

Managing Nematodes Without Methyl Bromide

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Abstract

Methyl bromide is an effective pre-plant soil fumigant used to control nematodes in many high-input, high-value crops in the United States, including vegetables, nursery plants, ornamentals, tree fruits, strawberries, and grapes. Because methyl bromide has provided a reliable return on investment for nematode control, many of these commodities have standardized their production practices based on the use of this chemical and will be negatively impacted if effective and economical alternatives are not identified. Alternative control measures based on other chemicals, genetic resistance, and cultural practices require a greater knowledge of nematode biology to achieve satisfactory results. Here, we provide an overview of nematode management practices that we believe will be relied upon heavily in U.S. high-value crop production systems in a world without methyl bromide. Included are case studies of U.S. high-value crop production systems to demonstrate how nematode management practices other than methyl bromide may be incorporated.

INTRODUCTION

In a day and age when many fumigant nematocides are being banned, phased-out, or their use is being heavily restricted, it is interesting to reflect that it was fumigant nematocides that made scientists and farmers realize the extent to which plant-parasitic nematodes damage crops. Although plant-parasitic nematodes have been known to affect plants since 1743 (71), the true economic impact of the damage they cause was not fully realized until the 1940s, when soil fumigants were developed, and their application resulted in appreciable yield gains due to the elimination of nematodes (64, 104). In 1947, Dr. R.M. Salter, chief of the Bureau of Plant Industry said, "New soil fumigants bid fair to become one of the greatest boons to agriculture since the development of fertilizers" (72). This point of view dominated the nematode control landscape for the next four decades. There are numerous historical documents extolling the benefits of fumigants and promoting their use as a stand-alone pest management practice. In a 1967 research bulletin written for the California Strawberry Advisory Board, it was stated, "Soil fumigation has become an integral part of land preparation for strawberry cultivation in California, has proved its worth hundreds of times over, and has provided valuable side-effects not anticipated at the out-set of experimentation to develop a control for soilborne diseases" (120).

Because of its broad spectrum of activity, methyl bromide has long been considered one of the premier soil fumigants for managing plant-parasitic nematodes and other soilborne pests. Research began as early as 1940 when Christie & Cobb experimented with methyl bromide for control of *Aphelenchoides ritzemabosi* on planting material (24, 104). Taylor & McBeth (102) obtained satisfactory results in field plots by releasing methyl bromide gas into tile lines buried under soil covered with a glue-coated paper, and good results were also obtained by simply covering the soil with paper and releasing methyl bromide between the cover and soil surface (103).

Methyl bromide is classified as a restricted-use pesticide and was registered for use in the United States in 1961 (112) as an effective herbicide, nematicide, insecticide, and fungicide. Widespread use of methyl bromide as a pesticide for soils, stored agricultural products, and other applications did not occur until the 1970s (3). In the late 1980s and early 1990s, methyl bromide was one of the five most used pesticides in the United States (87), with 75% of the use being for pre-plant soil fumigation. Characteristics of methyl bromide that led to its widespread use included: broad-spectrum pest control, better efficacy compared with other fumigants (64), and volatility sufficient to penetrate soils some distance from points of application (32).

The phase out of methyl bromide under the Montreal Protocol resulted from its ability to deplete stratospheric ozone (62, 87, 90). Initially, a 100% reduction of methyl bromide use from the 1991 domestic production level was scheduled for 2005 in developed countries and 2015 in developing countries, but as of 2008, the fumigant was still being used in the United States, Australia, Canada, and Japan. This is because the Montreal Protocol allows for critical use exemptions (CUE) to the ban if (a) there are no technically and economically feasible alternatives that are acceptable from a regulatory and bystander exposure perspective, and (b) the use is considered crucial to avoid a significant market disruption of selected commodities (109). In 2008, the United States accounted for 91% of the total global CUE approvals for high-value crops such as vegetables (cucurbit, eggplant, tomato, pepper), strawberries, deciduous fruit and nut trees, nursery crops, grapes (raisin, table, wine), ornamentals, and cut flowers and greens (9). Because of the long reliance upon and continued use of methyl bromide, these U.S. commodities will be the most challenged in managing plant-parasitic nematodes and other soilborne pests in the future without methyl bromide.

Methyl bromide soil fumigation has traditionally been used as a pre-plant management practice in high-input, high-value production

systems (87). Prior to planting, the fumigant, combined with a percentage of chloropicrin (2% to 50%), is typically injected into the soil and covered with plastic to keep the gas from immediately escaping into the atmosphere. These production systems have relied on methyl bromide for plant-parasitic nematode control because the expense of fumigating is relatively low and returns are potentially large (32). Producers of these crops have not adopted other methods of controlling nematodes because methyl bromide is extremely effective and well suited for these uses. In fact, high-value crop production systems have evolved around the use of methyl bromide, providing growers with a tool to avoid the expense of crop rotations and the problem of scarcity of new appropriate land (64).

In this review, we focus on U.S. high-value crop production systems that have relied heavily upon methyl bromide for plant-parasitic nematode control and try to envision a nematode management future without methyl bromide. Commodities that have become highly dependent on methyl bromide for nematode control stand to lose the most if effective alternatives are not identified (19). Research indicates that the future of nematode

control will depend more upon integrated techniques that incorporate cultural practices, genetic resistance, and alternative nematicides to keep populations below damaging levels. We include an overview of those nematode management practices that we believe will be widely utilized in U.S. high-value crop production systems in a world without methyl bromide. We also present case studies of several U.S. high-value crop production systems and demonstrate how nematode management practices other than fumigation with methyl bromide may be incorporated into these systems.

PLANT-PARASITIC NEMATODE MANAGEMENT PRACTICES

Chemical

Many studies evaluating methyl bromide alternatives in high-value crop production systems have focused heavily on chemical rather than nonchemical alternatives. The landscape of chemical nematode control is constantly changing because of registration and reregistration considerations at state and federal levels. Currently, there are only a handful of chemicals registered for pre-plant nematode control (Table 1) (2, 32, 62). The fumigants

Table 1 Fumigant and nonfumigant nematicides that will be relied upon by high-value crops in the United States for plant-parasitic nematode and soilborne disease control in a world without methyl bromide

Chemical name	Common name	Trade name [®]	Manufacturer
Trichloronitromethane	Chloropicrin	Chloropicrin	Dow Agrosciences, Indianapolis, IN
Sodium <i>N</i> -methylthiocarbamate	Metam sodium	Vapam	Amvac Chemical Corporation, Los Angeles, CA
Potassium <i>N</i> -methylthiocarbamate	Metam potassium	K-Pam	Amvac Chemical Corporation
Tetrahydro-3,5-dimethyl-2H-1,3,5-thiadiazine-2-thione	Dazomet	Basamid G	Certis, Columbia, MD
1,3-Dichloropropene		Telone II, Telone C-35, Telone C-17 Cordon, Inline	Dow AgroSciences
Methyl iodide	Iodomethane	Midas	Arvysta LifeScience, Cary, NC
Dimethyl disulfide	DMDS	Paladin	Arkema Inc., Philadelphia, PA
Sulfuryl fluoride			
[Methyl <i>N'</i> <i>N'</i> -dimethyl- <i>N</i> -[(methyl carbamoyl)oxy]-1-thioxamimidate]	Oxamyl	Vydate	DuPont Agricultural Products, Wilmington, DE
(<i>O</i> -Ethyl <i>S</i> -(1-methylpropyl)(2-oxo-3-thiazolidinyl)phosphonothioate)	Fosthiazate	Nemathorin	Syngenta International AG, Basel, Switzerland

chloropicrin, metam sodium, metam potassium, and dazomet have recently undergone reregistration eligibility decisions (REDs) by the U.S. Environmental Protection Agency (EPA) (114). Regulatory changes, including buffer zone requirements, are mandated to appear on the fumigant pesticide labels in 2010 and 2011, and the EPA plans to initiate reregistration reviews for all of the soil fumigants in 2013, four years earlier than previously planned (114).

Registered fumigants. Chloropicrin is commonly applied in combination with other fumigants such as methyl bromide, 1,3-dichloropropene, iodomethane, metam sodium, and metam potassium because of its fungicidal activity; however, it is generally less effective against nematodes and weeds than methyl bromide (32).

