PEPPERMINT PERFORMANCE AND WILT INCIDENCE, AS INFLUENCED BY SELECTED CULTURAL PRACTICES AND INOCULUM DENSITY OF *VERTIC1LLIUM DAHLIAE* [YEAR 61[1]

Abbreviated Final Report: 19891996. *This is a review of 1995-96 data with reference to previous reports. Readers are encouraged to review reports from 1990 through 1995 for additional background and detail. One or more detailed manuscripts, summarizing all data, will be prepared for formal publication during 1997, and included in the 1997 annual report.*

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Abstract

From plots in the long-term field trial at the COARC Powell Butte field, pre-plant inoculum densities of microsclerotia of V. dahliae (MS/g soil) from 1994 and 1995 were related to 1996 wilt disease incidence in a peppermint crop that had been replanted in the fall of 1995.

Using a complete, split-plot experimental design with five replications, soil in these plots was (a) artificially infested with various uniform levels of V. dahliae in 1989 (main plots) following 1987 fumigation with methyl bromide, (b) planted with verticillium- and nematode-free Todds rootstock in 1990, (c) and managed with either spring tillage without flaming or with post-harvest flaming without tillage (split plots) for three production seasons through 1993 until hay and oil yield declined in plots with the highest initial infestation levels. Peppermint in all plots was killed in the spring of 1994, plots were left fallow but irrigated in 1994, and plots were cropped to a combination of irrigated wheat and peas in 1995 using normal soil management, prior to planting of verticillium- and nematode free rootstock in the fall of 1995.

Based on calculation verified by preliminary soil assay recovery, plots were initially infested near 0, 0.01, 0.1, 1.0 and 5.0 MS/g soil using lab-grown microsclerotia. Changes in inoculum density within plots between 1990 and 1994 were expected but could not be measured until a consistent soil assay was developed in 1994. Inoculum densities based on reliable assays of soil samples were determined for 1994 and 1995. Inoculum density did not change in plots between 1994 and 1995. This suggests that MS had been released into soil from herbaceous mint stems by the August 1994 sampling and that the soil population had stabilized Prior to re-planting of peppermint in 1995, mean inoculum densities from soil in plots that had been flamed but not tilled during the 1990-93 peppermint crop were assayed to be 0.37, 0.02, 0.00, 0.12, and 0.74 MS/g soil, respectively, and a mean of 0, 0, 0.6, 2.4 and 7.2 percent of the peppermint plants, respectively, developed strong wilt symptoms in 1996. In contrast, mean inoculum densities from soil in plots that had been tilled but not flamed during the 1990-1993 peppermint crop were assayed to be 0.79, 0.07, 0.26, 5.70, and 18.60 MS/g soil, respectively, and a mean of 1.4, 1.8, 8.8, 15.7, and 62.8 percent of the peppermint plants, respectively, developed strong wilt symptoms during 1996. Among main plot treatments, inoculum densities in 1995 and wilt incidences in 1996 were significantly different ($p<0.05$), irrespective of whether these plots had been flamed but not tilled or whether they had been tilled but not flamed. Sub plot treatments (flaming with tillage vs. tilling without flaming) were significantly different)<0.05) with respect to both 1995 inoculum density and 1996 wilt incidence. ,

For several reasons, inoculum levels calculated for and recovered for 1989-90 should not be compared closely with those determined for 1994 and 1995. First, the lab-produced inoculum used in 1989 might have different size and behavior per unit inoculum than the naturally-produced inoculum most likely represented in 1994 and 1995. Second, the soil assay used to verify infestation level in 1990 was different from that used for estimating soil populations in 1994 and 1995.

The higher recovery of MS in 1994 and 1995 from initially non-infested plots in which wilt never occurred in 1990-93 or in 1996 seems anomalous and likely represents MS from a strain of V. dahliae nonpathogenic to mint.

