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Biodegradation and enhanced biodegradation: a reason for reduced biological efficacy of nematicides

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Summary. The phenomenon of enhanced biodegradation of fumigant and non-fumigant nematicides is reviewed. Several cases of reduced nematode control have been linked with rapid microbial degradation of nematicides by a specialized fraction of the soil microflora that has adapted to rapidly metabolize specific nematicides. The mechanisms involved in the development of enhanced degradation are described. High soil pH and optimal moisture and temperature conditions favour the development of enhanced biodegradation in soils. However, the persistence of enhanced biodegradation in the absence of further nematicide applications and the existence of cross-enhancement amongst nematicides are the most important factors controlling the practical significance of the phenomenon. The susceptibility shown to enhanced biodegradation by the majority of the currently available nematicides might intensify the problem in the future compared with the current situation. Sufficient chemical rotation *i.e.*, the use of active ingredients from different chemical groups, in combination with crop rotation and use of resistant cultivars may help to limit the establishment of enhanced biodegradation of nematicides in soils.

Key words: biological efficacy, enhanced biodegradation, nematicides, soil microorganisms.

Annual crop losses due to plant parasitic nematodes have been estimated as $78 billion worldwide (Barker *et al.*, 1998). Prior to the 1960s, control was mainly by crop rotation but more recently a variety of crop methods, including chemicals have been introduced to minimise nematode damage (Evans & Haydock, 1999), and this has focused the interest of researchers and farmers on chemical control.

Resistant cultivars of several crops that offer a satisfactory level of protection against root-knot (*Meloidogyne* spp), cyst (*Globodera* and *Heterodera* spp) and stem nematodes (*Ditylencus dipsaci*) are available to growers. However, resistant cultivars usually offer protection against one species of nematodes *i.e.*, the potato cultivar *Maris Piper* that confers full resistance to *G. rostochiensis* but has no resistance to *G. pallida*. The use of resistant varieties is not always sustainable and there are reports of breakdown in resistance because of high temperatures during the growing season and selection pressure due to large nematode populations (Tzortzakakis & Gowen, 1995). Because of the unpredictable behaviour of resistant varieties and difficulties dealing with cropping systems in intensive agricultural rotations growers have to employ chemical control as the main management scheme against nematodes.

Nematicides (Table 1) are classified according to their mode of delivery as fumigants and non-fumigants. Fumigants (Fig. 1) belong to two different chemical groups: the halogenated aliphatic hydrocarbons such as methyl bromide, 1,3-dichloropropene and chloropicrin, and the methyl isothiocyanate precursor compounds such as dazomet and metham sodium. They are volatile at normal environmental temperatures, volatilise soon after their application, and in their gaseous state kill nematodes. In contrast, non-fumigants (Fig. 2) are acetyl cholinesterase inhibitors that are incorporated in soils as granules and their principal mode of action is by paralyzing nematodes to such an extent that their ability to locate and feed from a suitable host is impaired (Woods *et al.*, 1999).

Also, aldicarb (Osborne, 1973), oxamyl (Evans & Wright, 1982), cadusafos (Ibrahim & Haydock, 1999) and fosthiazate (Woods *et al.*, 1999) have been reported to act by inhibiting nematode hatching. All of the non-fumigant nematicides are either organophosphorus or oxime carbamates that were introduced in the 1960s. Their main advantage was their ability to biodegrade and therefore not to accumulate in undesirable concentration in the environment. Paradoxically, biodegradation, which was initially viewed as a positive process for reducing environmental hazards, has turned into a double-edged sword with the development of enhanced degradation and the concomitant reduction in control of nematodes and other soil-inhabiting pests.

Non-fumigant nematicides are usually applied immediately prior to crop establishment and they have to persist in nematicidal concentrations for at least 6-8 weeks when nematodes are active. However, several reports revealed that some groups of pesticides, including organophosphorus and carbamate nematicides, were degraded at accelerated rates in soils that had a history of previous application of the same chemical. Often but not always, such rapid degradation in the laboratory was associated with ineffective nematode control. Further investigation revealed that the repeated application of the same pesticide to the same field for a number of years resulted in the establishment of an adapted microbial population conferring the catabolic systems to rapidly degrade the applied nematicide (Felsot & Shelton, 1993). Today, microbial adaptation for rapid pesticide metabolism is commonly known as enhanced biodegradation (Kaufman & Edwards, 1983).

The range of chemicals available for nematode control is relatively small compared with the numbers of available insecticides, fungicides and herbicides. Furthermore, only two new active ingredients (cadusafos, fosthiazate) have been introduced into the nematicide market during the last 15 years, and even the more effective ones may be banned due to toxicological and environmental problems (Nordmeyer, 1992). Therefore, the repeated use of the same few nematicides may pose a considerable risk for the development of enhanced biodegradation with the potential to develop into a substantial problem. The objective of this review is to examine the phenomenon of enhanced biodegradation of nematicides from the perspective of its implications for nematode control. This review focuses on different factors that favor or prevent the development of enhanced biodegradation. Also, theoretical and microbial aspects of the phenomenon and proposed means of coping with the problem once establish in the field are discussed. Finally, some positive aspects of enhanced biodegradation are mentioned.

Examples of enhanced biodegradation of nematicides

The first observation of rapid microbial degradation was reported for the herbicide 2,4-D by Audus (1949). However, it was the failure of the insecticide (and occasional nematicide) carbofuran to control corn rootworm (*Diabrotica* sp.) in the 1970s, which invoked the attention of scientists. Further entomological and degradation studies in the laboratory showed the loss of pesticide efficacy resulted from the rapid degradation of carbofuran by a population of soil microorganisms, which was adapted to catabolize carbofuran (Felsot *et al.*, 1981; Felsot *et al.*, 1982). Subsequently, several cases of nematicide failure have been reported and the majority of these were linked with enhanced biodegradation. The purpose of this section is to review such reports and link the phenomenon with field practices and nematode control problems.

Non-Fumigant Organophosphorus Nematicides

Ethoprophos. Ethoprophos is either applied as a granule at the rate of 1.5-10 kg a.i. ha^{-1} or as a liquid suspension at the rate of 5.2-20.8 kg a.i. ha^{-1}. Ethoprophos is useful in treating nematodes in many field cultivations such as potato, tobacco and bananas. The first observation of failure of ethoprophos to control nematodes was by Rhode *et al.* (1980) who reported that ethoprophos was ineffective against root-knot nematodes in a field cropped with corn or peas three years after prior use. This early report was followed by further observations (Smelt *et al.*, 1987) of poor nematode control in potato fields in the Netherlands. Further laboratory investigations revealed that ethoprophos was more rapidly degraded in soil from an annually treated plot than in soils from untreated plots. Similarly, Mojtahedi *et al.* (1991) observed a significant reduction in ethoprophos efficacy against root knot nematodes (*M. chitwoodi*) in soil treated with ethoprophos for the preceding two years. More recent studies (Karpouzas *et al.*, 1999a) in soils collected from a potato monoculture area in northern Greece linked reduced nematicidal performance of ethoprophos with enhanced biodegradation by using both laboratory degradation studies and bioassays with nematodes (Fig. 3) The problem soil had received annual applications of ethoprophos for the previous 30 years and the recommended dose of ethoprophos (5 mg a.i kg^{-1} dry

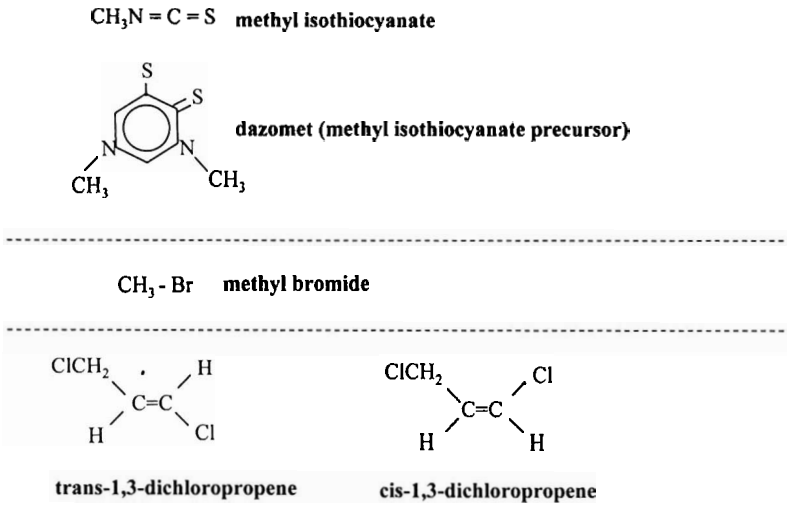

Fig. 1. Chemical structures of some important fumigant nematicides.