In many high-value commodities, 1,3-dichloropropene will be a viable alternative to methyl bromide for plant-parasitic nematode control; however, although 1,3-dichloropropene is a good nematicide, very few growers target nematodes alone, and this chemical provides no weed control. 1,3-Dichloropropene is marketed as a stand-alone fumigant (Telone II® and Cordon®, 96% to 97.5% 1,3-dichloropropene) or in combination with chloropicrin (Telone C-17®, 17% chloropicrin; Telone C-35® and Inline®, 35% chloropicrin). Application of 1,3-dichloropropene, however, has restrictions including township caps in California (20), prohibition of use on karst topography in Florida (90), and reduced efficacy in fine-textured soils in California (53).

The methyl isothiocyanate generators (metam sodium and metam potassium as liquid formulations and dazomet as a granular formulation) are very effective against nematodes and are used widely. However, although these are broad spectrum biocides, their performance is inconsistent because of inadequate volatility, which results in poor soil distribution and a relatively poor capability to penetrate and kill old woody roots or tubers (62, 64).

Another fumigant that has been proposed as a drop-in replacement for methyl bromide is iodomethane (90). Iodomethane has a broad spectrum of activity and is mobile in soil, but it is not an ozone depleter because it is rapidly destroyed by UV light (80). In 2008, EPA issued a conditional registration of iodomethane (113). Midas® (iodomethane combined with chloropicrin) is registered in 47 U.S. states for use on high-value crops, including ornamental plants, strawberries, tomatoes, peppers, fruit and nut trees, and vines.

For greater efficacy, it has been proposed to use the above-mentioned registered fumigants in combination with each other. An example would be a three-way system in which Telone II® is shank injected at 35 cm, followed by chloropicrin injected at 20 cm, and finally metam sodium is injected at 10 cm in depth (45).

Nonregistered fumigants. In the future, new fumigant nematicides will continue to be developed and evaluated for plant-parasitic nematode control. One product that is receiving attention is dimethyl disulfide (DMDS) alone or in combination with chloropicrin. DMDS is a ubiquitous natural product, common in the global sulfur cycle, and is detected as a metabolite in numerous biological processes (77). In field trials, DMDS controlled *Meloidogyne* spp. equivalent to methyl bromide (25). More recently surfuryl fluoride, a well-known commodity fumigant, has shown efficacy as a soil fumigant (16).

Despite the existence of chemical alternatives to methyl bromide, there are many challenges regarding their widespread adoption. The EPA REDs for soil fumigants will require buffer zones to minimize bystander exposure. The size of the buffer zone will depend upon the fumigant being applied and how it is applied. Emissions from soil fumigation are significant and can range from 20% to 90% of the total applied fumigant (124). Practices found to achieve fumigant emission reductions include modified fumigant placement (94), reduced rates of application (1), use of impermeable films (79),

water seals (47, 42), drip application (1, 81, 94, 96), bed fumigation (47), and coapplication of organic amendments (31, 40, 42), ammonium thiosulfate (118), or potassium thiosulfate (85). Examples of ways to reduce the buffer zone around a fumigated site include using high barrier films or potassium thiosulfate, or by applying fumigates to high-organic soils (>3% organic matter), (115). Regardless of the application scenario, federal and state restrictions on fumigants will continue, and managing nematodes with fumigants will become more complicated in the future. Economics is another concern in using fumigants other than methyl bromide. The use of fumigant emissions-reducing practices will add cost, and the prices of some of the alternative fumigants are higher in 2010 than that of methyl bromide. For example, unit for unit, the cost of Midas[®] is currently fivefold the 2009 cost of methyl bromide.

Pre-plant chemical controls have been the focus of most nematicide research because if nematodes are not controlled pre-plant, then it is very difficult to control them after a crop is established. This is especially true for high-value, long-term perennials, which can be in the ground for 5 to 100 years. Currently, there are very few post-plant nematicides registered. Oxamyl and fosthiazate are two nonfumigant nematicides that have been evaluated as partial methyl bromide alternatives since the early 1970s and 1990s, respectively (**Table 1**) (14). Oxamyl is currently registered in the United States for use on high-value crops such as pepper, tomato, eggplant, cucurbits, and some tree fruit crops. Fosthiazate is currently registered in the United States but only for use on tomatoes. These products could prove useful in some areas as a supplemental nematode control or where post-plant applications are needed to enhance fumigant performance or where nematode pressure is low (14).

Plant Resistance

The deployment of resistant crop plants may be the most effective and economical means of controlling plant-parasitic nematodes,

regardless of the availability of methyl bromide. That does not mean, however, that the loss of methyl bromide can be easily replaced by simply planting nematode-resistant plants. Although resistance to nematodes has been identified in a number of crops (88), much work remains to be done. Most of the plant resistance genes identified are effective against sedentary endoparasitic nematodes such as *Meloidogyne* spp. and those in the family Heteroderidae. Resistance to feeding by ectoparasitic or migratory endoparasitic nematodes has been more difficult to identify and is often expressed as reduced reproduction in comparison to a susceptible cultivar (28). The emphasis on sedentary endoparasitic nematodes is not surprising, as they have a more complex interaction with host plants and resistance is easier to evaluate. Most of the resistance genes against sedentary endoparasites described to date prevent or greatly reduce nematode population increase in the roots. Resistance typically is characterized by the failure or death of specialized feeding cells in the host (122). In some cases, resistance fits the gene-for-gene hypersensitive resistance model (7).

There are several examples of successful nematode management with resistance. The *Mi-1* gene for resistance to *Meloidogyne incognita*, *M. arenaria*, and *M. javanica* in tomato (121) has been used successfully for more than 25 years in California and elsewhere despite limitations due to high temperature breakdown of resistance and isolated cases of resistance-breaking pathotypes (73). Resistance to *Globodera* spp. in potato, conferred by the dominant, major-effect *H1* gene derived from *Solanum tuberosum* ssp. *andigena*, has remained effective against the Ro1 pathotype of *Globodera rostochiensis* for decades. Other pathotypes or species, such as *G. pallida*, may increase over time, but other sources of resistance are being developed (21). The identification and incorporation of resistance to a range of damaging nematodes is ongoing in high-value crops such as vegetables (105) and fruits (5, 35, 38, 116). Another method for utilizing plant resistance to control nematodes is through grafting (58). Grafting allows for the production of commercially

acceptable varieties on rootstocks that have some level of resistance or tolerance to nematodes. Grafting of commercial bell pepper varieties on nematode-resistant rootstock reduced damage caused by *M. incognita* (15). Marker-assisted selection may also increase the speed of resistant cultivar development in comparison to traditional methods of breeding, reduce problems associated with linkages to deleterious genes, and elucidate epistatic gene action (120).

Transgenic techniques allowing the transfer of cloned nematode resistance genes to susceptible crops hold great promise. Approaches such as transgenic introduction of genes encoding protease inhibitors may inhibit nematode feeding and potentially allow for the development of resistance to many different plant-parasitic nematodes (86). Gene silencing by RNA interference is also a promising approach for the development of transgenic plants resistant to nematodes (6). Successful transgenic varieties will require both regulatory approval and market acceptance. Plant resistance to nematodes holds great promise for effective and economical control of these important pests, but increased research efforts in both conventional plant breeding and the development of transgenic resistance are still needed.

Cultural Practices

In a discussion on plant disease control, Thurston (107) noted, "It is quite simple to apply a pesticide or utilize a high-yielding resistant variety to manage plant diseases, but one has to know a great deal about the biology of a situation in order to use cultural management." This simple but insightful observation applies to nematode management as well and underscores the importance of grower education. One of the great advantages of methyl bromide that is not often mentioned is the fact that growers need not have an appreciable understanding of nematode biology because the fumigant quickly and reliably kills whatever pathogens are present. However, effective cultural practices typically rely on specific information about

the nematode such as accurate species identification, host range, life cycle, survival strategies, and longevity. Success or failure of a particular practice often hinges on specific actions such as proper timing or host selection, and growers that do not understand why a particular step is taken may fail to control the problem using these techniques. Cultural management covers a wide range of activities designed to interfere with nematode survival and reproduction. Several commonly used cultural practices are described in greater detail below.

