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Glucosinolate-Containing Seed Meal as a Soil Amendment to Control Plant Pests

2000-2002

J. Brown, M.J. Morra
University of Idaho
Moscow, Idaho

Subcontract Report
NREL/SR-510-35254
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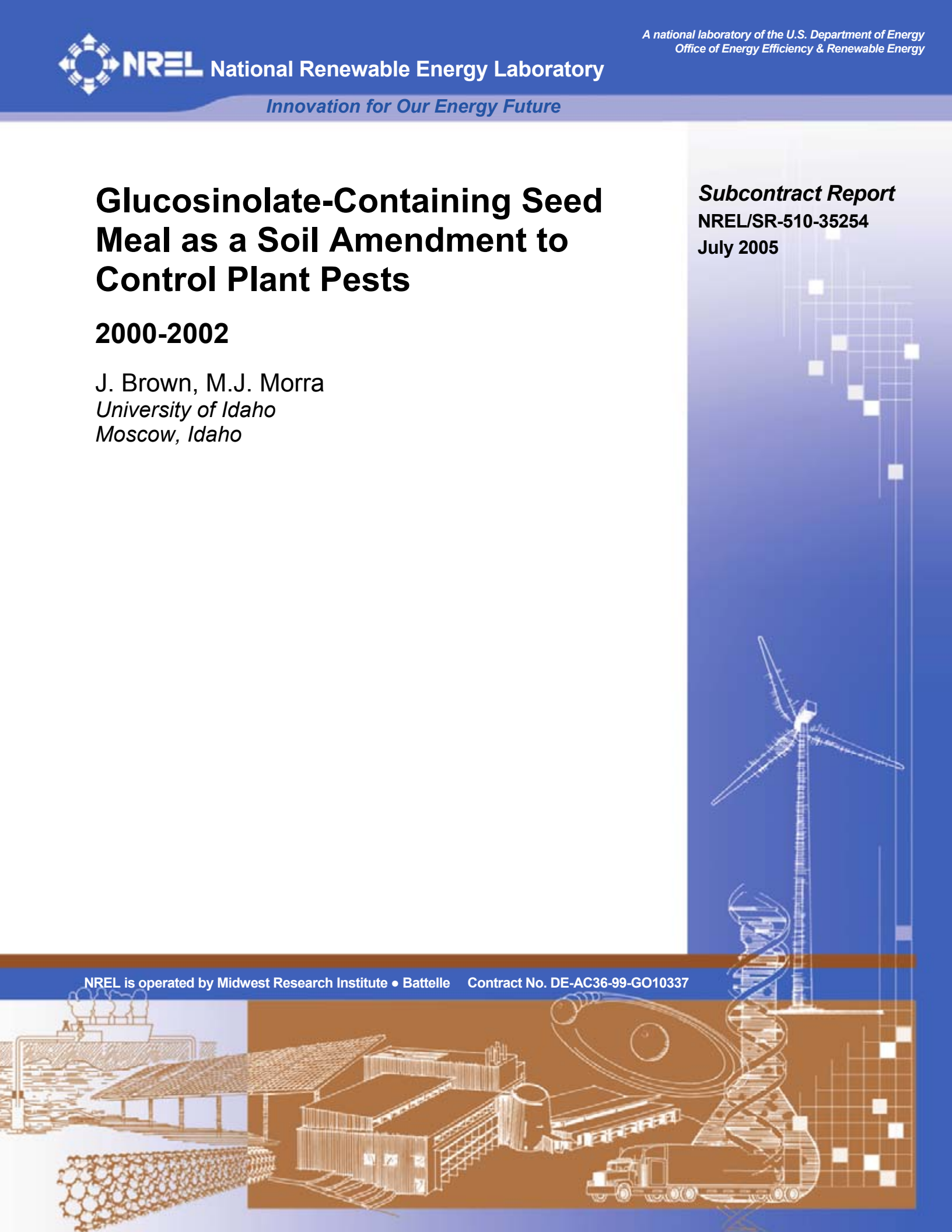