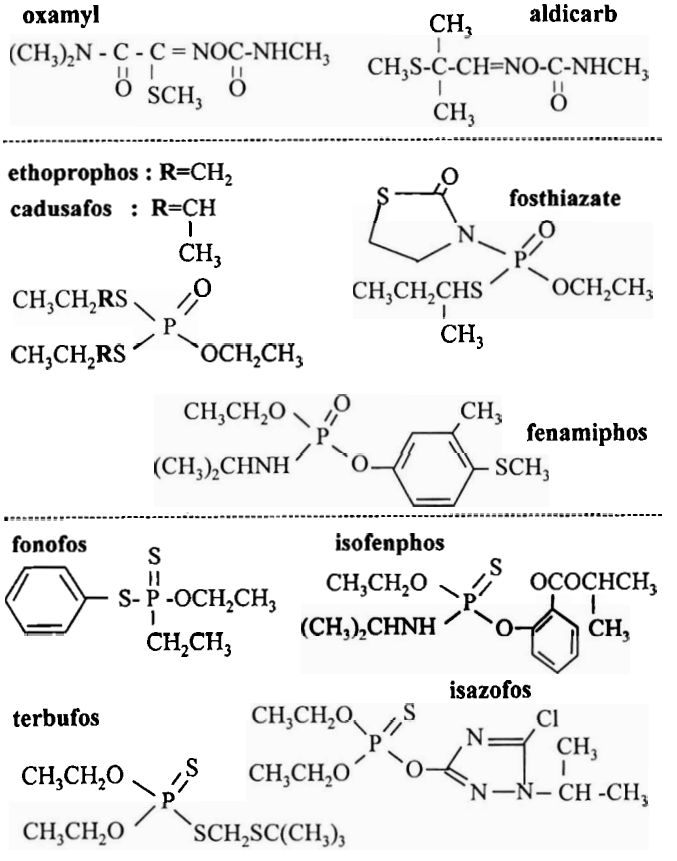

Fig. 2. Chemical structures of some important non-fumigant nematicides.

soil) completely degraded within two weeks of application, compared with only 30% degradation in a previously-untreated soil from the same area.

Fenamiphos. It is a systemic nematicide that can be translocated basipetally in plants (Homeyer, 1971). However, this downward translocation has not provided good results against nematodes. Thus, fenamiphos is mainly applied and rotavated into soil as a broadcast or band treatment either as a granule at the rate of 5-20 kg a.i. ha^{-1}, or as a liquid suspension at the rate of 5.2 kg a.i. ha^{-1}. It is

Table 1. The chemical names and properties of currently used nematicides.

Nematicides	Chemical name	Water solubility (mg l^{-1})	Vapor pressure (mPa)
Ethoprophos	O-ethyl S,S-dipropyl phosphorodithioate	700	46.5 (20°C)
Fenamiphos	Ethyl 4-methylthio-m-tolyl isopropylphosphoramidate	700	0.12 (20°C)
Cadusafos	S,S-di-sec-butyl O-ethyl phosphorodithioate	248	120 (25°C)
Fosthiazate	(RS)-S-sec-butyl O-ethyl 2-oxo-1,3 thiazolidin-3-yl phosphonothioate	9850	0.56 (20°C)
Fonofos	O-ethyl S-phenyl(RS)-ethylphosphonodithioate	13	28 (25°C)
Terbufos	S-tert-butylthiomethyl O,O-diethyl phosphorodithioate	4.5	34.6 (25°C)
Isazofos	O-5-chloro-1-isopropyl-1H-1,2,4-triazol-3-yl O,O-diethyl phosphorothioate	168	7.45 (20°C)
Isofenphos	O-ethyl O-2-isopropoxycarbonylphenyl isopropylphosphoramidothioate	18	0.22 (20°C)
Carbofuran	2, 3-dihydro-2, 2- dimethylbenzofuran-7-yl methylcarbamate	320	0.031 (20°C)
Aldicarb	2-methyl-2-(methylthio)propionaldehyde O-methylcarbamoyloxime	4930	13 (20°C)
Oxamyl	N,N dimethyl-2-methylcarbamoyloxyimino-2-(methylthio) acetamide	280000	31 (25°C)
Methyl bromide	bromomethane	13400	2.27×10^8(25°C)
1,3-D	(EZ)-1,3-dichloropropene	2000	3.7×10^6(20°C)
Dazomet	3,5-dimethyl-1,3,5-thiadiazinane-2-thione	3000	0.37 (20°C)
MITC	Methyl isothiocyanate	8200	2.13×10^6(25°C)

registered for use in field crops at least 60 days prior to harvesting or in greenhouses only at the beginning of cultivation of vegetables that have long growing periods. When degradation of fenamiphos in soil is determined, the two primary oxidation products fenamiphos sulfoxide and fenamiphos sulfone should also be monitored. Both oxidation products have similar nematicidal activity to the parent compound (Waggoner & Khasawinah, 1974). Fenamiphos was first observed failing to control root-knot nematodes in banana plantations to which it was applied three to four times a year (Anderson, 1989). This application strategy led to a gradual decline in the efficacy of fenamiphos. Further laboratory studies, where a soil was treated with fenamiphos every 12-14 weeks, showed that after the third and fourth treatment rates of degradation were 10-20 faster than in the corresponding untreated soils (Anderson & Lafuenza, 1992). However, in the field, development of enhanced biodegradation was slower.

Ou (1991) observed that enhanced biodegradation of total toxic residues (TTR) of fenamiphos (fenamiphos+f.sulfoxide+f.sulfone) occurred in soil after a single field application of fenamiphos to a site cropped with potato. Similar studies were initiated in Australia, where fenamiphos application is a standard practice for the control of root-knot nematodes in tomato, after growers reported loss of nematode control (Striling *et al.*, 1992). A bioassay using the fungal feeding nematode *Aphelenchus avenae* demonstrated that nematicidal activity in the previously treated soil was lost in two weeks, whereas in similar soil that had not been treated before application of fenamiphos retained its nematicidal activity for at least 6 weeks. Further experiments in sterilized and non-sterilized soil provided evidence for the involvement of microorganisms. Enhanced biodegradation of fenamiphos was also measured in soil from a plot treated with fenamiphos four times in two successive years (Davis *et al.*, 1993). The authors suggested that this enhanced degradation was due primarily to an increase in the degradation rate of fenamiphos sulfoxide in the previously-treated soil compared with its degradation in previously-untreated soils. These findings were in agreement with results reported by Ou *et al.* (1994) who noticed that only small amounts of fenamiphos sulfoxide were formed in previously treated soils, even though oxidation of the parent compound was rapid. It was considered that fenamiphos sulfoxide was rapidly hydrolyzed to fenamiphos sulfoxide phenol without undergoing further oxidation to fenamiphos sulfone, and that it was further mineralized by soil microorganisms. In contrast, in the previously untreated soil fenamiphos sulfoxide was also rapidly formed but it was then partly oxidized to fenamiphos sulfone and partly hydrolyzed to the