Crop rotation. Farmers have recognized the benefit of rotating crops since ancient times (26, 29). Crop rotation improves arable land in various ways and can be a very effective nematode management tool in some cropping systems. The basic concept of crop rotation is to separate the nematode from its host for a sufficient length of time to keep damaging population levels from developing (89). The strategy is simple; however, in some cropping systems effective rotations may be difficult or impossible to develop because of biological, practical, and/or economic constraints. This is especially true for high-value crops produced on prime agricultural land where the economic return for lesser-valued rotation crops cannot be justified. Rotations typically have their greatest application in annual production systems where a different crop or cultivar can be planted each season (13). Rotations may include nonhosts, resistant hosts, fallow, allelopathic plants, trap crops, or green manure crops (52). Although the goal is nematode management, other issues that affect production practices cannot be ignored, including the interaction of the alternate crop with other pests, availability of other management tactics, length of the rotation sequence, and value of the rotation crop. Ultimately, the success will be determined by the economics of the overall rotation management strategy.

Biofumigation. Reports of the nematode suppressive effects of the Brassicaceae occurred as early as 1925 when Morgan noted a decline in nematode populations exposed to mustard (70);

however, only in the past 15 to 20 years has the cause been understood. Secondary metabolites known as glucosinolates are sequestered within the plant's tissues along with the hydrolyzing enzyme myrosinase. When the tissues are ruptured or lysed, these come together to produce toxic and volatile isothiocyanates (82). Glucosinolates are regarded as a natural chemical defense to protect the plant against disease and herbivory (37, 54); however, when a field of brassica plants is mechanically chopped and quickly incorporated into the soil, a flush of isothiocyanate can be released in sufficient concentration to impact plant-parasitic nematode populations (50, 82). The practice of incorporating brassicaceous plant material into the soil to control soilborne organisms has been coined biofumigation (57).

Biofumigation for control of plant-parasitic nematodes has met with variable results in high-value crop production systems (60, 61, 101). To a large degree, this variability can be explained by considering the principal components of the biofumigation process. A major factor is the species and cultivar used because there is considerable variability in the types and concentrations of glucosinolates present in plant tissues (27, 91); this, in turn, will determine the specific isothiocyanates and concentrations released. Other factors that affect efficacy include the stage of plant development, method of tissue maceration, method and speed of incorporation of the tissue into soil, soil type, soil temperature, and soil moisture (63). In addition, it appears that different nematode genera have different tolerances to isothiocyanates (125).

Research has shown that other plants with different biochemical makeups may also have potential as biofumigation crops (79, 119), whereas other studies have expanded the concept of biofumigation to include the nematode-suppressive effect of incorporating various organic residues into soil (8). In general, these alternative biofumigation techniques appear promising, but the mode of action is not as well understood as the glucosinolate-isothiocyanate system of the Brassicaceae, and more research

is needed to develop these into practical and reliable nematode control practices.

Soil solarization. Soil solarization was first described in 1976 as a pre-plant soil treatment for controlling soilborne pathogens and weeds (55). Since that time, soil solarization has received much attention as a methyl bromide replacement, especially in locales in California and Florida where methyl bromide has been heavily relied upon. Soil solarization is the passive heating of soil covered with a plastic mulch. Tomato research trials in Florida demonstrated that soil solarization was cost effective, compatible with other pest management practices, readily integrated into standard production systems, and, thus, an alternative to methyl bromide (23). In these trials, densities of *Paratrichodorus minor* and *Criconebella* spp. were lower in solarized plots. However, in another trial soil solarization did not provide adequate control of *M. incognita* (93). Differences between the trials may have been due to insufficient soil temperatures to achieve nematode suppression; 38°C is considered the base temperature needed to kill *M. incognita* juveniles and eggs (117). In the central valley of California, soil solarization reduced population densities of *M. incognita* and other plant-parasitic nematodes (98, 99) including *Tylenchulus semipenetrans* (126), but in the coastal regions where high-value strawberries and flowers are grown, soil solarization was not effective in reducing *T. semipenetrans* (126).

A combination of solarization with other pest management techniques is frequently suggested for marginal environmental conditions to decrease treatment duration or to improve nematode suppression (100). *Meloidogyne* spp. control was improved when solarization was combined with 1,3-dichloropropene (93). Solarization can also be combined with manures and plant residues, potentially increasing the nematicidal activity of the amendments. Combining soil solarization with broccoli residues did not improve nematode suppression compared with untarped broccoli (126), but when soil solarization was combined with sorghum green manure, *Mesocriconebella xenoplax*

populations were suppressed 11 months longer in tarped versus nontarped plots (79). More recently, solarization has been combined with anaerobic soil disinfestation (17, 97) and steam injection (43) with good results. Anaerobic soil disinfestation combines solarization and flooding with an organic carbon source to stimulate anaerobic decomposition, which then leads to the production of nematotoxic byproducts (97). Control of plant-parasitic nematodes with this technique prior to planting bell pepper was equivalent to methyl bromide (17). Injecting steam into soil with a mobile steam generator can also be used to supplement soil solarization. Results from trials combining solarization and steam injection demonstrated that steam, with or without solarization, controlled pests equal to or better than methyl bromide (43).

Although the execution of solarization is simple, the overall mode of action is complex (i.e., heat penetration, variability across environments) (100), limiting its widespread adoption. Furthermore, solarization is most effective during the hottest part of the year; thus, in most cases, at least one year of production will be lost. In high-value crop production systems, where preharvest production costs are high, this may not be an economically viable option. Solarization is probably best suited to shallow soils, to applications prior to planting shallow-rooted (annual) crops, and to situations in which plant-parasitic nematodes are not deeply distributed in soil (98).

CASE STUDIES

Florida Vegetables

The crisis of a methyl bromide phase-out in Florida agriculture began to be addressed prior to the year 2000. Probably the most significant outcome has been the construction of a new integrated pest management strategy (90). The process has not been a simple substitution, but rather a coupling and integration of approaches, followed by an examination of interactions (75).

Florida is a primary producer of winter vegetables with tomato, eggplant, and pepper crops

being produced on 20,440 ha with an estimated annual value of \$889.7 million in 2008 (111). Strawberry production occurred on 3,400 ha in Florida in 2008 with an assessed value of \$329.3 million. The high crop values, long growing seasons, and the susceptibility of these crops to nematode damage make it very important to minimize nematode populations prior to planting, particularly because post-plant control strategies are unavailable or are of limited value. The management of nematodes in these systems currently relies on the integrated use of chemical, cultural, and biological tactics. Host plant resistance is extensively used when available but seldom embodies the polygenic resistance to the key pest species found in these production systems. For some nematode species, including *Belonolaimus longicaudatus*, there are no resistant or tolerant strawberry varieties available. Short-term fallow, with or without nonhost rotation crops, is practiced in most Florida crops to minimize erosion and to provide organic substrate for bed construction. Even with these tactics, Florida growers still rely heavily on soil fumigation for crop production and nematode control.

Since 1994, all of the federally registered and experimental fumigants, applied alone or in combination, have been evaluated and compared with methyl bromide for their broad spectrum pest control and yield enhancement activity in Florida (45, 46, 48). Chloropicrin has repeatedly proven to be very effective against soilborne diseases but not nematodes. Because chloropicrin has poor nematicidal activity, it must be combined with other fumigants to replace the nematode control attributes of methyl bromide. With these alternative fumigants, nematode control efficacy is more highly dependent upon proper placement, uniform delivery, and spatial distribution within the field (34, 74, 76). Consistently effective nematode control can be obtained with prebedding applications of Telone C-35[®] utilizing specialized equipment to ensure deep soil placement and improved fumigant containment (44). More recently, studies have demonstrated the consistency of the three-way

system for soilborne pest control in Florida (48). However, because of use restrictions for all products containing 1,3-dichloropropene in Dade County, FL, either metam sodium or metam potassium, in combination with shank injections of chloropicrin, are currently defined as the best alternatives to methyl bromide. With repeated long-term use or under conditions of high nematode pressure, other integrated practices are required to achieve adequate nematode control and economic crop productivity. In Florida, grower transition to the use of alternative fumigants represents a change from 40 years of total reliance on methyl bromide to a multi-tactic pest control and crop production system. Ultimately, grower transition to these new integrated methods will be largely economic, being driven by reduced methyl bromide supply, higher product price, and many other on-farm considerations.