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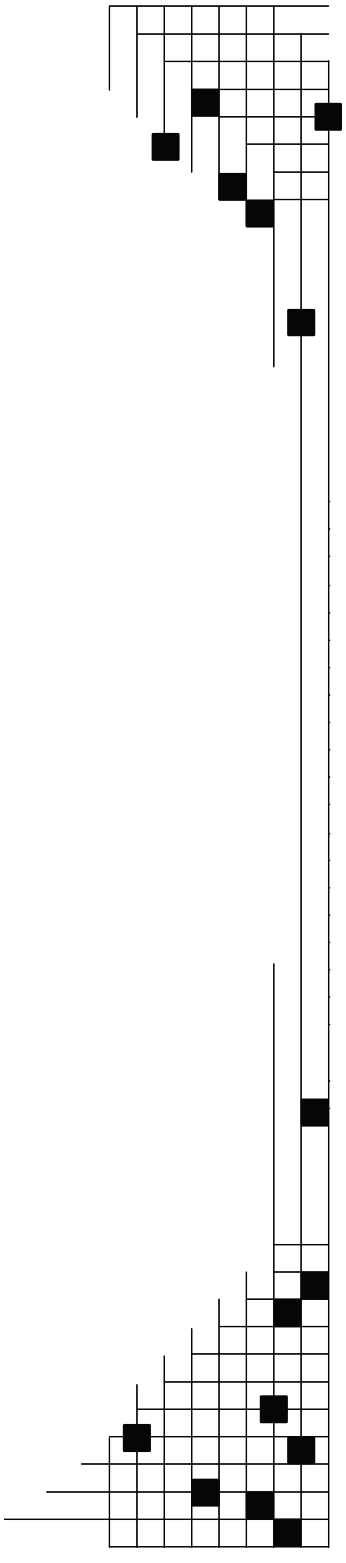

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Glucosinolate-Containing Seed Meal as a Soil Amendment to Control Plant Pests

I. Introduction

Plants may produce compounds that directly or indirectly affect their biological environment. These compounds fall within a broad category of compounds called allelochemicals, and are exclusive of food that influences growth, health, or behavior of other organisms (Whittaker and Feeney 1971). One reason for interest in allelochemicals is their potential for use in alternative pest management systems. Using plant-produced allelochemicals in agricultural and horticultural practices could minimize synthetic pesticide use, reduce the associated potential for environmental contamination, and contribute to a more sustainable agricultural system.

Glucosinolates, compounds that occur in agronomically important crops, may represent a viable source of allelochemic control for various soil-borne plant pests. Extensive studies of several hundred species of the Brassicaceae (Cruciferae) family indicate that virtually all may be capable of producing glucosinolates (Kjaer 1976). Insecticidal, nematicidal, fungicidal, and phytotoxic effects are often associated with tissues of cruciferous plants. As such, glucosinolates are commonly considered to be ultimately responsible for pest suppression.

In this review we consider what is known about glucosinolates and the factors involved in potential application of glucosinolate-containing tissues in pest control strategies. We will focus on the use of seed meal, but supporting work involving the use of other parts of the plant will be presented when necessary. However, glucosinolates are not biologically active, but are the precursors for the formation of a variety of potential allelochemicals. Much of the past emphasis and available literature have focused on isothiocyanates (ITCs), apparently the most important of those allelochemicals. Any delivery system designed to take advantage of this chemistry must consider the fact that glucosinolates must be enzymatically hydrolyzed and that multiple pesticidal compounds may be produced. As such, we will first provide an overview of glucosinolate chemistry and the relevant hydrolytic reactions. The most recent and comprehensive reviews concerning glucosinolates are those of Brown and Morra (1997), Fahey et al. (2001), and Rosa et al. (1997).