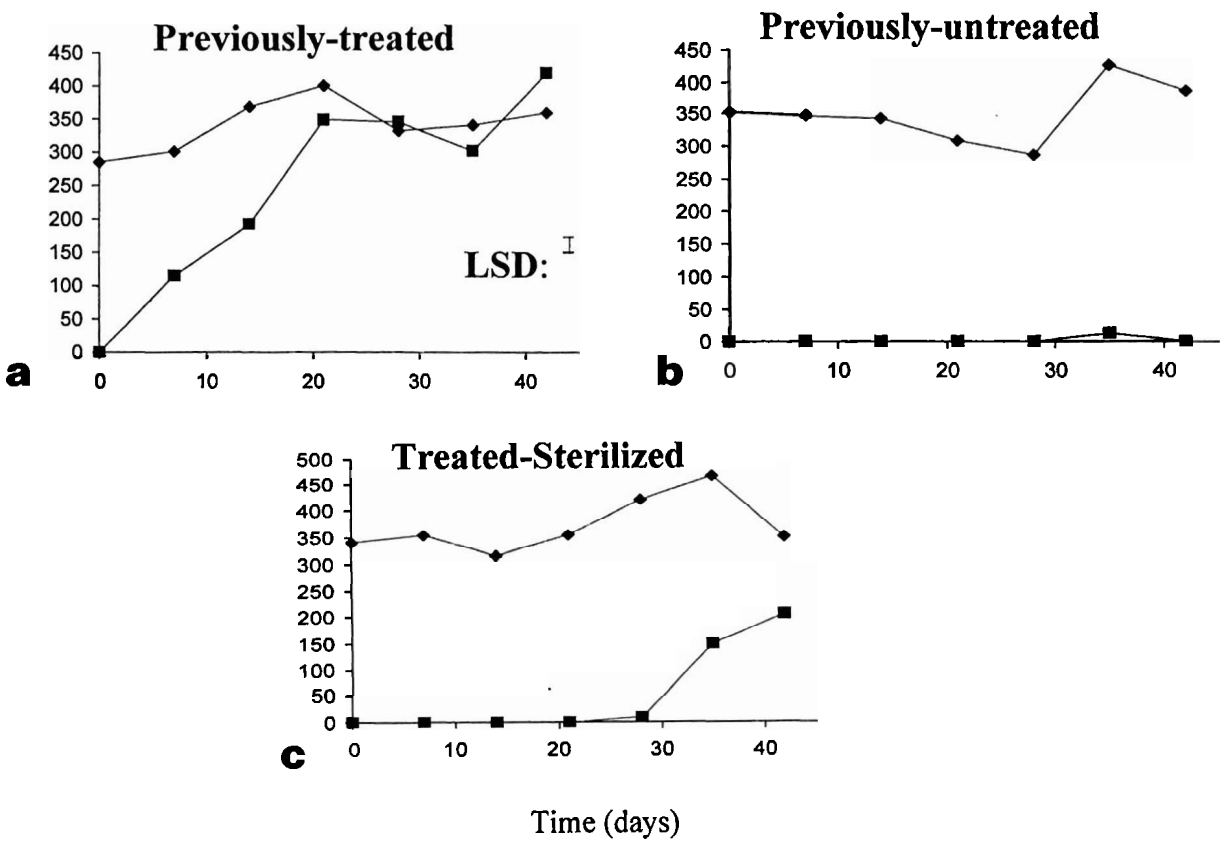

Fig. 3. Numbers of *Meloidogyne javanica* juveniles extracted from soils taken from fields: a, previously treated with ethoprophos for 30 years; b, previously-untreated with ethoprophos; c, previously-treated but sterilized in the laboratory. (■) samples with a fresh addition of 5 mg kg^{-1} ethoprophos; (◆) control samples (0 mg kg^{-1}). Each value is the mean of four replicates. The vertical bar represents the least significant difference (P=0.05) for comparing data points derived by ANOVA following transformation of the data to $\log_{10}(n+1)$ (adapted from Karpouzas *et al.*, 1999a).

corresponding phenol (Chung & Ou, 1996). The metabolic pathway described above is illustrated in Fig. 4.

Although numerous occurrences of reduced nematicidal activity of fenamiphos were reported from the United States and Australia, it was not until 1996 that its failure was first reported in Europe (Smelt *et al.*, 1996). The half-life of the total toxic residues (TTR) of fenamiphos in a soil from an experimental field in the Netherlands was 37 days compared with 75 days in a soil collected from a nearby-untreated plot. Recently, Pattison *et al.* (2000) reported a reduction of fenamiphos performance against burrowing nematodes in several banana plantations in Queensland, Australia. Subsequent bioassay studies showed that within 2 weeks of application the numbers of nematodes surviving in the treated soil (5 mg kg^{-1}) were not significantly different from the numbers in samples not treated with the nematicide. Sterilization of the adapted soil recovered the nematicidal activity of fenamiphos, which then lasted for at least six weeks.

Cadusafos. This substance is a relatively new nematicide *i.e.*, first registered in USA in 1988 (Michell, 1988), and no problems of enhanced biodegradation of cadusafos have been reported. However the similarity of its chemical structure to that of ethoprophos (Fig. 2), which is liable to enhanced biodegradation, suggests that enhanced biodegradation may become a problem in the near future. Significant reductions in nematicidal efficacy of cadusafos have been reported by growers in Northern Greece (Giannakou, per. comm.) and the possibility of the development of enhanced biodegradation in those fields is currently under investigation in our laboratory. In the same area combination of metham sodium with cadusafos greatly increased the level of nematode control

(Giannakou *et al.*, 2002).

Fosthiazate. No reports of reduced biological efficacy of fosthiazate have been reported. However, fosthiazate was first introduced in the market in 1998 (Koyanagi *et al.*, 1998) and as yet no fields have been repeatedly treated with it.

Isofenphos-Fonofos-Terbufos-Isazofos. These organophosphates are registered for the control of soil-dwelling pests and nematodes. However, they are only occasionally used to control nematode infestations. It has been well documented that the insecticidal performance of isofenphos (Abou-Assaf *et al.*, 1986; Chapman *et al.*, 1986a; Niemczyk & Chapman, 1987), fonofos (Racke & Coats, 1988; Wilde, 1990) and terbufos (Horng & Kaufman, 1987) was seriously affected by enhanced biodegradation. Probably, the only reason for the lack of reports associating reduction of nematicidal efficacy of these organophosphates and enhanced biodegradation is their limited use against nematodes. However, repeated applications of isofenphos, fonofos and terbufos as insecticides will probably result in loss of efficacy of subsequent applications of these chemicals for nematode control. The potential of isazofos to undergo enhanced biodegradation was studied by Somasundaram *et al.* (1993) who found that its rapid degradation was biologically mediated, but they could not correlate closely pretreatment history and enhanced biodegradation. They concluded that soil pH was the most important factor controlling rapid degradation, with isazofos degradation being rapid in soils with a pH of 6.9 or higher.

Carbamate nematicides

Aldicarb and Oxamyl. Aldicarb is widely used to control nematodes, and because it moves systemically to the top of the plants insects and mites are also effectively controlled. It is one of the most toxic and also potentially harmful substances used in crop protection with an LD_{50} of about 1 mg kg^{-1}. Aldicarb has a high solubility in water (4930 mg l^{-1}), but oxamyl is much more soluble in water (280000 mg l^{-1}) and breaks down quickly to the relatively non-toxic oxime (Smelt *et al.*, 1983). Studies with oxamyl in moist soils at 15 °C showed its half-life to range between 6 and 39 days (Smelt *et al.*, 1983). In similar studies by Smelt *et al.* (1978) the half-life of aldicarb ranged from 2 to 9 days. However, aldicarb is rapidly oxidized in soils to aldicarb sulfoxide which is then slowly oxidized to aldicarb sulfone. Both aldicarb sulfoxide and sulfone possess nematicidal activity and their concentration should be monitored along with the parent compound TTR. In studies employed by Smelt *et al.* (1978) the TTR of aldicarb monitored in soil samples after 58 days of incubation at 15 °C ranged from 40 to 93% of the initially applied aldicarb and the main component of the TTR was aldicarb suldoxide. Jones & Norris (1998) reviewed the results from more than 30 field studies with aldicarb and reported that the half-life of the TTR of aldicarb ranged from 15-100 days and no parent aldicarb remained 30 days after application. It appears that aldicarb itself is less persistent than oxamyl but its TTR persist in soil much longer than those of oxamyl.

The failure of aldicarb and oxamyl to control nematode infestation was first noted in the Netherlands, where annual application of the chemical for two to three successive years led to a significant decrease in nematode control (Smelt *et al.*, 1987). Laboratory incubation studies revealed that both TTR of aldicarb and oxamyl were degraded more rapidly in samples from the previously treated fields than in the previously untreated controls. The complete inhibition of degradation of both nematicides in steam-sterilized soils established the role of soil microorganisms. Smelt *et al.* (1987) suggested that in previously treated soils, aldicarb was rapidly oxidized to aldicarb sulfoxide, which as soon as it was formed was degraded to less toxic oxime or non-toxic nitriles which were then further mineralized. This metabolic pathway (Fig. 5) was also suggested by Suett & Jukes (1988), who noted that aldicarb failed to control stem nematodes (*Ditylenchus dipsaci*) on strawberries where it had been successfully used once every one or two years for a period of 8 years. TTR of aldicarb completely disappeared within 4 weeks of application, compared with 10% of the initial TTR remaining in the previously untreated soil 8 weeks after the application.

Aharoson & Katan (1993) suggested a different metabolic pathway for aldicarb in soils in Israel previously treated with aldicarb annually for the previous 10 years. They suggested that the major metabolic pathway of aldicarb was its direct hydrolysis to oximes and nitriles, whereas oxidation of aldicarb to the sulfoxide and sulfone metabolites was only a minor metabolic pathway.

The best documented case of enhanced biodegradation of aldicarb was reported by Bromilow *et al.* (1996) who conducted a 20-year study in which aldicarb was applied annually to spring barley at 6 kg a.i ha^{-1}. At the end of the study the hydrolysis of aldicarb sulfoxide and sulfone was 6 and 18 times faster respectively in soil samples col-

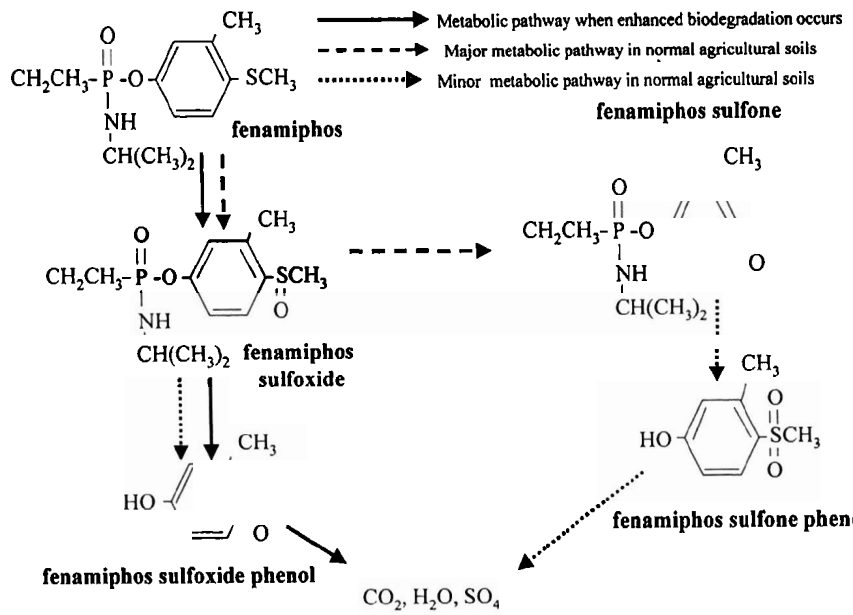

Fig. 4. The metabolic pathway of fenamiphos in a previously treated soil as described by Ou *et al.* (1994).