California Orchards and Vineyards

In California, there is strong economic incentive to fumigate orchard and vineyard sites. Soil fumigation allows growers to replant orchards and vineyards within a year of removing the old trees and vines so that the new plantings come into bearing within three to seven years. The estimated cost for loans, taxes, and land maintenance for nonproductive land approximates 10% of the land value per year or approximately \$2500 ha⁻¹ year⁻¹. It is therefore critical to get fruit land back into production quickly. Currently, half of the 1.3 M ha of perennial crops in California are impacted by elevated plant-parasitic nematode populations (65).

The pre-plant fumigants used on perennial crops include 1,3-dichloropropene, metam sodium, and chloropicrin (64, 65, 66). Some reductions in fumigant use have occurred because of strip or spot fumigation treatments; however, these approaches are often shortsighted if the new rootstock has no nematode resistance. Cost and regulatory requirements have increased for each of the fumigants, and there are serious restrictions to the use of 1,3-dichloropropene in California. Its use is not approved for

fine-textured soils, and greater inputs are required for soil preparation and moisture management when it is used. In addition, there are township caps and buffer zone requirements, and air quality standards related to volatile organic compounds (VOCs) are enforced (20, 53).

A long-term fallow, with or without nonhost rotation crops, is the traditional nonchemical alternative for California orchards and vineyards (39). The alfalfa variety California Common and sudangrass are two of the best rotation crops as long as there is attention to nematodes and weeds. These rotation crops provide enough financial return to support the cost of weed control during the rotation but little repayment of capital costs, which is approximately \$10,000 ha⁻¹ over four years.

Host plant resistance is the preferred nonchemical alternative for California orchards and vineyards. There are 18 popular perennial crops in California, and their resistance or susceptibility and tolerance or intolerance to nematodes differs greatly (54, 66, 68). The search for new and improved nematode resistance has focused on four crop groupings, almond, grape, stone fruit, and walnut, that comprise 70% of perennial cropland in California. There are currently two examples of perennial cropping systems in California where resistance has been deployed successfully. First, almond orchards on Nemaguard (10) rootstock are replanted with Hansen 536 (56) rootstock. The Nemaguard trees are killed with herbicide just after their final harvest, and the land is idle for one full year. The new orchard is then replanted on Hansen 536. This rootstock is useful against *Meloidogyne* spp. and *Pratylenchus* spp., but is highly susceptible to *M. xenoplax*. In a second example, old vineyards are replanted with grapes grafted onto 10-17A (*Vitis simponi* × *V. muscadinia*) or O39-16 (*V. vinifera* × *V. rotundifolia*) rootstocks after the removal of own-rooted vines. During mid-winter, the old vines are cut off above ground, and the trunks are painted with a mixture of herbicide and an appropriate adjuvant. After one year of fallow, the new rootstock of choice is O39-16 if the only major

disease is *Grapevine fan leaf virus* (GFLV) plus its vector *Xiphinema index* (68). The rootstock 10-17A provides broader and more durable nematode resistance to most nematode species, including *X. index*, but is intolerant of GFLV (4, 5, 68).

Perennial Crop Nursery Production

Perennial crop nursery production in the United States was a \$4.65 billion industry in 2006 (110). Within this industry, the following sectors requested CUE in 2009 because no alternative had been identified to control plant-parasitic nematodes and other soilborne pathogens: deciduous fruit and tree nurseries (California), nursery roses (California), forest nurseries (Southeastern United States), and strawberry and raspberry nursery stock (Southeastern United States and California). Under California regulatory laws, nursery crops must be “free of especially injurious pests and disease symptoms” in order to qualify for a California Department of Food and Agriculture (CDFA) Nursery Stock Certificate for Interstate and Intrastate Shipments (18). If an approved fumigation is not used in the nursery, a nematode sampling procedure is imposed by CDFA, and if any plant-parasitic nematodes are found, all nursery stock in an area must be destroyed. Currently, only methyl bromide, and under certain soil conditions 1,3-Dichloropropene, meet certification guidelines in California. Because of this zero tolerance for nematodes, the loss of methyl bromide could severely impact the California nursery industry. Consequences of the presence of plant-parasitic nematodes potentially include: yield loss, total loss of crop, increased production costs, and quality losses.

The only fumigant other than methyl bromide sanctioned for field-grown nursery stock in California is 1,3-dichloropropene (18, 53). Rose nursery trials at two locations in California indicated that 1,3-dichloropropene combined with standard high density polyethylene (HDPE) film or virtually impermeable film (VIF) resulted in *T. semipenetrans* control

comparable to methyl bromide-chloropicrin used with standard HDPE film (53). In the same trials, there were few differences in crop establishment, crop quality, and plant-parasitic nematode populations between fumigant treatments with 1,3-dichloropropene and iodomethane both combined with chloropicrin and methyl bromide. At harvest, only methyl bromide treatment resulted in nondetectable nematode populations in grape and bramble (95). However, California restrictions, including township caps and buffer zone requirements, exist for 1,3-dichloropropene. Practices to minimize the effects of some of these restrictions may include reduced rates of 1,3-dichloropropene or applying 1,3-dichloropropene to a smaller area through bed fumigation or drip irrigation.

Adoption of methyl bromide alternatives by the perennial crop nursery industry has been slow because of the required duration and depth of nematode control, stringent regulations on materials being nematode-free, and high economic risks due to non-certification (53). Many nursery operations follow the nursery stock crop with one or two years of green manure crops, grain crops, or fallow before the next nursery cycle. However, these management practices do not ensure nematode-free nursery stock. In perennial nursery production systems where plants are in the ground for three to five years, the problems with maintaining nematode-free nursery stock are further exacerbated. Although a nonchemical treatment may initially control plant-parasitic nematodes at shallow depths, over time roots will grow to depths where the treatments do not reach, and roots may become infested with nematodes. For example, many tree, vine, and woody perennials are grown in the field for 14 to 26 months and may produce roots that penetrate 1.5 m into the soil (53). In the short-term future, it is likely that the nursery industries will have to utilize technologies that reduce fumigant emissions in order to continue to be able to use fumigants. However, as stated above, the restrictions on fumigant use are increasing in California.

Northeastern U.S. Orchards and Vineyards

Xiphinema americanum is one of the most serious nematode problems facing fruit growers in the mid-Atlantic region of the United States (51, 78). This nematode species is widespread throughout the Northeastern United States and has a broad host range. All stages of the nematode persist in soil, and its lifespan is estimated to be two to three years. The nematode is a weak pathogen by itself, but it is an efficient vector of *Tomato ring spot virus* (ToRSV) (11). Stone fruit, wine grapes, and certain apple cultivars infected with ToRSV become unhealthy and decline over a period of several years. The virus is difficult to contain because common broadleaf weeds within the host range of *X. americanum* can serve as reservoirs (84). Dispersal of ToRSV is aided by the fact that the virus is pollen- and seedborne transmitted in many of its weed hosts (12).

Pre-plant soil fumigation is a quick and efficient method of simultaneously suppressing both *X. americanum* and weeds that harbor ToRSV. The efficacy of fumigation allows growers to replant on nematode-infested sites the following year with little risk of virus infection. However, the loss of methyl bromide and tighter restrictions placed on the remaining fumigants have generated a need for other remediation techniques that are designed to suppress the *X. americanum* population and to purge the site of weeds that serve as reservoirs of ToRSV. Despite the fact that its host range includes *Brassica* spp., *X. americanum* is sensitive to biofumigation with high glucosinolate-containing cultivars of rapeseed (49). Two seasons of successful biofumigation with rapeseed variety Dwarf Essex can reduce the *X. americanum* population to levels similar to fumigation (50). Although *X. americanum* is slow to reproduce, the nematode population will eventually rebound to pretreatment levels. Therefore, it is important to include and maintain an aggressive weed management program to prevent the establishment of ToRSV hosts. Weeds can be effectively managed during the two years

of biofumigation with a combination of herbicides and cultural practices.