II. Glucosinolates

A. Structure

Ettlinger and Lundeen in 1956 (Fig. 1) described the general structure for glucosinolates. Found in dicotyledonous plants, they are a class of organic anions usually isolated as potassium or sodium salts (Larsen 1981), but occasionally in other forms. For example, *p*-hydroxybenzyl glucosinolate is isolated as a salt complex with sinapine; an organic cation derived from choline (Challenger 1959; Kjaer 1960; Van Etten and Tookey 1979). Features common to the class are a ß-D-thioglucose moiety, a sulfate attached through a C=N bond (sulfonated oxime), and a side group (designated R) that distinguishes one glucosinolate from another. More than 100 different R groups, and thus glucosinolates, have been identified or inferred from degradative products (Table 1).

B. Occurrence

Glucosinolates are especially abundant among families of the order Capparales: Tovariaceae, Resedaceae, Capparaceae, Moringaceae, and Brassicaceae. Families outside the order exhibit occasional occurrence and include the Caricaceae, Euphorbiaceae, Gyrotemonaceae, Limnathaceae, Salvadoraceae, and Tropaeolaceae families (Fenwick et al. 1983). A recent literature review provides a comprehensive list of all species known to contain glucosinolates (Fahey et al. 2001).

Glucosinolate types in plant species are highly variable. For example, the main glucosinolate in radish seed (*Raphanus sativus*) is 4-methylsulphinyl-3-butenyl glucosinolate, while mustard seed (*Brassica juncea*) is dominated by propenyl glucosinolate. Cabbage seed (*Brassica oleracea*) contains mainly propenyl and 2-hydroxy-3-butenyl glucosinolate; rapeseed (*Brassica napus*) contains 4 major glucosinolates: 2-hydroxy-3-butenyl, 3-butenyl, 4-pentenyl, and 2-hydroxy-4-pentenyl (Sang et al. 1984). Similar differences in glucosinolate types are observed when comparing vegetative plant parts (Hill et al. 1987; Josefsson 1967b).

Numerous authors have shown that glucosinolate concentrations vary within plants of a single species, and that fluctuations occur with plant age (Carlson et al. 1987; Chong and Bible 1974; Clossais-Besnard and Larher 1991; Elliott and Stowe 1971; Freer et al. 1989; Griffiths et al. 1991; Johnston and Jones 1966; Josefsson 1967a; Josefsson and Appelqvist 1968; Kondo et al. 1985; Macfarlane-Smith and Griffiths 1988; Paxman and Hill 1974). Additional environmental factors such as spacing, moisture regime, and nutrient availability affect concentration (Freeman and Mossadeghi 1973; Josefsson 1970a, 1970b; Ju et al. 1982; Louda et al. 1987; MacLeod and Nussbaum 1977; Mailer and Pratley 1990). Glucosinolate type and quantity also vary within tissues of an individual plant. The major glucosinolate in radish seed is not detected in radish leaves or roots; propenyl glucosinolate is found in all *B. juncea* tissues (Sang et al. 1984).

C. Hydrolysis Reactions

Toxicity is not attributed to intact glucosinolates, but instead to biologically active products such as ITCs, organic cyanides, oxazolidinethiones (OZTs), and ionic thiocyanate (SCN^-) released upon enzymatic degradation by myrosinase (thioglucoside glucohydrolase, EC 3.2.3.1) in the presence of water. Degradation also occurs thermally or by acid hydrolysis (Kjaer 1976; MacLeod et al. 1981).

Myrosinase is not properly identified as a single enzyme, but rather as a family or group of similar-acting enzymes. Multiple forms of the enzymes exist, both among species and within a single plant (Bones and Slupphaug 1989; Falk et al. 1992, 1995a; Lenman et al. 1990, 1993a; Xue et al. 1993), and all perform a similar function (Björkman 1976). Although their genetic sequences are similar to other ß-glycosidases (Lenman et al. 1993b), myrosinases are fairly specific toward glucosinolates (Durham and Poulton 1990). These enzymes cleave the sulfur-glucose bond regardless of either the enzyme or substrate source. However, the particular enzyme and glucosinolate substrate influence reaction kinetics (Bones 1990; MacLeod and Rossiter 1986). In addition to plants, the enzymes have been discovered in the bacterium *Enterobacter cloacae* and the fungus *Aspergillus sydowi* (MacLeod and Rossiter 1986). Myrosinase-like activity has also been observed in soils (Borek et al. 1996a; Chae and Tabatabai 1983).