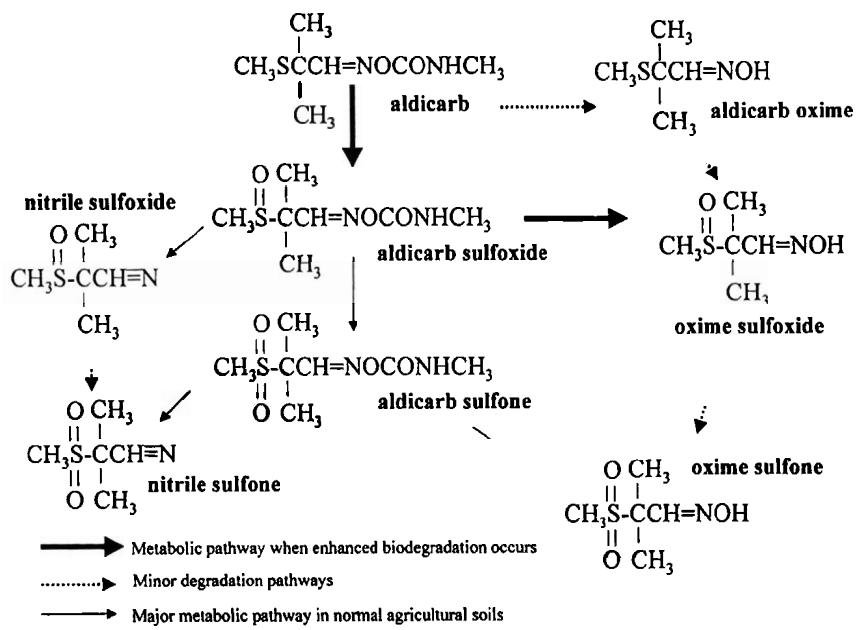

Fig. 5. The metabolic pathway of aldicarb in a previously treated soil as described by Smelt *et al.* (1987).

lected from the treated plot compared to the control plot. However, the development of enhanced biodegradation was relatively slow in the field and aldicarb failed to increase barley yield only in the final 4-year period of the study. Suett *et al.* (1996a) also reported the failure of aldicarb and oxamyl to reduce the population of free-living nematodes in glasshouse rose cultures in the Netherlands.

Carbofuran. It is applied to soil at 5-50 mg ai kg^{-1}. It can persist for 12 to 50 weeks in acidic soils (pH<5.5), but this period is reduced 10 times when the soil is alkaline (pH>7.5) (Hassal, 1990). It has given good control of some important species of nematodes such as *M. incognita* on tomato (Overman & Jones, 1975), and *Radopholus similis* on banana (Gowen, 1975, 1976). This carbamate insecticide-nematicide is one of the most reported

and discussed pesticide as far as enhanced biodegradation is concerned. Carbofuran is only occasionally used as a nematicide. However, in general, the formulation, and time and frequency of application are similar when carbofuran is used against soil-dwelling insects or nematodes. Therefore, the reported cases of failures of carbofuran to control corn rootworm *Diabrotica* sp. (Felsot *et al.*, 1981; Felsot *et al.*, 1982), cabbage root fly (*Delia radicum*) or carrot fly (*Psila rosae*) (Suett, 1986; Suett *et al.*, 1993) highlight the problems that might develop if carbofuran is repeatedly used in the same field for two or more years.

Fumigant nematicides

Methyl bromide. It is a colourless, odourless, highly poisonous gas. It has a boiling point of 4.6 °C and must be applied under polyethylene sheets. It can give very good control of nematodes as it diffuses rapidly and penetrates easily into soil. Production of several high input crops such as vegetables in greenhouses rely on the use of methyl bromide as a general soil sterilant. It was believed that as methyl bromide is a gas (above 4 °C) it does not undergo microbial degradation. However, it is now well documented that soil is a significant sink for methyl bromide as about 50% of the applied dose usually remains in the soil (Shorter *et al.*, 1995) and soil microorganisms are involved in its degradation (Ou *et al.*, 1997). According to Gan *et al.* (1994) methyl bromide is considered to be mainly degraded in soil by chemical hydrolysis and methylation. However, degradation of methyl bromide was greatly stimulated in soil containing methanotrophic microorganisms with the ability to oxidize methyl bromide (Oremland *et al.*, 1994). In a recent study, Ou *et al.* (1997) found that methyl bromide degraded more rapidly in a sandy Florida soil pretreated with ammonium sulphate than in untreated soil. These authors also observed that pretreatment of soils with ammonium sulphate caused a significant decrease in soil pH, but stimulated the activity of ammonia monoxygenases, which oxidized methyl bromide to formaldehyde and bromide ion. In conclusion, degradation of methyl bromide in soils can be stimulated in methanotrophic soils, or soils treated with ammonia containing compounds, where soil microflora can produce methane and ammonia monoxygenases and co-oxidize methyl bromide (Ou, 1998). However, enhanced biodegradation of methyl bromide in soils from field sites that have been treated repeatedly with methyl bromide has not been reported.

1,3-dichloropropene (1,3-D). It was introduced as a soil fumigant by Shell Limited (Cremlyn, 1991). It is injected into the soil at rates of 200-1000 l ha^{-1} and has proved to be a very reliable chemical for the control of many types and different stages of plant parasitic nematodes. Enhanced biodegradation of 1,3-dichlorpropene in soil was not known until 1989, when Lebbink *et al.* (1989) reported that rapid degradation of 1,3-D occurred in soil in a field in the Netherlands that had received annual treatments of 1,3-D for the previous 12 years. Nematicidal activity in the field soil progressively declined with a 70% reduction of efficacy in killing potato cyst nematodes. Parallel studies by Smelt *et al.* (1989) showed that some sandy and reclaimed peat soils in the northeast Netherlands had the ability to rapidly degrade 1,3-D and MITC, regardless of their pretreatment history. Ou *et al.* (1995) conducted similar studies in a soil from Florida, which had received six applications of 1,3-D during a 12-year period. They showed that a 40 mg kg^{-1} dose of the fumigant degraded significantly faster in the soil from the previously-treated as compared to the soil from the previously-untreated site. Moreover, the difference in degradation rates between the treated and the untreated soils had resulted from the faster degradation of the trans-1,3-D in the treated soil as compared with the slower degradation of this isomer in the untreated soil. Degradation rates of the cis-isomer in the treated and untreated soil were similar. Probably, biological hydrolysis was the main factor responsible for enhanced degradation of the trans-isomer in treated soil, but both chemical and biological hydrolysis contributed to degradation of the cis-isomer. These results contrast with those of Smelt *et al.* (1996) who did not find any difference in the degradation rate of the two isomers.

More recent studies, by Verhagen *et al.* (1996) demonstrated that extensive repeated applications of cis-1,3-D at two-month intervals for a period of one year, resulted in the rapid degradation of the isomer as compared with the degradation rate in untreated plots.

Methyl isothiocyanate. It can be applied as a soil drench or injected in the form of metham sodium, or as a powder rotavated into soil in the form of dazomet. Its efficacy in controlling nematodes depends on the type of soil, the humidity and temperature. Recent reports from Australia (Warton *et al.*, 2001) showed enhanced biodegradation of MITC in soils from a carrot farm where metham sodium (methyl isothiocyanate is liberated when

metham sodium comes in contact with moist soil) was regularly applied for nematode control.

Proposed mechanisms explaining the development of enhanced biodegradation

Knowledge of the mechanisms involved in the development of enhanced biodegradation in a field is important for understanding the practical aspects of the relationship between the phenomenon and nematode control. Soil microorganisms can either co-metabolize or mineralize organic substrates (Alexander, 1985). In co-metabolism, the substrates are slowly degraded by soil microorganisms that possess enzymes with broad specificity. Metabolites produced are either resistant to further metabolism, or become bound to soil colloids. Co-metabolism is characterized by the inability of the soil microorganisms to proliferate at the expense of the organic substrate, and with pesticides, the rate of change of concentration in the medium remains relatively constant. Microorganisms that co-metabolize a pesticide usually grow on other carbon or nitrogen substrates that are abundant in soils.