These data constitute a general verification of earlier studies in the Willamette Valley that showed that wilt can be held static under a program of post-harvest flaming without tillage, but that wilt worsens

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under a program of tillage without flaming. For the first time, our data provide a quantitative basis with respect to soil inoculum density for these responses. The earlier Willamette Valley studies were done with highly susceptible Black Mitcham. We show a similar pattern with the moderately tolerant variety Todds. The 1990 and 1996 disease incidences resulted strictly from new root infections (at least those which become systemic) on the replanted mint. As the mint stand aged, additional new root infections undoubtedly developed. Nevertheless, the data support the concept that a substantial proportion of the wilt in subsequent years is carried over within rhizomes. This was most likely true for flamed and untilled plots since the initial infestation levels did not support the high levels of wilt eventually seen as stands aged. But this pattern of disease intensification also was likely true for tilled plots — not only were new MS incorporated into soil from infected stems, but infected rhizomes were chopped into pieces and redistributed during tillage.

It is not clear from this study what levels of inoculum are critical in various soils, or for various varieties. As in 1990 through 1993, wilt incidence in 1996 varied with soil type across the COARC Powell Butte field, associated with a statistically significant block effect ($p<0.05$). For example, in plots which were tilled but not flamed from 1990-93, wilt incidence in the highest two infested treatments ranged from 2-45 percent and 25-100 percent, respectively, with the lower incidences occurring on the west end of the trial area, and the higher incidences occurring on the eastern side. In contrast, inoculum densities determined in 1994 and 1995 were not higher in the east than in the west. This suggests that soil characteristics rather than inoculum density were responsible for the consistent range in wilt development across the trial area. These data support Idaho potato data for verticillium that an inoculum density vs. disease incidence relationships vary with respect to soil type or other factors. Thus, whereas soil assays may be useful research tools, they may not provide reliable prediction of commercial disease losses among diverse field situations.

Our reports from 1990-1993 document greater weed problems in plots that were not tilled [This likely was directly related to the soil disturbance during spring tillage, but also may have been related to weed establishment in bare areas of untilled plots.] Our earlier reports document the value of tillage for redistribution of rootstock in thin stands. Other studies indicate the value of tillage for control of invertebrate pests. A possible detrimental effect of post-harvest flaming on predatory mites has been suggested Nevertheless, our data support the concept of reducing tillage to a bare minimum, while retaining flaming as a critical component of mint culture as long as V. dahliae remains a dominant influence. Our investigation did not determine what pattern of wilt and soil inoculum changes would develop under a program of tillage plus flaming, or a program of no tillage and no flaming. The earlier Willamette Valley studies suggested intermediate results with these two programs with Black Mitcham, but these variations might be worth investigating further.

Our earlier reports also documented an interaction between high soil population of V. dahliae and winter kill. In fact, in the most highly infested plots that were flamed but not tilled, yield losses in 1993 resulted from the combination of low stand and verticillium wilt, rather than wilt alone. Similar interactions might occur between V. dahliae and other stress factors. Thus, whether from a wilt response alone, or from wilt interactions with other factors, this study underscores the difficulty in retaining mint productivity in the presence of high soil inoculum density of the peppermint wilt fungus.

Introduction

On this long-term project, readers are referred to previous reports of progress from this project from 1990 through 1995 (Crowe, 1992, 1993, 1994, 1995). The initial intent was several-fold: (1) To determine the general ranges of infestation of microsclerotia (MS) of mint strains of *V. dahliae* that induce various levels of verticillium wilt, and the type of soil assay most likely to detect these ranges, (2) to determine whether reduced tillage combined with propane flaming after harvest would limit the increase of verticillium wilt in central Oregon (Homer & Dooley 1965 and 1966, McIntyre & Homer 1973), (3) to determine whether winter damage of consistently untilled mint might be more adverse to production in central Oregon than damage due to wilt aggravated by tillage, (4) to determine actual changes in soil inoculum levels of MS over time, which had only been assumed previously but not measured, and (5) to serve as a basis for evaluation of inoculum density and "wilt potential" in commercial field soils using the inoculum density vs. disease loss relationships determined from this field trial.

Plots at the COARC Powell Butte field were fumigated with methyl bromide in 1987. In

1989, the widely used Butterfield soil assay (Butterfield & DeVay 1977, Joaquim et al. 1988, Nicot & Rouse 1987) indicated that few MS of *V. dahliae* were present following fumigation. Field history suggested that any MS present likely were associated with potatoes and not with peppermint. Objectives 1, 2, and 3 above were largely assessed during 1990-1993, following uniform infestation of large field plots and planting of Todds peppermint in the spring of 1990. In general, wilt incidence increased on tilled but not flamed mint and remained static on flamed but not tilled mint for all initially calculated levels of infestation (0, 0.01, 0.1, 1.0 and 5.0 MS/g soil) except at the highest level of initial infestation (5.0 MS/g soil). At the highest initial level, oil and hay yields declined in 1993 for both tilled and flamed plots, a result of a combination of reduced stand and in-season wilt (Table 1).