Strawberry Nursery Production

Strawberry fruit production has been a major focus of research on alternatives to methyl bromide. Strawberries are a high-value crop grown at high plant density and often replanted in the same locations for years. As a result, methyl bromide has been widely depended upon as a pre-plant soil fumigant to control weeds, pests, and soilborne plant pathogens, including nematodes. An important component of managing plant pathogens in strawberry nurseries without methyl bromide is the establishment of pathogen-free transplants into clean soil. Nursery transplant production is not aimed at increasing plant vigor and fruit yield, but rather aims to generate plant material free of pathogens, nematodes, and viruses, including those transmitted by nematodes (36, 83).

The use of alternatives to methyl bromide to achieve relatively clean soils and increased vigor and yield has been widely studied and implemented in strawberry fruit production systems (2). In contrast, for strawberry transplant production, the development of alternatives has been much more difficult given the higher standards of pathogen, weed, and nematode control required for certification (36, 83). Nonchemical alternatives such as solarization, steam, rotation, biofumigation and green manure, disease resistance, and the use of disease-free plug plants are not efficacious enough for use in nursery plant production (2). Nematode resistance in strawberry, described as reduced numbers in roots or plant tolerance (28, 33), has not been well exploited. The fumigant 1,3-dichloropropene was demonstrated to reduce *Xiphinema* spp. and *Longidorus* spp. to levels in soil that would likely be effective at reducing the risk of virus infection in strawberry transplants (22), especially in combination with effective weed controls. A survey of commercial strawberry production fields found fumigation with methyl bromide to be much more effective

in reducing nematode numbers in the following strawberry crop than 1,3-dichloropropene or metam sodium, which had nearly 50 times as many nematodes (59).

Strawberry nursery production often involves testing and meristem culture for elimination of viruses and other pathogens, followed by greenhouse propagation and finally field propagation to produce the final transplant product. The field propagation stage (even with fumigation) can be the most difficult part of the production of pathogen-free transplants. Methyl bromide is widely used to protect both field-grown propagation stock and certified plant stock from soilborne pathogens, nematodes, and weeds (36). Without the use of this fumigant, more expensive plug plants produced in soilless mixes may be required to achieve the low pathogen populations necessary for certification.

CONCLUSIONS

Although no stand-alone replacement for methyl bromide exists, numerous chemical and nonchemical nematode control practices have been developed for different cropping systems. Viable management practices need not be identical to methyl bromide treatment but must effectively and economically manage the targeted nematode pests (106). As noted by Roskopf et al. (90), “An integrated approach that utilizes biologically-based pest management tactics, such as plant growth-promoting rhizobacteria, soil solarization, and biological control agents combined with crop rotations and cover crops will be a necessity in the future. A multi-tactic approach is becoming increasingly important as many agricultural chemicals undergo intense scrutiny with regard to human toxicity and environmental impact.”

In Taylor’s review of nematicide history (104), he reminisced about his time as an employee of the Shell Chemical Corporation and made the following remark regarding nematicide education: “We were asking them (farmers) to invest money in chemicals and equipment to control pests they had never seen in

all the years they had been working the soil. The application methods were unlike any they had ever used before, and the results were unknown.” It appears we have come full circle and once again face the challenge of educating growers of high-value crops on how to manage nematodes with unfamiliar management practices. Similar to the extensive educational activities that occurred at the advent of fumigant technology, current outreach must be directed toward making growers comfortable with transitioning to using chemicals or management systems other than methyl bromide. As stated above, many of the nonchemical nematode management practices will require specific information about the nematode, such as accurate species identification, host range, life cycle, survival strategies, and longevity. When using management practices other than soil fumigation, growers will need a basic knowledge of nematode biology and access to resources such as nematode identification services. Plant breeders and scientists from other disciplines will need to work in teams with field-savvy nematologists to develop and implement alternative nematode management strategies. The expectation that these services and this expertise will be available are not a given in a future where fewer nematology positions are being filled and less money is being spent on nematode taxonomy, extension, and applied research.

It is likely that we cannot yet foresee all the challenges that we will face in managing plant-parasitic nematodes without methyl bromide. The change from methyl bromide fumigation to another nematode management practice is expected to create changes in pest species diversity and density, and possibly result in the emergence of different pest problems over time (75). If we look toward those parts of the agricultural sector that have not relied on methyl bromide, we are provided with a glimpse of a future without methyl bromide. An international survey (92) determined annual crop losses due to nematodes as: cotton, 10.7%; peanut, 12%; wheat, 7%; and soybean, 10.6%. The bottom line is that we struggle to control plant-parasitic

nematodes in all crops, and this struggle will be no different for U.S. high-value crop production systems that have been reliant on methyl bromide for decades.

SUMMARY POINTS

1. Methyl bromide is classified as a restricted-use pesticide and was registered for use in the United States in 1961 as an effective herbicide, nematocide, insecticide, and fungicide.
2. Initially a 100% reduction of methyl bromide use from the 1991 domestic production level was scheduled for 2005 in developed countries and 2015 in developing countries, but as of 2008 the fumigant was still being used in the United States, Australia, Canada, and Japan.
3. High-input, high-value crop production systems, including vegetables, nurseries, ornamentals, tree fruits, and grapes, have relied heavily upon methyl bromide for plant-parasitic nematode control and will be the most challenged by the loss of methyl bromide.
4. Research indicates that the future of nematode control will depend more on integrated techniques that incorporate cultural practices, genetic resistance, and alternative pesticides.

FUTURE ISSUES

1. Federal, state, and international regulations regarding soil fumigants used to control plant-parasitic nematodes are likely to become more restrictive in the future.
2. An increased need for nematological expertise in response to adoption of methyl bromide alternatives will occur at a time when fewer nematology positions are being filled and less money is being spent on nematode taxonomy, extension, and applied research.

DISCLOSURE STATEMENT

Mention of trade names or commercial products in this article is solely for the purpose of providing specific information and does not imply recommendation or endorsement by the U.S. Department of Agriculture.

LITERATURE CITED

1. Ajwa HA, Trout T, Mueller J, Wilhelm S, Nelson SD, et al. 2002. Application of alternative fumigants through drip irrigation systems. *Phytopathology* 92:1349–55
2. Ajwa HA, Klose S, Nelson SD, Minuto A, Gullino ML, et al. 2003. Alternatives to methyl bromide in strawberry production in the United States of America and the Mediterranean region. *Phytopathol. Mediterr.* 42:220–44
3. Andersen SO, Sarma KM. 2002. *Protecting the Ozone Layer: The United Nations History*. London: Earthscan Publ. Ltd. 490 pp.
4. Anwar SA, McKenry MV. 2002. Penetration and development of *Meloidogyne arenaria* on two new grape rootstocks. *J. Nematol.* 34:143–145
5. Anwar SA, McKenry MV, Ramming D. 2002. A search for more durable grape rootstock resistance to root knot nematode. *Am. J. Enol. Vitic.* 53:9–23