In mineralization, nematicides and other pesticides are rapidly degraded by soil microorganisms which carry specific catabolic enzymes. Metabolites produced are smaller molecules which are further metabolized with concurrent production of energy. The rapid reduction of nematicide concentration in the medium coincides with a similar increase in the population of the microorganisms degrading the nematicide. Microorganisms responsible for pesticide mineralization contain specific enzymic properties and the pesticide is their primary growth substrate. An example of pesticide mineralization is presented in Fig. 6, where rapid degradation of ethoprophos in a selective growth medium coincides with concurrent proliferation of the population of the degrading-microorganism, which was utilising ethoprophos as a carbon source (Karpouzas & Walker, 2000a).

The exact mechanism involved in the development of the phenomenon in the field is not well documented. In enhanced biodegradation of a nematicide an initial lag phase of slow degradation is followed by an extremely rapid phase of degradation. Three mechanisms have been proposed to explain this lag phase following application of the chemical and thus the development of enhanced biodegradation:

1) The lag phase is the time required for an initially small population of the specific degrading microorganisms to proliferate to a threshold population, which is adequate to rapidly metabolize the chemical (Felsot & Shelton, 1993). However, the amount of energy that a pesticide offers to soil microorganisms is minimal to support such substantial changes (Turco & Konopka, 1990). It is possible that this mechanism is important in soils with inherent small populations of specific-pesticide degraders (Hendry & Richardson, 1988).

2) The lag phase is the time required for the induction of specific nematicide-degrading catabolic enzymes in the presence of the nematicide. According to this mechanism the rapid degradation of pesticides results from an increase in the enzymic activity of the indigenous soil microorganisms rather than a population increase. This mechanism offers a satisfactory explanation of the phenomenon in cases where enhanced biodegradation of pesticides was not associated with concurrent increases in the population of the specific pesticide-degrading microorganisms (Merica & Alexander, 1990; Scow *et al.*, 1990).

3) The lag phase is the time required for the evolution and spread of novel catabolic genes as a result of genetic exchanges amongst soil microorganisms. Several soil microorganisms carry sequences in plasmid DNA that encode the production of enzymes responsible for the metabolism of some naturally-occurring soil organic molecules (*e.g.*, xylene) which structurally resemble pesticide molecules (Head *et al.*, 1990). Therefore, a single genetic change may lead to the development of novel catabolic genes encoding pesticide catabolic enzymes.

None of the proposed mechanisms can individually explain the development of enhanced biodegradation in the field, and probably all three mechanisms contribute to the development of the phenomenon.

Factors controlling the development and practical significance of enhanced biodegradation

Laboratory incubation studies have often been employed to measure degradation rates of pesticides in soils collected from a field with pretreatment history. Frequently, laboratory confirmation of enhanced biodegradation is not accompanied by poor field performance. This inconsistency may be explained by the complex interactions between soil-microorganisms and pesticides combined with the effects of various climatic conditions.

Soil factors

The effect of pH on the development of enhanced biodegradation has been stressed by several workers. Read (1987) noticed that soils with pH< 5.6 could not be conditioned for enhanced bio-

Table 2. Isolated bacteria reported to rapidly degrade various nematicides.

Nematicide	Bacteria	Reference
Ethoprophos	*Pseudomonas putida*	Karpouzas *et al.* (2000a)
Fenamiphos	*Arthrobacter* sp.	Ou & Thomas (1994)
Isofenphos	*Corynebacterium* sp.	Murphy & Cohick (1985)
	Streptomyces sp.	Gauger *et al.* (1986)
	Pseudomonas sp.	Racke & Coats (1987)
	Arthrobacter sp.	Racke & Coats (1988)
Carbofuran and Aldicarb	*Achromobacter* sp.	Karns *et al.* (1986)
	Pseudomonas sp.	Chaudhry & Wheeler (1988)
	Flavobacterium sp. *Pseudomonas* sp.	Chaudhry & Ali (1988)
Methyl bromide	*Nitrosomonas europea, Nitrosolobus multiformis*	Rasche *et al.* (1990)
	Methylcoccus capsullatus	Oremland *et al.* (1994)
1,3 - dichloropropene	*Pseudomonas* sp.	Lebbink *et al.* (1989)
	Pseudomonas pavonaceae	Verhagen *et al.* (1995)
	Rhodococcus sp.	Ou *et al.* (2001)

degradation of aldicarb and suggested that repeated applications of aldicarb in such soils is unlikely to result in reduced nematicidal activity. Smelt *et al.* (1996) did not observe enhanced biodegradation of ethoprophos, aldicarb or oxamyl in a soil with pH 5.4, which had been treated annually with the nematicides for the previous 10 years. Similar results were obtained by Karpouzas *et al.* (1999b) who did not observe enhanced biodegradation of ethoprophos in soils that had received annual applications of ethoprophos, or a combination of ethoprophos+carbofuran for the previous seven years. They concluded that the acidic soil pH prevented the development of enhanced biodegradation of ethoprophos and carbofuran. In the same study, enhanced biodegradation of ethoprophos developed after a single field application in a soil with pH 8 compared with 30 years of successive ethoprophos application required for the development of the problem in a soil with pH 5.6. Soil pH probably affects enhanced biodegradation either directly by affecting the chemical stability of the pesticide, or indirectly by affecting the composition and activity of soil microflora (Suett *et al.,* 1996b). Generally, alkaline pH favors bacteria and not fungi and actinomycetes, whereas low pH dramatically reduces bacterial numbers and activity (Burns, 1976). Somasundaram *et al.* (1993) found that rapid degradation of isazofos was associated with pretreated soils with pH>6.9. Similarly, Simon *et al.* (1992) found a good correlation between soil pH and organic matter with degradation rates of fenamiphos.

Jones & Norris (1998) suggested that organic matter content was inversely related to degradation. Soil organic matter has a conflicting double effect on pesticide degradation: soils with high organic matter content are characterized by higher microbial activity, but conversely high organic matter content increases pesticide adsorption resulting in reduced amounts of nematicide in soil solution and therefore reduced bio-availability. Chapman *et al.* (1986b) reported that higher amounts of carbofuran were required to condition an organic soil than a sandy loam soil; presumably, adsorption was greater in the organic than in the sandy loam soil because of higher organic matter content. The effect of soil organic matter on microbial degradation was demonstrated by Karpouzas & Walker (2000b), who found that ethoprophos-degrading microorganisms degraded ethoprophos significantly more slowly when introduced in an organic soil (8.5%), as compared with degradation rates in sandy soils with organic matter contents of 2.3 and 0.3%.

Climatic factors

Factors such as soil moisture and temperature affect rates of degradation and of the development of enhanced biodegradation. Low levels of moisture in soil inhibited the development of enhanced biodegradation of carbofuran (Chapman *et al.,* 1986b). Also, Felsot & Shelton (1993) did not observe enhancement of fonofos degradation when soil, which was treated with the nematicide for the previous five years, was kept at low moisture levels (<15% w/w), whereas enhanced biodegradation was evident when soil moisture was higher (>15-30% w/w). The effect of soil moisture was also demonstrated by Karpouzas & Walker (2000b), where the degrading ability of ethoprophos-degrading microorganisms was significantly impaired

in soils that were kept at low moisture levels (-1500 kPa). Shelton & Parkin (1991) found that mineralization of carbofuran in adapted soils was significantly slower when soils were kept at −700 and −1500 kPa (dry soils). Moisture content affects the rate of biodegradation by influencing the physiological status of the microorganisms. Another effect of soil moisture on degradation rates of nematicides was demonstrated by Chapman *et al.* (1986b) who reported that degradation of carbofuran was not affected by moisture levels when the technical grade was applied. In contrast, slower degradation of carbofuran was observed in the dry soil when granular formulations were applied. These observations suggest that the effect of soil moisture was manifested through an effect on liberation rate from the granules rather than an effect on the physiological status of the microflora.

Jones & Norris (1998) reviewed the effects of several factors on degradation of ethoprophos and aldicarb and concluded that for both nematicides, temperature is the most important variable affecting degradation rates. Low incubation temperatures inhibited the development of enhanced biodegradation of carbofuran (Chapman & Harris, 1990). However, once established enhanced biodegradation of carbofuran was relatively insensitive and microorganisms maintained their ability to degrade carbofuran in enhanced soils after a period of incubation at 3 °C and moisture levels of 4.5%. The effect of soil temperature on microbial degradation of ethoprophos was demonstrated by Karpouzas & Walker (2000b) in soils inoculated with ethoprophos-degrading bacteria. The degradation rate of ethoprophos was reduced at 5°C but not at 20 and 35°C. It can be concluded that enhanced biodegradation of nematicides would develop in soils where moisture and temperature of soil favor microbial growth and activity.