Following the record cold winter of 1990-91, major stand decline occurred only in highly infested plots that had been flamed but not tilled in the fall of 1990. In this treatment combination, the mint never really recovered full stand during 1991, 1992, or 1993 (Table 1). The winter injury likely was associated with lack of winter hardiness on wilt-infected rhizomes in the fall of 1990. Lack of winter hardiness was never observed at initially lower levels of infestation. Undoubtedly, the winter kill also occurred in the highly infested plots that were tilled in the early spring of 1991, but any such winter kill was obscured by redistribution of surviving rhizomes.

The 1991-93 disease data suggested that inoculum density was not increasing greatly in flamed and unfilled plots, and that it could even be dropping if much of the year to year wilt incidence was resulting from carryover of *V. dahliae* through active rhizome infections rather than new infections through roots, as suggested by Nelson (1950). The wilt data also suggested that inoculum density for tilled mint might be a "moving target," assuming inoculum was building up due to tillage along with the increase in incidence of wilt symptoms (although carryover in rhizomes also could complicate this argument).

Beginning later in 1990 and extending through 1994 (when we stopped using it altogether), we failed to recover *V. dahliae* consistently from the Powell Butte soil using the Butterfield assay, even when some variations were tried. On many sample dates, we cultured no colony forming units from any samples. Soil samples were shipped to other laboratories, and these labs also failed to recover *V. dahliae*. In our laboratory, a fusarium fungus consistently overgrew our culture plates and precluded growth of *V. dahliae*. This did not happen from most other soils from elsewhere in the region. The reasons for initial success in 1990, followed by consistent failure are not clear, but may relate to the short time in which lab-produced inoculum had been resident in the soil — perhaps the contaminating fusarium became tightly associated with MS directly after the first several months, or perhaps the fusarium developed in the soil system more in association with the presence of mint roots. Whatever the reason, the failure to recover *V. dahliae* for several years in spite of seemingly normal disease progression created some confusion. The net result was that we were unable to document the changes in soil inoculum as the disease progressed between 1990-93

Because of the problems encountered with several standard soil assays for MS during 1990-1993, objectives 4 and 5 above could not be addressed by the end of 1993. In 1994 it was proposed that yet another assay be attempted that had proven useful in England on cooler soil where standard assays had failed (Harris et al. 1993). This Harris assay seemed to provide reasonable data on a limited series of tests in 1994.

As an alternative to dependency on soil assays, to verify that soil inoculum had changed, and to avoid confounding the inoculum density vs. disease incidence relationship with infected rhizome carryover with root infections from MS, it was proposed in 1993 that the mint in the Powell Butte trial be killed, that mint roots and rhizomes be allowed to decay for a period of time, and that the plots be replanted to mint for evaluation of wilt on the subsequent crop. For cotton, release of MS into soil from decaying cotton stems takes one to two years (Huisman & Ashworth 1976), and for potatoes it takes about two years before MS become released into soil from decaying potato stems (Davis & Huisman, personal communication). Two seasons were allotted for MS to become released into soil prior to mint replanting.

Methods

Triply-replicated soil samples from 1994 and doubly-replicated soil samples from 1995 were assayed as described in 1995 (Harris et al, 1993). Each soil sample was composed of two 20-core sub-samples that were separately assayed, and this sampling procedure was repeated_ Briefly, soil in each sub-sample was air dried, ground, and soil

volume was reduced by washing on 400-mesh screens. Concentrated soil residue was placed onto semi-selective medium in Petri plates, and characteristic growth of *V. dahliae* was noted after two weeks. Data were expressed as colony forming units (CFU) per gram of soil. Even though the soil sieving process and the culture medium used in the Harris assay were similar to the Butterfield assay (Butterfield & DeVay, 1977), certain variations must have been crucial to overcoming the influence of competitive organisms on the culture plates. Data from 1994 and 1995 soil sampling provide reasonable estimates of the soil population of *V. dahliae* into which mint was replanted in the fall of 1995 (Table 1).