6. Atkinson HJ, Urwin PE, McPherson MJ. 2003. Engineering plants for nematode resistance. *Annu. Rev. Phytopathol.* 41:615–39
7. Bent AF, Mackey D. 2007. Elicitors, effectors, and R genes: the new paradigm and a lifetime supply of questions. *Ann. Rev. Phytopathol.* 45:399–436
8. Bello A, Lopez-Perez JA, Garcia-Alvarez A, Sanz R, Lacasa A. 2004. Biofumigation and nematode control in the Mediterranean region. In *Nematology Monographs and Perspectives: Proceedings of the 4th International Congress of Nematology*, ed. R Cook, DJ Hunt, pp. 133–149. Leiden: Brill
9. Brennen R. 2008. EPA update: critical use exemptions. *Annu. Int. Res. Conf. Methyl Bromide Altern. Emiss. Reduct., Orlando, FL*. <http://mbao.org>
10. Brooks RM, Olmo HP. 1961. Register of new fruit and nut varieties. List 16. *Proc. Am. Soc. Hortic. Sci.* 78:225–229
11. Brown DLF, Halbrendt JM, Jones AT, Vrain TC, Robbins RT. 1994. Transmission of three North American nepoviruses by populations of four distinct species of the *Xiphinema americanum* group. *Phytopathology* 84:646–49
12. Brunt AA, Crabtree K, Dallwitz MJ, Gibbs AJ, Watson L, et al. 1996. *Plant Viruses Online: Descriptions and Lists from the VIDE Database*. <http://www.agls.uidaho.edu/ebi/vdic/refs.htm>
13. Bullock DG. 1992. Crop rotation. *Crit. Rev. Plant Sci.* 11:309–26
14. Burelle N. 2005. Review of the non-fumigant nematicides oxamyl and fosthiazate. *Annu. Int. Res. Conf. Methyl Bromide Altern. Emiss. Reduct., San Diego, CA. Abstr. 110*. <http://mbao.org>
15. Burelle NK, Bausher MG, Roskopf EN. 2009. Greenhouse evaluation of *Capsicum* rootstocks for management of *Meloidogyne incognita* on grafted bell pepper. *Nematropica* 39:121–32
16. Busacca J. 2009. Surfuryl fluoride: summary of field trials in Florida and Georgia. *Annu. Int. Res. Conf. Methyl Bromide Altern. Emiss. Reduct., San Diego, CA. Abstr. 23*. <http://mbao.org>
17. Butler DM, Roskopf EN, Kokalis-Burelle N, Muramoto J, Shennan C. 2009. Field evaluation of anaerobic soil disinfestations in a bell pepper–eggplant double crop. *Annu. Int. Res. Conf. Methyl Bromide Altern. Emiss. Reduct., San Diego, CA. Abstr. 43*. <http://www.mbao.org>
18. California Department of Food and Agriculture. 2009. *Nursery Inspection Procedures Manual*. <http://www.cdffa.ca.gov/phpps/pe/Nursery/NIPM.html>
19. Carpenter J, Gianessi L, Lynch L. 2000. *The Economic Impact of the Scheduled Phase-out of Methyl Bromide in the U.S.* Washington, DC: Nat. Cent. Food Agric. Pol. 466 pp.
20. Carpenter J, Lynch L, Trout T. 2001. Township limits on 1,3-D will impact adjustment to methyl bromide phase-out. *Calif. Agric.* 55:12–18
21. Castelli L, Bryan G, Blok VL, Ramsay G, Phillips MS. 2005. Investigation of resistance specificity amongst fifteen wild *Solanum* species to a range of *Globodera pallida* and *G. rostochiensis* populations. *Nematology* 7:689–99
22. Chapman PJ. 1983. The effectiveness of 1,3-dichloropropene for controlling virus vector nematodes with reference to the MAFF certification scheme for strawberry nursery stock. *Plant Pathol.* 32:273–79
23. Chellemi DO, Olson SM, Mitchell DJ, Secker I, McSorley R. 1997. Adaptation of soil solarization to the integrated management of soilborne pests of tomato under humid conditions. *Phytopathology* 87:250–58
24. Christie JR, Cobb GS. 1940. The inefficiency of methyl bromide fumigation against the chrysanthemum foliar nematode. *Proc. Helminthol. Soc. Wash.* 7:62
25. Church GT, Roskopf EN, Holzinger J. 2004. Evaluation of DMDS for production of ornamental cockscomb (*Celosia argentea*). *Annu. Int. Res. Conf. Methyl Bromide Altern. Emiss. Reduct., Orlando, FL, Abstr. 87*. <http://mbao.org>
26. Conklin HC. 1961. The study of shifting cultivation. *Curr. Anthropol.* 2:27–61
27. Craig SC, Saxton AM, Sams CE. 2005. Relationship of climate and genotype to seasonal variation in the glucosinolate-myrosinase system. I. Glucosinolate content in ten cultivars of *Brassica oleracea* grown in fall and spring seasons. *J. Sci. Food Agric.* 85:671–81
28. Dale A, Potter JW. 1998. Strawberry cultivars vary in their resistance to northern lesion nematode. *J. Nematol.* 30:577–80
29. De la Vega GE. 2006. *Royal Commentaries of the Incas and General History of Peru, Abridged*. Indianapolis, IN: Hackett Publ. 232 pp.

30. Desaegeer JAJ, Eger JE, Csinos AS, Gilreath JP, Olson SM, Webster TM. Movement and biological activity of drip-applied 1,3-dichloropropene and chloropicrin in raised mulched beds in the southeastern USA. *Pest Manag. Sci.* 60:1220–1230
31. Dungan RS, Gan J, Yates SR. 2001. Effect of temperature, organic amendment rate and moisture content on the degradation of 1,3-dichloropropene in soil. *Pest Manag. Sci.* 57:1107–13
32. Duniway JM. 2002. Status of chemical alternatives to methyl bromide for pre-plant fumigation of soil. *Phytopathology* 92:1337–43
33. Edwards W, Jones H, Schmitt DP. 1985. Host suitability and parasitism of selected strawberry cultivars by *Meloidogyne hapla* and *M. incognita*. *Plant Dis.* 69:40–42
34. Eger JE, Gilreath JP, Noling JW. 2001. Effect of irrigation times on wetting patterns in Florida vegetable soils. *Annu. Int. Res. Conf. Methyl Bromide Altern. Emiss. Reduct., San Diego, CA, Abstr.* 48. <http://mbao.org>
35. Esmenjaud D, Voisin R, Van Ghelder C, Bosselut N, Lafargue B, et al. 2009. Genetic dissection of resistance to root-knot nematodes *Meloidogyne* spp. in plum, peach, almond, and apricot from various segregating interspecific *Prunus* progenies. *Tree Genet. Genomes* 5:279–89
36. European Mediterranean Plant Protection Organization. 2008. Certification scheme for strawberry. *EPPO Bull.* 38:430–37
37. Feeny P. 1977. Defensive ecology of the Cruciferae. *Ann. Missouri Bot. Gard.* 64:221–34
38. Felipe AJ. 2009. “Felinem,” “Garnem,” and “Monegro” almond x peach hybrid rootstocks. *HortScience* 44:196–97
39. Flint ML. 2002. Integrated pest management for almonds, *Univ. Calif. Ag. Nat. Res. Pub.* 3308. p. 199, 2nd ed.
40. Gan J, Yates SR, Papiernik S, Crowley D. 1998. Application of organic amendments to reduce volatile pesticide emissions from soil. *Environ. Sci. Technol.* 32:3094–98
41. Gao S, Trout TJ. 2006. Using surface water application to reduce 1,3-dichloropropene emission from soil fumigation. *J. Environ. Qual.* 35:1040–48
42. Gao S, Qin R, McDonald JA, Hanson BD, Trout TJ. 2008. Field tests of surface seals and soil treatments to reduce fumigant emissions from shank injection of Telone C35. *Sci. Total Environ.* 405:206–14
43. Gilbert C, Fennimore S, Subbarao K, Hanson B, Rainbolt C, et al. 2009. Systems to disinfest soil with heat for strawberry and flower production. *Annu. Int. Res. Conf. Methyl Bromide Altern. Emiss. Reduct., Orlando, FL, Abstr.* 15. <http://mbao.org>
44. Gilreath JP, Santos BM, Busacca JD, Eger JE, Mirusso JM, et al. 2006. Validating broadcast application of Telone C-35 complemented with chloropicrin and herbicides in commercial tomato farms. *Crop Prot.* 25:79–82
45. Gilreath J, Jones J, Motis T, Santos B, Noling J, et al. 2003. Evaluation of various chemical treatments for potential as methyl bromide replacements for disinfestations of soilborne pests in polyethylene-mulched tomato. *Proc. Fl. State Hort. Soc.* 116:151–58
46. Gilreath JP, Santos BM. 2004. Methyl bromide alternatives for bell pepper (*Capsicum annuum*) and cucumber (*Cucumis sativus*) rotations. *Crop Prot.* 23:347–51
47. Gilreath JP, Motis TN, Santos BM, Mirusso JM, Gilreath PR, et al. 2005. Influence of supplementary in-bed chloropicrin application on soilborne pest control in tomato (*Lycopersicon esculentum*). *Crop Prot.* 24:779–84
48. Gilreath JP, Santos BM. 2008. Managing weeds and nematodes with combinations of methyl bromide alternatives in tomato. *Crop Prot.* 27:648–52
49. Halbrendt JM, Jing G. 1994. Nematode suppressive rotation crops for orchard renovation. *Acta. Hort.* 363:49–56
50. Halbrendt JM. 1996. Allelopathy in the management of plant-parasitic nematodes. *J. Nematol.* 28:8–14
51. Halbrendt JM. 2003. Nematodes. In *Concise Encyclopedia of Temperate Zone Tree Fruits*, ed. T Baugher, S Singha, pp. 177–184. Binghamton, NY: Haworth Press
52. Halbrendt JM, LaMondia JA. 2004. Crop rotation and other cultural practices. In *Nematology, Advances and Perspectives, Vol. 2: Nematode Management and Utilization*, ed. ZX Chen, SY Chen, DW Dickson, pp. 909–930. Wallingford/Cambridge, UK: CABI Publ.