Frequency, rate and formulation of application

From the viewpoint of crop protection, the number of prior treatments required for development of enhanced biodegradation is important. A single application of fenamiphos was adequate to condition a soil for its enhanced biodegradation (Ou, 1991). Conversely, 5 years of annual application of fonofos was necessary for enhanced biodegradation to develop (Felsot & Shelton, 1993). The number of applications needed for enhanced biodegradation to develop appears to depend mainly on the pesticide and on certain soil properties such as pH whose effect has been described previously (Karpouzas *et al.*, 1999b). However, a soil pesticide that is applied 3-4 times a year, *e.g.*, fenamiphos in banana plantations (Anderson & Lafuenza, 1992), is more likely to suffer efficacy problems as compared with other nematicides such as cadusafos or ethoprophos that are applied once a year.

The rate of application may also significantly affect the development of enhanced biodegradation. Read (1987) reported a marked delay in the degradation of aldicarb in previously-treated soils at doses exceeding 750 mg a.i kg^{-1} soil, whereas smaller doses activated soil microflora for rapid degradation. Application of such high doses of aldicarb had adverse effects on bacterial activity and inhibited fungal growth in the soil. Similarly, increasing amounts of ethoprophos (25 mg a.i kg^{-1}) inhibited the enhanced biodegradation of carbofuran (Racke & Coats, 1990). Similar observations were reported by Karpouzas *et al.* (1999b) where repeated applications of ethoprophos led to the accumulation of high ethoprophos residues and a significant reduction in the non-adapted soil microflora. In a subsequent study, Karpouzas & Walker (2000b), observed complete degradation of a 50 mg kg^{-1} dose of ethoprophos in a soil inoculated with ethoprophos-degrading bacteria. Apparently, adapted microorganisms possess the enzymatic mechanisms to rapidly degrade the nematicide, thus circumventing any toxic effects that such a high concentration might impose. Conversely, the non-adapted microorganisms could not rapidly detoxify the high concentrations of ethoprophos and consequently suffered adverse effects. The type of formulation used for nematicide application can also affect the development of enhanced biodegradation. Findings supporting this argument were reported by Chapman & Harris (1990), where enhanced biodegradation of isofenphos was more readily expressed when an analytical formulation instead of the granular formulation was used.

Cross-enhancement

The problem of enhanced biodegradation of nematicides became more acute after observations that a nematicide can be degraded rapidly in soil from a site to which it has never been applied before, but which has been exposed to a pesticide from the same chemical group (Racke & Coats, 1990). Cross conditioning between carbamates is relatively common. Enhanced biodegradation of carbofuran in soils previously treated with aldicarb and oxamyl was reported by Chapman & Harris (1990). Similar cross-adaptation studies revealed increased rates of degradation of aldicarb and oxamyl in soils exhibiting enhanced biodegradation

of carbofuran (Harris *et al.*, 1984). Suett & Jukes (1988) also observed faster degradation of aldicarb after a carbofuran pretreatment as compared with an aldicarb pretreatment. Probably, both oxime carbamate nematicides are liable to cross-enhancement with carbofuran. Also, Smelt *et al.* (1987) observed rapid degradation of aldicarb in an oxamyl field-treated soil and *vice versa*. Therefore, the alternating use of aldicarb or oxamyl should not be encouraged, especially when carbofuran is also used as either an insecticide or nematicide.

In contrast to the carbamate nematicides, there are no reports of cross-enhancement between organophosphorus nematicides. Therefore, Racke & Coats (1988), did not observe increased degradation rates of ethoprophos, fonofos and terbufos in a soil that contained a microbial population with the ability to mineralize 60% of isofenphos within 2 days. Similarly, Anderson & Lafuenza (1992) and more recently Smelt *et al.* (1996) found no evidence of cross-enhancement between fenamiphos and ethoprophos indicating that these two nematicides can be alternated safely. A more recent study (Karpouzas & Walker, 2000c) did not observe any cross-adaptation between ethoprophos and other nematicides such as cadusafos (which is structurally related to ethoprophos), fenamiphos, fonofos and isazofos.

No incidents of cross-enhancement between carbamate and organophosphorus nematicides have been reported. Ethoprophos degraded slowly in soils adapted to rapidly degrade aldicarb or oxamyl (Smelt *et al.*, 1996). Similarly, the degradation rates of aldicarb and oxamyl were not significantly different in soils collected from fields previously treated with ethoprophos and previously-untreated (Karpouzas & Walker, 2000c). Cross enhancement between fumigants 1,3-D and MITC was not observed by Verhagen *et al.* (1996) who reported that application of MITC or 1,3-D alone did not condition soil for enhanced biodegradation of the other. However, frequent alternating use of these fumigants did not decrease the development of enhanced biodegradation for both.

It is possible that similarity in chemical structure may be important in the development of cross-enhancement between carbamates. This is probably the case with aldicarb and oxamyl that are structurally very similar and their hydrolysis leads to the production of similar metabolites which can be further used by the same soil bacteria. Conversely, microbial degradation of organophosphorus nematicides proceeds *via* initial hydrolysis and secondary metabolism of the produced metabolites. As hydrolytic metabolites of organophosphorus nematicides tend to be somewhat unique, this might explain the high specificity of enhanced biodegradation among these compounds (Racke & Coats, 1990).

Stability of enhanced biodegradation

In addition to cross enhancement, another important factor that controls the expression of the phenomenon in the field is its stability. Racke & Coats (1988) reported that soil from a field treated with fonofos for the previous five years lost its capacity to actively degrade fonofos after the winter period. In complementary studies, Chapman & Harris (1990), showed that enhanced biodegradation of fonofos and terbufos lasted for about a year as compared with over three years for isofenphos. Similarly, enhanced biodegradation of fenamiphos persisted in a soil collected three years after the field was previously treated, but disappeared the following year (Ou, 1991). However, Anderson & Lafuenza (1992), found that 12 months after the previous fenamiphos application, field degradation rates of the nematicide were not significantly different in soils from previously treated and untreated fields. Smelt *et al.* (1996) studied the persistence of enhanced biodegradation of aldicarb, oxamyl and ethoprophos in adapted fields in the Netherlands and observed that the phenomenon persisted for at least five years for the oxime carbamates. Conversely, enhanced biodegradation of ethoprophos persisted for at least 3 years, but had disappeared after 5 years. Karpouzas & Walker (2000c), also found that enhanced biodegradation of ethoprophos persisted for at least two years.

Fumigation of adapted soil with 1,3-D, which kills some fungi but only a few bacteria, did not decrease the accelerated degradation of aldicarb and oxamyl (Smelt *et al.*, 1996). In the same study a soil adapted to rapidly degrade 1,3-D, after a five-year interval without further 1,3-D application, did not significantly decrease the degradation rate of the fumigant. These results are in agreement with Verhagen *et al.* (1996) who reported that degradation rates of 1,3-D, in a soil adapted to rapidly degrade the fumigant, had not returned to normal even after a five-year interval without further chemical treatment. However, this time interval was sufficient to obtain a complete recovery of MITC effectiveness in adapted soils.

Agronomic practices

It has been demonstrated that just 0.1 g of soil from an adapted soil added to 1 kg of initially unadapted soil is adequate to transfer ethoprophos-degrading ability (Karpouzas *et al.*, 1999a).