In November of 1995, verticillium- and nematode-free Todds rhizomes were dug from the COARC Madras research farm. This rootstock planting had been established in 1992 from Oregon-certified rooted cuttings planted into land never previously irrigated nor cropped to mint. Rhizomes were separated into 6-8 in pieces by hand on the day of digging, and planted every row-foot into 5 rows per plot on the next day into open 4in-deep furrows opened into the established 10 ft x 80 ft plots in the long term COARC Powell Butte field trial. Roots were covered by machine and irrigated

Peppermint emerged erratically in the spring of 1996, but the field pattern was unrelated to any experimental treatments. More likely, poor emergence was related to the long, cool winter that somehow similarly effected many new plantings in the entire Powell Butte region in 1996. A stand count was taken in early June.

Mint was irrigated and remained relatively weed free during 1996. Wilt symptoms developed initially in July, and worsened into September. Wilt ratings were taken at about 10 percent bloom on September 10, 1996, but plots were not harvested Wilt ratings were the proportion of wilted plants to the number of emerged plants, expressed as a percentage (Table 1).

With the erratic stand, it was determined that future inoculum shifts and wilt disease would not occur in a consistent manner, even if the trial was replanted. In the fall of 1996, the mint was killed, and the soil in the entire trial area was fumigated to reduce the risk of spread of wilt around the COARC Powell Butte farm. Thus, this field trial was terminated.

Results & Discussion

The 1996 disease rating can be directly compared to the 1995 inoculum density rating as determined by soil sampling (Table 1). The 1990 disease rating cannot be directly compared to 1989 inoculum density because we did not attempt to recover microsclerotia from all levels uniformly infested in 1989. Early in 1990, the Butterfield assay was successfully used to confirm that the initially calculated infestation rates were reasonable estimates of recoverable MS/g soil. In the spring of 1990, an average of 1.2 and 6.3 MS/g soil were recovered from soil in which the calculated infestation was 1.0 and 5.0 MS/g soil, respectively. These recovered estimates from 1990 were reasonably similar to calculated rates of infestation. Thus, for convenience and necessity, the calculated numbers were used to generally describe the entire initial infestation range, and these calculated estimates are included in Table 1.

The relationships between 1996 disease incidence in replanted Todds peppermint and the preplant infestation rates estimated in 1994 and 1995 are stridng. All plots had been uniformly infested in 1989, and populations were expected to diverge based on cultural management. Inoculum levels in plots in which mint had been tilled but not flamed in 1990-1993 were many times higher ($p<0.05$) prior to the 1996 replanting than in plots that had been flamed but not tilled in 1990-93 and, accordingly, wilt incidence was at least 10-fold higher ($p<0.05$) in the 1996 replanting for previously tilled vs. flamed plots (Table 1). Many plots in the previously tilled and not flamed treatments were perceived to be at "wilt-out" levels in the 1996 replanting year. In summary then, these soil inoculum density estimates provide a quantitative basis for the Homer model. Inoculum seemed to not increase with a regime of flaming without tillage, and inoculum clearly comparatively increased with a regime of tillage without flaming

Based on the relatively low recovery of MS in 1994 and 1995 from soil sampled from previously flamed and unfilled plots, much of the disease progression that occurred in those plots (especially at the highest rate of initial infestation) must have involved carryover of systemic infections from mature to developing rhizomes. Just as likely, tillage operations in tilled but unnamed plots broke new rhizomes into several infected pieces and redistributed these, enhancing wilt in tilled plots well above that which would be directly attributable to root infections from soil-borne microsclerotia. Of course, such tillage also would be incorporating senescent stems from the previous year, together with newly formed microsclerotia in those stems, into soil at the same time.

For various reasons, the inoculum density vs. disease incidence relationship for the first and second mint plantings cannot be directly compared. (a) It is not clear whether the Harris assay and the Butterfield assay would yield the same inoculum density estimates. Relative recovery efficiency for these two methods should be compared, perhaps on several different soils, with both lab and naturally-formed microsclerotia. At this time, we have not determined this. (b) The lab-produced inoculum used for artificial infestation was uniformly sized. Recovery of most such sclerotia was expected in the spring of 1990 in order to verify their placement. In contrast, by 1994 and 1995, many or most sclerotia in the soil system likely were naturally produced on wilted plant material between 1990 and 1993, and released into soil over various periods of time. Such inoculum represents a wider size range, and the smaller fraction likely is lost during assay. (c) The biological activity of lab-produced Vs natural inoculum may not be equal. (d) Disease estimates for 1990 through 1993 were based on the number of discrete wilt loci per plot, whereas disease estimates for 1996 were a proportion of the emerged rhizomes planted.