Myrosinase and glucosinolates are separated from each other in intact plant tissues; however, the precise nature of the arrangement has not been easy to determine. Evidence suggesting myrosinase is a cytosolic enzyme associated with membranes, perhaps surrounding a vacuole containing glucosinolates (Lüthy and Matile 1984; Thangstad et al. 1990), has been supplanted by that obtained using more precise methodologies. Glucosinolates are probably contained in vacuoles of various types of cells (Grob and Matile 1979; Pocock et al. 1987). In contrast, myrosinase is contained only within structures, called myrosin grains, of specialized myrosin cells that are distributed among other cells of the plant tissue (Höglund et al. 1992; Thangstad et al. 1991). As glucosinolate vacuoles do not appear to be present within myrosin cells, intercellular rather than intracellular separation occurs. Disrupting cellular tissues allows glucosinolates and myrosinase to mix, resulting in the rapid release of glucosinolate degradation products. Myrosinase activity and glucosinolates are preserved in cold-pressed meal and are no longer physically separated. Thus, adding water immediately results in the production of the hydrolysis products, including isothiocyanate, without the need for additional tissue maceration.

Enzymatic degradation is influenced by a number of variables, and reviews are available (Chew 1988a; Fenwick et al. 1983; McDanell et al. 1988; McGregor et al. 1983; Sørensen 1990; Tookey et al. 1980; Van Etten and Tookey 1979; Van Etten and Wolff 1973; Van Etten et al. 1969). In the presence of moisture, glucosinolate hydrolysis produces glucose, sulfate, and an additional aglucon product(s) from the remaining N, C, S, and R groups (Figure 2). The latter product is proposed to go through at least one unstable intermediate, the ultimate form controlled by reaction conditions including pH, R-group, and the presence of metal ions such as Fe^{+2}. In addition, smaller proteins or coenzymes accompany

myrosinase and may alter the product profile (Falk et al. 1995b; Taipalensuu et al. 1996). Several possible products that exhibit some form of biological activity may be formed (Fig. 2). The products are all interrelated in that they are isomers or result from further fission of the isomers.

D. Hydrolysis Products

ITCs have historically been considered the "normal" products of glucosinolate breakdown. They are often volatile with pungent flavors or odors. The presence of propenyl ITC in mustards and horseradish is responsible for much of the flavor; thus, ITCs are sometimes called mustard oils. Formation requires that the initial unstable aglucon intermediate undergo a Loessen rearrangement to the R-N=C=S configuration. Isothiocyanates are quite reactive, although less so than the related isocyanates (R-N=C=O). A few commercially available soil fumigants depend on the activity of methyl ITC either as the parent compound or as produced from precursors such as sodium N-methyldithiocarbamate or tetrahydro-3,5-dimethyl-2*H*-1,3,5-thiadiazine-2-thione. Because of known toxicities, ITCs are often considered likely candidates for pesticidal activity.

The ability of ITCs to form cyclic thione compounds (Hughes 1975) is believed to occur in a spontaneous intramolecular reaction when the ITC contains a ß hydroxyl group on the side chain (R-group) (Fig. 2). The goitrogenic OZTs so formed are major products from rapeseed (*B. napus*).