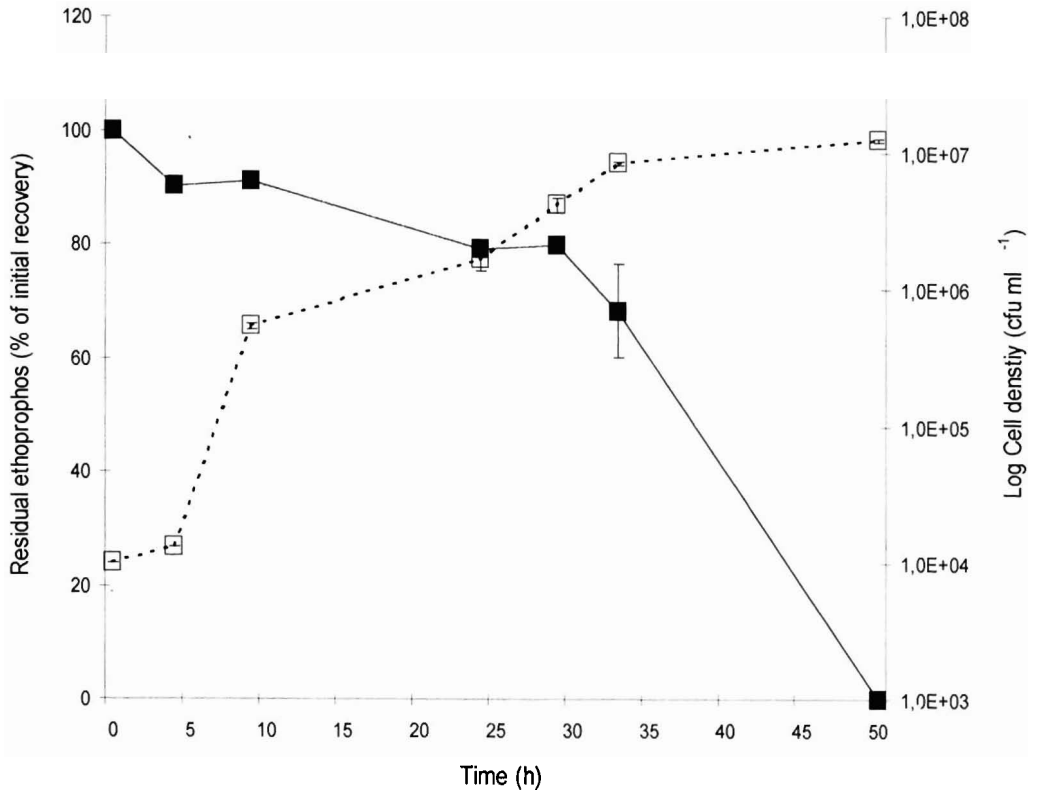

Fig. 6. Degradation of ethoprophos (■) and cell growth (□) of *P. putida* epI in Mineral Salts Medium supplemented with Nitrogen. Each value is the mean of three replicates. Error bars represent the SD of the mean (adapted from Karpouzas & Walker, 2000a).

Therefore, it is possible that enhanced biodegradation problems can be transferred from one field to another on machinery carrying soil residues.

Microbial studies and isolation of nematicide-degrading microorganisms

An important component of the study of enhanced biodegradation is investigation of the microbial relationships that control the phenomenon. Firstly, the involvement of microorganisms in the rapid degradation of the nematicide should be identified. This can be achieved by measuring changes in degradation rates in samples from an adapted soil, following steralization. Secondly, the specific degrading microorganisms should be enumerated. Finally, the responsible microorganisms should be isolated and the genetics involved in the expression of the phenomenon investigated.

Enumeration of nematicide-degrading microorganisms

Numbers of specific nematicide degrading microorganisms have been estimated in several studies. The 'most probable number' technique, by which microbial numbers are statistically estimated from a series of dilutions, has been employed to determine the levels of microorganisms capable of metabolizing carbofuran, isofenphos and fonofos in soils which had been previously treated and not treated with the nematicides. Racke & Coats (1990), reported no isofenphos-degrading microorganisms in soils that had not received previous applications of isofenphos as compared with 6-12000 cells g^{-1} soil present in the previously treated soils. No fonofos-degrading microorganisms were found in previously treated and untreated soils. When counts were made in soils with, and without, a history of carbofuran treatments results were contradictory. No significant increases in the number of carbofuran-degrading microorganisms occurred in soils pretreated with 0.1 to 50 mg kg^{-1} of carbofuran (Merica & Alexander, 1990), and the initial population of carbofuran-degraders appeared high ($>10^8$ cells/kg soil) at the commencement of the experiment. However, soils with an initial low population of specific degraders ($<10^6$ cells kg^{-1} soil) responded with population increases (Hendry & Richardson, 1988). It is be-

lieved that the most probable number enumeration method provides only a rough estimate of the numbers of pesticide-degrading microorganisms and is insensitive to small changes of the specific microbial population (Felsot & Shelton, 1993)

Isolation of nematicide-degrading microorganisms

Several microbial studies related to enhanced biodegradation have been conducted. Such studies resulted in the isolation of nematicide-degrading microorganisms that were able to utilize nematicides an as energy source. Most evidence suggests that soil bacteria form the main component responsible for enhanced biodegradation of nematicides. Some of the isolated bacteria involved in enhanced biodegradation of nematicides are presented in Table 2. Ou & Thomas (1994) isolated a mixed bacterial culture able to rapidly mineralize fenamiphos in soil extract medium. However, none of the individual components, which were all gram-negative bacteria, had any capacity to mineralize fenamiphos. In a more recent study, Karpouzas *et al.* (2000a) identified two isolates of *Pseudomonas putida* (epI and epII) able to metabolize high concentrations of ethoprophos (up to 50 mg l^{-1}), within 48 h in liquid cultures. These isolates retained their degrading ability at a range of pH and temperatures in liquid cultures (Karpouzas & Walker, 2000a). Also, *Pseudomonas putida* epI was able to rapidly degrade fresh and aged residues of ethoprophos when inoculated in soil samples (Karpouzas & Walker, 2000b). A *Pseudomonas* (Racke & Coats, 1987) and an *Arthrobacter* (Racke & Coats, 1988) strain were isolated from soil exhibiting enhanced biodegradation of isofenphos. The *Arthrobacter* was more efficient in rapid metabolism of isofenphos to isopropyl salycilate and salycilate that were further mineralized. None of the ethoprohos and isofenphos-degrading bacteria mentioned previously were able to degrade any other organophosphorus (cadusafos, fonofos, isazofos, isofenphos) or carbamate nematicides (aldicarb, oxamyl). Other workers have also isolated isofenphos-degrading bacteria such as *Corynebacterium* sp. (Murphy & Cohick, 1985) and a *Streptomyces* sp. (Gauger *et al.*, 1986).

A large number of bacteria capable of rapidly degrading carbofuran have been isolated in enhanced biodegradation related studies (Singh *et al.*, 1993; Karpouzas *et al.*, 2000b). In contrast, no isolates have been obtained from soils exhibiting enhanced degradation of aldicarb or oxamyl. However, some carbofuran-degrading bacteria carried broad-spectrum enzymic capabilities and could also degrade aldicarb in liquid cultures where the nematicide was the sole source of carbon or nitrogen. Karns *et al.*, (1986) isolated an *Achromobacter* sp. that could rapidly degrade aldicarb. Similarly, Chaudhry & Wheeler (1988), showed that a carbofuran-degrading *Pseudomonas* was able to rapidly degrade aldicarb with concurrent microbial growth. In complementary studies, Chaudhry & Ali (1988) isolated a number of carbofuran-degrading *Pseudomonas* and *Flavobacterium* strains that were also able to grow on aldicarb.

Bacteria have been isolated that can metabolize methyl bromide. Rasche *et al.* (1990) were the first to report the isolation of two ammonia-oxidation bacteria *Nitrosomonas europea* and *Nitrosolobus multiformis* that can co-oxidize methyl bromide to formaldehyde and bromide ion. Subsequently, Oremland *et al.* (1994) showed that a strain of the methane oxidation bacterium, *Methylcoccus capsullatus,* had the capacity to mineralize methyl bromide.

Bacteria that can rapidly degrade the fumigant 1,3-D have also been isolated. Lebbink *et al.* (1989) isolated a *Pseudomonas* sp., which was able to completely degrade the fumigant in liquid culture in less than 6 days. This isolate degraded the trans-isomer more rapidly than the cis-isomer. Verhagen *et al.* (1995) isolated 15 bacteria capable of degrading cis-1,3-D from microplot soil that showed enhanced biodegradation. These bacteria metabolized cis-1,3-D to cis-3-chloroallyl alcohol (3-CAA) that was further metabolized by the bacteria (Fig. 7) (Ou *et al.*, 2001). Ou (1989) also reported the isolation of a bacterial culture that was capable of mineralizing 1,3-D to CO_2. In a more recent study, Ou *et al.* (2001) isolated a *Rhodococcus* sp. that was able to co-metabolically degrade 1,3-D in the presence of a suitable second substrate. This strain metabolized trans-1,3-D and trans-3-CAA, and also trans-3-CAAC, more rapidly than the corresponding cis-isomers, but eventually mineralized the fumigant.