The recovery of MS from plots in 1994 that had received no added pathogenic MS in 1989 was higher than from the plots initially infested at 0.01 and 0.1 MS/g soil, even though no wilt or very little wilt occurred in "non-infested" plots. This result seems anomalous and the colonies that formed on the lab medium may represent MS from a strain of *V. dahliae* nonpathogenic to mint, one which does not appear to have been recovered from plots in which the mint strain of *V. dahliae* was added. This suggests some unanticipated relationship between populations of strains. [The Butterfield assay was used prior to 1989 infestation to determine the background level of *V. dahliae*. Any such background level likely was low, due to fumigation, but our ability to measure the background can now be questioned due to the later problems experienced with the Butterfield assay.]

Inoculum density estimates for 1994 and 1995 were very similar, suggesting that the population of MS (as measured by CFU) did not increase. This further suggests that the herbaceous mint stems had decayed and released MS following tillage operations during 1991 through 1993, and that the population had stabilized prior to August 1994 soil sampling.

For this Powell Butte field, one might integrate the pattern of disease progression during 1990-93, the mean soil inoculum density data for 1995, and the disease levels in 1996 to suggest pre-plant economic thresholds. We believe one such economic threshold might be 0.25 MS/g soil (based on the Harris assay) if the field was regularly tilled without flaming and if stand longevity was restricted to about 4 years — at which time the field might be too highly infested to recrop successfully. In contrast, if the field was not tilled after planting and if it was regularly post-harvest flamed, the economic threshold might be elevated as high as 1.0 MS/g soil, or even higher, with the stand longevity likely to be sustained substantially longer than 4 years.

However, it remains to be determined whether assays prove to be useful predictors of wilt incidence for commercial crops, although they will be useful in research trials. Recent worldwide comparisons among several *V. dahliae* assays, using identical soil samples that were divided among 13 different laboratories, indicated that within-lab results were consistent, but between-lab results were rather variable (Termordhuizen 1995). This would suggest that different labs might communicate different levels of infestation, which would complicate interpretation with respect to disease incidence. Further, in potatoes, it seems as if even the same inoculum densities can result in a wide variation of wilt when they occur in different soil types (J. Davis, University of Idaho, personal communication), which would further complicate interpretation.

The Powell Butte trial demonstrates this same problem. In 1990-93, wilt incidence was associated with soil type on the COARC Powell Butte field [significant block effect ($p<0.05$)]. Similarly, in plots that were tilled but not flamed from 1990-93, wilt incidence in 1996 in the highest two infested treatments ranged from 2-45 percent and 25-100 percent, respectively, with the lower incidences occurring on the west end of the trial area, and the higher incidences occurring on the eastern side. In contrast, however, inoculum densities determined in 1994 and 1995 were not clearly higher in the east than in the west. This suggests that soil characteristics rather than inoculum density may have been responsible for this range in wilt development across the trial area. On this basis, then, the economic threshold of inoculum density on the west side of the field might be as high as 5 MS/g soil for the flamed and not tilled scenario, whereas an economic threshold on the east side of the field might be substantially less than 1 MS/g soil.

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Table 1. Mint disease resulting from various infestation levels of microsclerotia of *Verticillium dahliae*, at Powell Butte, OR, 1989-1996[1].
Using the Fisher LSD Procedure

