raspberry, Vrain et al. (1997) found 80% or more of the population was in soil at most sample dates. Root biomass was greatest from November to March of each year and dropped to approximately one-third of winter levels during summer. *Pratylenchus penetrans* populations peaked from September to October in the first year and from June to July in the second year, indicating that seasonal population growth was controlled primarily by climatic conditions rather than the availability of roots. Low soil temperatures may have prevented the nematodes from fully exploiting the increased availability of roots during winter. Merrifield and Ingham (1996) found that the percentage of the total population in peppermint roots reached 70% to 90% in early April, decreased to 20% to 40% in August, and returned to higher percentages during winter. Root population peaks usually preceded soil population peaks during spring, whereas August soil, root, and rhizome population peaks were usually simultaneous. In our trial, *P. penetrans* appeared to be more easily detectable in soil during the summer and in roots during the fall. On clover in Prince Edward Island, Canada, egg-laying and hatching were evident when soil temperature at a depth of 7 cm was 3.4 °C (Kimpinski, 1975), indicating that *P. penetrans* can reproduce at relatively low soil temperatures. Thus, the nematode may be active most of the year in Easter lily fields.

Olthof (1971) found that soil moisture and temperature trends could not be consistently correlated with population densities of *P. penetrans* under a rye-tobacco rota-

tion. In our trials on Easter lilies, with the exception of nematodes within stem roots, nematode populations were strongly correlated with both temperature and rainfall and could be related to these variables with regression equations whose slopes were significantly different from zero. This information, combined with the potential to predict the timing of generations, could lead to improved timing of postplant applications and a reduction in nematicide usage.

Our research could affect nematode management decisions made by lily growers with respect to the choice of rotation crops, fallowing land for a prescribed period of time, and timing of various cultural procedures. Because of the length of time land would need to be left fallow to significantly reduce nematode populations, a cover crop that would minimize reproduction of *P. penetrans* and minimize erosion would be essential. Of the crops examined, salina clover, Fancy White Dutch subterranean clover, and all of the fescues except Zorro would be the most desirable candidates. Such a mixture would reduce erosion and permit use of the land for pasture while producing nematode levels similar to that of a fallow condition.

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