53. Hanson BD, Gao S, Gerik J, Wang D, Qin R. 2008. Pest control with California approved nursery stock certification 1,3-D treatments. *Annu. Int. Res. Conf. Methyl Bromide Altern. Emiss. Reduct., Orlando, FL, Abstr. 25*. <http://mbao.org>
54. Hopkins RJ, van Dam NM, van Loon JJA. 2009. Role of glucosinolates in insect-plant relationships and multitrophic interactions. *Annu. Rev. Entomol.* 54:57–83
55. Katan J, Greenberger A, Alon H, Grinstein A. 1976. Solar heating by polyethylene mulching for the control of diseases caused by soilborne pathogens. *Phytopathology* 66:683–88
56. Kester DE, Asay RN. 1986. Hansen 2168 and Hansen 536: two new *Prunus* rootstock clones. *HortScience* 21:331–332
57. Kirkegaard JA, Gardner PA, Desmarchelier JM, Angus JF. 1993. Biofumigation: using *Brassica* species to control pests and diseases in horticulture and agriculture. In *Proc. 9th Aust. Res. Assem. Brassicas*, ed. N Wratten, R Mailer, pp. 77–82. Wagga Wagga, NSW: NSW Agric.
58. Kubota C, McClure MA, Kokalis-Burelle N, Bausher MG, Roskopf EN. 2008. Vegetable grafting: history, use, and current technology status in North America. *Hortscience* 43:1664–69
59. LaMondia JA, Cowles RS, Los L. 2005. Prevalence and potential impact of soil-dwelling pests in strawberry fields. *HortScience* 40:1366–70
60. Lawrence L, Matthiessen J. 2004. Biofumigation: using *Brassica* rotations to manage soil-borne pests and diseases. *Outlooks Pest Manag.* 15:42–44
61. Lazzeri L, Baruzzi G, Malaguti L, Antoniaci L. 2003. Replacing methyl bromide in strawberry production. *Pest Manag. Sci.* 59:983–90
62. Martin FN. 2003. Development of alternative strategies for management of soilborne pathogens currently controlled with methyl bromide. *Annu. Rev. Phytopathol.* 41:325–50
63. Matthiessen JN, Warton B, Shackleton MA. 2004. The importance of plant maceration and water addition in achieving high *Brassica*-derived isothiocyanate levels in soil. *Agroindustria* 3:277–80
64. McKenry MV. 1994. Nematicides. In *Encyclopedia of Agriculture Science*, ed. CJ Arntzen, 3:87–95. San Diego, CA: Acad. Inc.
65. McKenry MV, Buzo T, Kretsch J, Kaku S, Otomo E, et al. 1994. Soil fumigants provide multiple benefits: alternatives give mixed results. *Calif. Agric.* 48:22–28
66. McKenry MV, Hutmacher B, Trout T. 1998. Nematicidal value of eighteen pre-plant treatments one year after replanting susceptible and resistant peach rootstocks. *Annu. Int. Res. Conf. Methyl Bromide Altern. Emiss. Reduct., Orlando, FL, Abstr. 34*. <http://www.mbao.org>
67. McKenry MV. 1999. *The Replant Problem and Its Management*. Fresno, CA: Catalina Publ. 124 pp.
68. McKenry MV, Luvisi D, Anwar SA, Schrader P, Kaku S. 2004. Eight-year nematode study from uniformly designed rootstock trials in fifteen table grape vineyards. *Am. J. Enol. Vitic.* 55:218–227
69. McKenry MV, Buzo T. 2009. Evaluation of “starve and switch” approach to replanting trees. *Annu. Int. Res. Conf. Methyl Bromide Altern. Emiss. Reduct., San Diego, CA, Abstr. 48*. <http://mbao.org>
70. Morgan DO. 1925. Investigations on eelworm in potatoes in south Lincolnshire. *J. Helminthol.* 3:185–92
71. Needham T. 1743. A letter concerning certain chalky tubulous concretions called malm; with some microscopical observations on the farina of the red lily, and of worms discovered in smutty corn. *Philos. Trans. R. Soc.* 42:173,174; 634–41
72. *New York Times*. 1947. Treatment of soil. Jan. 26
73. Noling JW. 2000. Effects of continuous culture of a resistance tomato cultivar on *Meloidogyne incognita* soil population densities and pathogenicity. *J. Nematol.* 32:452
74. Noling JW, Gilreath JP, Eger JE. 2001. Effect of irrigation volume on wetting patterns in Florida vegetable soils. *Annu. Int. Res. Conf. Methyl Bromide Altern. Emiss. Reduct., San Diego, CA, Abstr. 49*. <http://mbao.org>
75. Noling JW. 2002. The practical realities of alternatives to methyl bromide: concluding remarks. *Phytopathology* 92:1373–75
76. Noling JW, Gilreath JP, Nance J. 2003. Influence of soil compaction layers on fumigant diffusion in soil. *Annu. Int. Res. Conf. Methyl Bromide Altern. Emiss. Reduct., San Diego, CA, Abstr. 38*. <http://mbao.org>
77. Ntow WJ, Ajwa H. 2009. Behavior of fumigants in soil. In *Recent Developments in Management of Plant Disease*, ed. U Gisi, I Chet, M Lodovica Gullino, pp. 329–48. New York: Springer