Inoculum Density (initial)		Seasonal Wilt Incidence in 1st Crop Per Area Covered by Mint Growth in the Spring						Inoculum Density During Crop Rotation		Wilt Incidence in 2nd Crop at Harvest	
1989 Preplant		1990 1st crop, 1st yr	1991 1st crop, 2nd yr		1992 1st crop, 3rd yr		1993 1st crop, 4th yr	1994, 1995 between mint crops		1996 2nd crop, 1st yr	
MS/g Soil [2]		Numerator = No. of Cumulative Wilt Loci at Harvest[3] Denominator = Percent Area of Plot from which Mint Emerged in the Spring (800 ft^2=100%)[4]						MS/g Soil[5]		% Wilted Plants[6]	
Calculated	(Verified)	Prior to Trt	Flamed	Tilled	Flamed	Tilled	Flamed / Tilled	Flamed	Tilled	Flamed	Tilled
0	(NA)[7]	0/94	0.2/79	0.8/96	0.2/88	3/97	2/85 / 9/83	0.4 b[8]	0.7 b	0 a[8]	1.4 b
0.01	(NA)	0.2/96	0.2/75	0/96	0.6/89	1/98	4/83 / 9/92	0.2 b	0.1 ab	0 a	1.8 b
0.1	(NA)	0.3/96	0.8/79	0.8/96	0.2/87	14/97	7/84 / 76/90	0 a	0.3 b	0.6 b	8.8 c
1.0	(1.2)	3./82	3/82	19/97	4/87	39/96	18/82 / 264/91	0.1 ab	5.7 c	2.4 b	15.7 cd
5.0	(6.3)	52/97	92/299	164/949	88/51	401/96	400+/5410 / 800+/58[10]	0.7 b	18.8 d	7.2 c	62.8 d

1. The trial was a randomized split block design with five replications. Main plots were rates of initial infestation of *V. dahliae*, and split plots were either post-harvest flamed without spring tillage in 1990, 1991 and 1992, or were spring tilled without post-harvest in 1991, 1992 and 1993. Todds peppermint was planted in the spring of 1990 and managed through 1993. Tilled but not flamed plots were again flamed in 1993. Mint was killed in the spring of 1994, and wheat+peas were grown in 1994 and 1995 following common soil management practices. Todds peppermint was replanted in the fall of 1995 and managed through September 1996.
2. Microsclerotia (MS) were produced in the laboratory on cellophane agar, distributed uniformly over 80'x10' plot areas and tilled 10 cm into soil in the late fall of 1989. Soil from plots with the two highest calculated rates was assayed (Butterfield & DeVay, 1977) to verify infestation level.
3. Discrete wilt infections were flagged periodically during the season until harvest. Loci nearer than 20 cm could not be distinguished. Figures above 400 wilt loci per 800 ft2 are estimates rather than exact counts. Statistical analyses for 1990-93 wilt incidence are discussed in previous reports.
4. Spring plant stands were estimated by determining the area from which mint emerged in the May of each year, and expressed as a percentage of 800 ft^2 plot area. Statistical analyses for spring stands are discussed in previous reports.
5 Inoculum as MS/g soil were estimated from soil samples which were processed as per Harris et al. 1993. Inoculum measurements in 1994-95 likely represents microsclerotia which were produced naturally in mint during previous years, and which were released into soil. Inoculum density estimates for 1989 and 1994-95 are not necessarily comparable.
6 A second crop of mint was space planted in the fall of 1995, and 1996 wilt was expressed as the percentage of emerged mint from the spring of 1996 which developed wilt symptoms during 1996. Yields were not determined for 1996 due to erratic stands unrelated to *V. dahliae*. Based on visual observations, yields would have been very low for all 5 replications of the most highly infested plots which had been tilled 1991-93, and for 2 of 5 replications in the next-most highly infested plots which had been tilled 1991-93. Yields likely would not have been reduced in all other treatments, at least for 1996.
7. NA = not applicable, the lowest calculated rates were not assayed to verify initial infestation level.
8. Within and across Flamed and Tilled columns, means followed by the same letter were not statistically significant ($p<0.05$).
9. The winter of 1990-91 reached below -35 F, which resulted in winter kill but only in the most highly infested plots (as seen in a statistically significant infestation vs. spring stand interaction, $p<0.05$). Spring stands were greatly reduced in plots which were flamed but not tilled, but surviving rhizomes were separated and redistributed in tilled plots such that the effect of winter kill was obscured. Mint growth compensated even for low stands, and yields were not significantly different for any treatments in 1991 (or 1992).
10. Yields are not shown, and within each year were not statistically different among infestation levels or between flaming/tillage treatments until 1993. In 1993, mint yields were reduced ($p<0.05$) at the highest level of infestation for both flamed but not tilled treatment and the tilled but not flamed treatment. Boldface is used to emphasize the onset of such yield loss as described commonly as "wilt out". "Wilt out" at the highest initial levels of infestation was due to a combination of reduced stand and in-season wilt.