Molecular biological aspects

Several studies have shown that the genes encoding the production of enzymes responsible for the degradation of carbofuran are located on plasmids (Topp *et al.*, 1993; Feng *et al.*, 1997). Karns & Tomasek (1991) cloned the gene (*mcd*) carried in an *Achromobacter* sp. responsible for carbofuran degradation. Six of the bacteria isolated by Verhagen *et al.* (1995) contained a 50 to 60 kb plasmid that was probably involved in the degradation of cis-1,3-D. However, apart from the extensive molecular biological research concerning carbofuran, no such studies have been conducted for fenami-

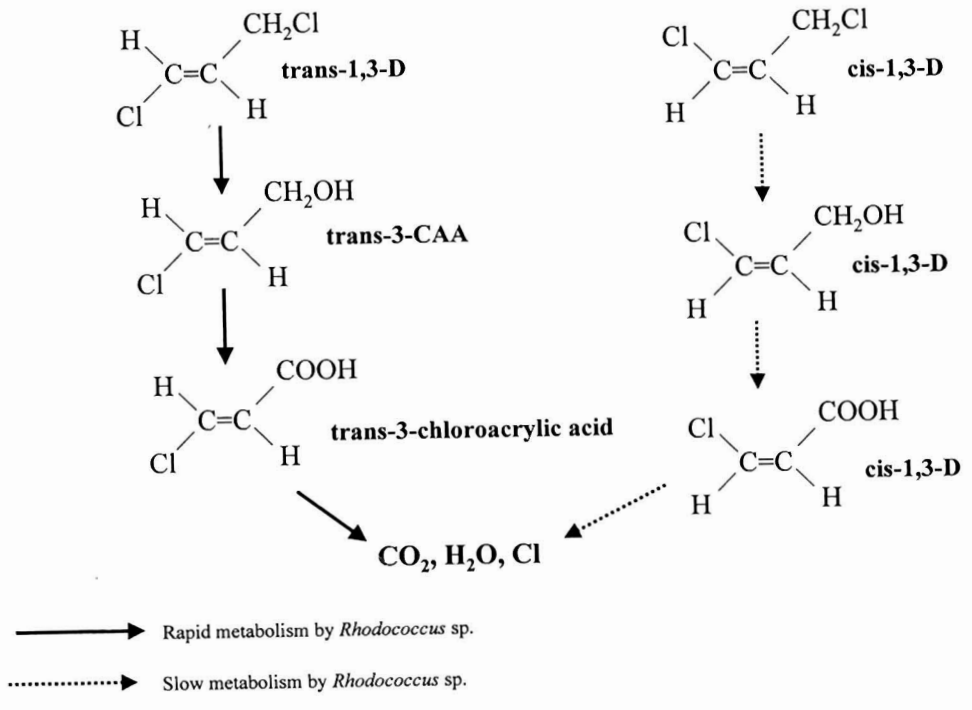

Fig. 7. The metabolic pathway of 1,3-dichloropropene by *Rhodococcus* sp. as described by Ou *et al.* (2001).

phos or ethoprophos-degrading microorganisms.

Coping with enhanced biodegradation

Microbial degradation of modern nematicides is a natural process that cannot be completely eliminated. However, in its extreme form enhanced microbial degradation can create significant problems for crop protection. The effects of enhanced biodegradation of nematicides can be minimized through the application of two kinds of strategies: operational and technological.

Operational Strategies

These strategies include crop and nematicide rotation and optimal application timing. Crop rotation can be a useful technique for minimizing the effects of enhanced biodegradation of nematicides. The alternation of potatoes with crops that are poor or non-hosts for potato cyst nematodes in a four or five year rotation scheme can reduce the nematode density, and also avoid the use of nematicides. This strategy may be of limited use in monoculture areas of the Netherlands and northern Greece where a one-year rotation with beans, or even no rotation at all, is employed by growers.

Chemical rotation is probably the most effective measure in preventing the development of enhanced biodegradation, or minimizing the problems once established. The lack of cross enhancement amongst the organophosphate nematicides and between organophosphate and carbamate nematicides allow alternating application of either organophosphates alone, or organophosphates and carbamates. In the latter case, the utilization of aldicarb and oxamyl in the same application scheme should be avoided due to the cross-enhancement problems arising from their use. Also, application of aldicarb or oxamyl should be restricted to once every three to four years due to research results indicating that if adaptation for the oxime carbamates occurs it might persist for three or more years. Another important consideration is the minimization of the use of the oxime carbamate nematicides in particular areas *i.e.*, potato monocultures in northern Greece, where carbofuran is used as a standard soil insecticide for the control of *Leptinotarsa decemlineata* (Say).

In instances where enhanced biodegradation of a nematicide has already been established it is important to have knowledge of the time required for the nematicide degradation rate to return to normal. Therefore, studies at individual field sites should be employed that will offer information on the duration of enhanced biodegradation and pos-

sible involvement of cross-enhancement. For example, Anderson & Lafuenza (1992) proposed a nematicide rotation program in banana plantations in the Ivory Coast where fenamiphos is alternated with other organophosphorus nematicides such as ethoprophos, isofenphos, or isazofos. It will be useful to examine if the application of fumigants once every three or four years might prevent the development of enhanced biodegradation of non-fumigant nematicides. The application of broad-spectrum soil sterilants every two or three years may minimize the risk of the development of enhanced biodegradation by killing some of the active nematicide-degrading bacteria. Also, such treatments will prevent high nematode infestations by decreasing the infective population of nematodes surviving in soil during the winter period.

Application time is critical for efficient nematode control. Knowledge of the nematode species present in soil at a field site and their biological life cycle under local soil and environmental conditions is necessary to determine the most effective nematicide application period. In this case, even smaller doses of the chemical may be sufficient to keep the nematode infestation below an acceptable level. As previously mentioned, smaller doses retard the development of enhanced biodegradation.

Technical Strategies

Technical strategies have been developed that include new formulation technology, novel nematicide molecules and the use of inhibitors or extenders. If the availability of the nematicides to soil microorganisms could be reduced without affecting the uptake by nematodes, then longer effective residual life would result. Therefore, alternative formulation technologies such as controlled release formulations may be useful for extending the biological efficacy of nematicides.

Synthesis of novel nematicide molecules should be directed towards the discovery of new molecules that are resistant to mineralization by soil microflora, but which will be co-metabolized thus environmental pollution will be minimized. Another significant target for nematicide production is research towards the production of novel molecules with increased activity, which will be used at lower application rates. For example, sulfonylurea herbicides are used at low application rates (10-50 g ai ha^{-1}) that do not activate soil microflora.

Beneficial aspects of enhanced biodegradation

The negative aspects of enhanced biodegradation for nematode control have been presented. However, the study of enhanced biodegradation can result in the isolation of nematicide-degrading microorganisms that can be used for the decontamination of polluted waters and soils. Fenamiphos-degrading bacteria can be used for decontaminating underground water regimes containing fenamiphos sulfoxide and sulfone, each of which are mobile chemicals that can move down the soil profile in percolating water. Bioremediation-type experiments have been employed with other soil bacteria (*e.g.*, the ethoprophos-degrading strains of *Pseudomonas putida*), and have shown promising results (Karpouzas & Walker, 2000b). Enhanced biodegradation of nematicides is also beneficial for preventing the accumulation of residues of neurotoxic chemicals such as organophosphorus and carbamate nematicides. Studies of the molecular aspects of enhanced biodegradation will be useful for isolating DNA catabolic sequences encoding the production of catabolic enzymes. Such sequences may be cloned and universal probes, which can identify homologous sequences in soil and water *in situ,* could be used for detecting biodegrading organisms thus preventing the development of enhanced biodegradation.

CONCLUSIONS

This review reveals that the efficacy of most nematicides is adversely affected by enhanced biodegradation. The occurrence of enhanced biodegradation can be predicted from the knowledge of pesticide characteristics, treatment histories, soil properties and environmental conditions. Although there is an extensive literature concerning the reduction in nematicide efficacy due to enhanced biodegradation, growers and many researchers are not fully aware of the phenomenon. Reduction in nematicidal performance is usually attributed to poor application or to movement out of the root zone due to heavy precipitation. Growers need to be informed of the fundamentals and consequences of the problem in order to use practices that minimize the risk of the development of enhanced biodegradation. It is more practical to prevent the development of biodegradation rather than to attempt to eradicate or suppress the phenomenon once it is established.

There are two aspects of enhanced biodegradation of nematicides that appear to be important for future problems associated with modern crop protection. The first concern arises from the fact that the majority of available nematicides are susceptible to enhanced biodegradation, with the exception of cadusafos and fosthiazate each of which are relatively new active ingredients and thus there are

no fields repeatedly treated with these chemicals. The other concern arises from the fact that methyl bromide, which has been very effective against nematodes, will be withdrawn from the market by the end of 2004. This will result in increasing applications of other fumigant and non-fumigant nematicides to replace methyl bromide, and subsequently increasing the risk of the development of enhanced biodegradation. The best strategy to avoid enhanced biodegradation is careful pesticide rotation, along with utilization of resistant cultivars and crop rotation.

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Karpouzas D. G., Giannakou, I. O. Биодеградация и ускоренная биодеградация – причины пониженной биологической эффективности нематицидов.

Резюме. Рассмотрен феномен ускоренной биодеградации нематицидов фумигационного и нефумигиционного применения. Несколько случаев снижения эффективности борьбы с нематодами были связаны с высокой скоростью микробиологической деградации этих нематицидов определенной частью почвенной микрофлоры, адаптированной к быстрому усвоению некоторых препаратов. Высокие значения pH, оптимальная влажность и температура почвы приводят к ускоренной биодеградации. Продолжительное сохранение условий ускоренной биодеградации в отсутвие применения нематицидов, а также усиление биодеградации при внесении в почву любых нематицидов, представляют собой наиболее важные практические аспекты данного феномена. Повышенная чувствительность используемых в настоящее время нематицидов к ускоренной бидеградации может составить серьезную проблему в будущем. Использование активных ингредиентов нематицидов с различными активными химическими группами вместе с севооборотом и использованием устойчивых сортов могут существенно понизить эффект ускоренной биодеградации нематицидов в почве.