78. Nyczepir AP, Halbrecht JM. 1993. Nematode parasites of fruit trees. In *Plant Parasitic Nematodes in Temperate Agriculture*, ed. K Evans, D Trudgill, J Webster, pp. 381–425. Wallingford, UK: CAB Intl.
79. Nyczepir AP, Rodríguez-Kábana R. 2007. Preplant biofumigation with sorghum or methyl bromide compared for managing *Criconeimoides xenoplax* in a young peach orchard. *Plant Dis.* 91:1607–11
80. Ohr HD, Sims JJ, Grech NM, Becker JO, McGriffen ME Jr. 1996. Methyl iodide, an ozone-safe alternative to methyl bromide as a soil fumigant. *Plant Dis.* 80:731–35
81. Papiernik SK, Yates SR, Dungan RS, Lesch SM, Zheng W, Guo M. 2004. Effect of surface tarp on emissions and distribution of drip-applied fumigants. *Environ. Sci. Technol.* 38:4254–62
82. Ploeg A. 2008. Biofumigation to manage plant-parasitic nematodes. In *Integrated Management and Biocontrol of Vegetable and Grain Crop Nematodes*, ed. A Ciancio, KG Mukerji, pp. 239–48. Dordrecht: Springer
83. Porter I, Mattner S, Mann R, Gounder R. 2006. Strawberry nurseries: summaries of alternatives and trials in different geographic regions. *Acta Horticult.* 708:187–92
84. Powell CA, Forer LB, Stouffer RF. 1982. Reservoirs of tomato ringspot virus in fruit orchards. *Plant Dis.* 66:583–84
85. Qin R, Gao S, McDonald JA, Ajwa H, Shem-Tov S, et al. 2008. Effect of plastic tarps over raised-beds and potassium thiosulfate in furrows on chloropicrin emissions from drip fumigated fields. *Chemosphere* 72:558–63
86. Rashed NA, MacDonald MH, Matthews BF. 2008. Protease inhibitor expression in soybean roots exhibiting susceptible and resistant interactions with soybean cyst nematode. *J. Nematol.* 40:138–46
87. Ristaino JB, Thomas W. 1997. Agriculture, methyl bromide, and the ozone hole: can we fill the gaps. *Plant Dis.* 81:964–77
88. Roberts PA. 1992. Current status of the availability, development, and use of host plant-resistance to nematodes. *J. Nematol.* 24:213–27
89. Rodríguez-Kábana R, Canullo GH. 1992. Cropping systems for the management of phytonematodes. *Phytoparasitica* 20:211–24
90. Rosskopf EN, Chellemi DO, Kokalis-Burelle N, Church GT. 2005. Alternatives to methyl bromide: a Florida perspective. *Plant Health Prog.* doi:10.1094/PHP-2005-1027-01-RV
91. Sang JP, Minchinton IR, Johnstone PK, Truscott RJW. 1984. Glucosinolate profiles in the seed, root, and leaf tissue of cabbage, mustard, rapeseed, radish and swede. *Can. J. Plant Sci.* 64:77–93
92. Sasser JN, Freckman DW. 1987. A world perspective on nematology: the role of society. In *Vistas on Nematology*, ed. JA Veech, DW Dickson, pp. 7–14. Maryland: Soc. Nematol.
93. Schneider SM, Rosskopf EN, Leesch JG, Chellemi DO, Bull CT, et al. 2003. United States Department of Agriculture—Agricultural Research Service research on alternatives to methyl bromide: pre-plant and post-harvest. *Pest Manag. Sci.* 59:814–26
94. Schneider SM, Ajwa HA, Trout TJ, Gao S. 2008. Nematode control from shank- and drip-applied fumigant alternatives to methyl bromide. *HortScience* 6:1826–32
95. Schneider SM, Hanson BD. 2009. Effects of fumigant alternatives to methyl bromide on pest control in a deciduous fruit and nut plant nursery. *HortTechnology* 19:526–32
96. Schneider SM, Hanson BD, Gerik JS, Trout TJ, Shrestha A, Gao S. 2009. Comparison of shank- and drip-applied methyl bromide alternatives in perennial crop field nurseries. *HortTechnology* 19:331–39
97. Shennan C, Muramoto J, Koike ST, Daugovish O. 2009. Optimizing anaerobic soil disinfestation for non-fumigated strawberry production in California. *Annu. Int. Res. Conf. Methyl Bromide Altern. Emiss. Reduct., San Diego, CA. Abstr. 101.* <http://www.mbao.org>
98. Stapleton JJ, DeVay JE. 1983. Response of phytoparasitic and free-living nematodes to soil solarization and 1,3-dichloropropene in California. *Phytopathology* 73:1429–36
99. Stapleton JJ, Heald CM. 1987. Management of phytoparasitic nematodes by soil solarization. In *Solarization*, ed. J Katan, JE DeVay, pp. 51–60. Boca Raton: CRC Press
100. Stapleton JJ. 2000. Soil solarization in various agricultural production systems. *Crop. Protect.* 19:837–41
101. Sterling GR, Sterling AM. 2003. The potential of *Brassica* green manure crops for controlling root-knot nematode (*Meloidogyne javanica*) on horticultural crops in a subtropical environment. *Aust. J. Exper. Agric.* 43:623–30
102. Taylor AL, McBeth CW. 1940. Preliminary tests of methyl bromide as a nematicide. *Proc. Helminthol. Soc. Wash.* 7:93–96

103. Taylor AL, McBeth CW. 1941. A practical method of using methyl bromide as a nematocide in the field. *Proc. Helminthol. Soc. Wash.* 8:26–28
104. Taylor AL. 2003. Nematocides and nematicides—a history. *Nematropica* 33:225–32
105. Thies JA, Ariss J. 2009. Comparison between the N and Me3 genes conferring resistance to the root-knot nematode (*Meloidogyne incognita*) in genetically different pepper lines (*Capsicum annuum*). *Europ. J. Plant Pathol.* 125:545–50
106. Thomas WB. 1996. Methyl bromide: effective pest management tool and environmental threat. *J. Nematol.* 28:586–89
107. Thurston HD. 1992. Sustainable practices for plant disease management in traditional farming systems. Boulder: Westview. 280 pp.
108. Trout T, Schneider S, Ajwa H, Gartung J. 2003. Fumigation and fallowing effects on replant problems in California Peach. *Annu. Int. Res. Conf. Methyl Bromide Altern. Emiss. Reduct., San Diego, CA. Abstr.* 55. <http://mbao.org>
109. UN Environ. Prog. 2000. *Montreal Protocol on Substances that Deplete the Ozone Layer*. <http://www.unep.org/OZONE/pdfs/Montreal-Protocol2000.pdf>
110. US Dept. Agric. 2007. *Nursery Crops 2006 Summary*. US Dept. Agric., NASS Sp Cr 6–3(07)
111. US Dept. Agric. 2008. *Florida Vegetables*. US Dept. Agric., NASS. http://www.nass.usda.gov/Statistics_by_State/Florida/Publications/Vegetables/apv/vegapv08.pdf
112. US Environ. Prot. Agency. 1986. *Pesticide Fact Sheet Number 98: Methyl Bromide*. Washington DC: U.S. Gov. Print. Off.
113. US Environ. Prot. Agency. 2009. *Extension and Conditional Registration of Iodomethane (Methyl Iodide)*. http://www.epa.gov/opp00001/factsheets/iodomethane_fs.htm
114. US Environ. Prot. Agency. 2009. *Implementation of Risk Mitigation Measures for Soil Fumigant Pesticides*. http://www.epa.gov/opprrrd1/reregistration/soil_fumigants/
115. US Environ. Prot. Agency. 2009. *Buffer Zones Fact Sheet*. http://www.epa.gov/opprrrd1/reregistration/soil_fumigants/buffer-zones-fs.htm
116. Walker A. 2006. New nematode-resistant grape rootstocks are nearing release. *Found. Plant Serv. Grape Prog. Newslet.* pp. 8–10
117. Wang K-H, McSorley R. 2008. Exposure time to lethal temperatures for *Meloidogyne incognita* suppression and its implication for soil solarization. *J. Nematol.* 40:7–12
118. Wang Q, Gan J, Papiernik SK, Yates SR. 2000. Transformation and detoxification of halogenated fumigants by ammonium thiosulfate. *Environ. Sci. Technol.* 34:3717–21
119. Widmer TL, Abawi GS. 2002. Relationship between levels of cyanide in sudangrass hybrids incorporated into soil and suppression of *Meloidogyne hapla*. *J. Nematol.* 34:16–22
120. Wilhelm S. 1967. Bringing our knowledge up to date on soil fumigation. *California Strawberry Advisory Board, Strawberry News Bull.* 13:5
121. Williamson VM. 1998. Root-knot nematode resistance genes in tomato and their potential for future use. *Annu. Rev. Phytopathol.* 36:277–93
122. Williamson VM, Kumar A. 2006. Nematode resistance in plants: the battle underground. *Trends Genet.* 22:396–403
123. Wu XS, Blake S, Sleper DA, Shannon JG, Cregan P, et al. 2009. QTL, additive and epistatic effects for SCN resistance in PI 437654. *Theor. Appl. Genet.* 118:1093–105
124. Yates SR, Gan J, Papiernik SK, Dungan R, Wang D. 2002. Reducing fumigant emissions after soil application. *Phytopathology* 92:1344–48
125. Zasada IA, Ferris H. 2003. Sensitivity of *Meloidogyne javanica* and *Tylenchulus semipenetrans* to isothiocyanates in laboratory assays. *Phytopathology* 93:747–50
126. Zasada IA, Ferris H, Elmore CL, Roncoroni JA, MacDonald JD, et al. 2003. Field application of brassica-ceous amendments for control of soilborne pests and pathogens. *Plant Health Progress* doi:10.1094/PHP-2003-1120-01-RS



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Errata

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