Nitrile character is common to four additional products. Forming a nitrile (R-C≡N, also known as an organic cyanide), which does not require rearrangement, involves sulfur loss from the molecule. Nitrile formation is favored over ITC at low pH, but occurs in some crucifers at a pH where ITC is normally the dominant product (Gil and MacLeod 1980). The presence of Fe^{+2} or thiol compounds increases the likelihood of nitrile formation (Hasapis and MacLeod 1982; Uda et al. 1986a, 1986b). Epithionitrile formation requires the same conditions as for nitriles, plus terminal unsaturation of the R-group and the presence of an epithiospecifier protein. The epithiospecifier protein possesses a rare property in that it is an enzyme cofactor that allosterically directs an enzyme to yield a different product (MacLeod and Rossiter 1985; Petroski and Kwolek 1985; Petroski and Tookey 1982). Thiocyanate (R-S-C≡N) is sometimes produced, particularly in members of the Alyssum, Coronopus, Lepidium, and Thlaspi families (Fenwick et al. 1983). Factors controlling organic thiocyanate formation are not well understood (Larsen 1981).

SCN^- production from glucosinolates is controlled by the presence of specific R-groups. Evidence suggests the anion is a resonance hybrid with greater charge on the S (Hughes 1975; Witczak 1986); however, charge can be localized on either the sulfur ($^-$S-C≡N) or the nitrogen (S=C=N^-), depending on the environment (Beekhuis 1975). Indole and 4-hydroxybenzyl glucosinolates yield SCN^- thought to arise from a highly unstable ITC intermediate. SCN^- is formed from indole glucosinolates over a wide pH range, whereas 4-hydroxybenzyl glucosinolates is typically thought to yield SCN^- only at a more basic pH. We have recently determined that 4-OH benzyl isothiocyanate was not stable even at pH

values of 3.0 (Borek and Morra, 2003). The half-life decreases with an increase in pH from 3.6 h at pH 3.0 to less than 5 min at pH 7.0.

Indolylic compounds also result during SCN^- production from indole glucosinolate hydrolysis. 3-Indolylmethanol, the immediate product, may form ascorbigen or 3,3'-diindolylmethane (McDanell et al. 1988). 3-Indolylacetonitrile, indole acetic acid, and dioxindoles may be formed under conditions favoring nitrile formation (McDanell et al. 1988; Monde et al. 1991). Indolylic compounds in these plant tissues are also formed by routes other than glucosinolate degradation (Monde et al. 1991; Takasugi et al. 1988).

III. Pesticidal Activity of Glucosinolate Hyrolysis Products

A. Herbicidal Activity

Glucosinolate-containing plants have a reputation for affecting successive or nearby plant communities. Various negative or inhibitory effects can occur. At one time dyer's woad (*Isatis tinctoria*) cultivation was restricted because of a negative influence on following crops (Elliott and Stowe 1971; Fenwick et al. 1983). Yields of legumes (such as clover) and, to a lesser extent, grass are reduced following a *Brassica* crop (Campbell 1959; Kutácek 1964). Campbell (1959) showed that pieces of *B. oleracea* roots placed in a petri dish with seeds of clover (*Trifolium repens*) inhibited germination, suggesting direct involvement of compounds from the *Brassica* plants. Flax yields decrease if species of *Camelina* are present as weeds (Grümmer and Beyer 1960). *Brassica* herbage reduced stand establishment of five crop species more than twice as much as barley (*Hordeum vulgare*) amendments (Vera et al. 1987). Similarly, canola stubble was more inhibitory to wild oat (*Avena sterilis*) emergence than wheat or pea (Jones 1992). Stands of wild *Brassica nigra* appeared to inhibit germination of annual grasses (Bell and Muller 1973), and broccoli (*B. oleracea*) residues amended to soil reduced germination and growth of lettuce for 10-21 d (Patrick et al. 1963). Researchers in Sweden demonstrated that *Sinapis alba* seed meal applid to the soil suppresses weed emergence (Ascard and Jonasson 1991; Johansson 1992; Johansson and Ascard 1994; Oleszek et al. 1994). For example, mustard meal or "cake," applied in rows between cole crops with the intent of attracting enemies of the cabbage root fly also reduced numbers of several annual weeds (Ascard and Jonasson 1991).

Results with respect to plant inhibition are not always clear, however, and sometimes appear inconsistent or contradictory. For example, heavy rape residues (*Brassica campestris* L.) reduced wheat, barley, and oat growth in a field trial, but soil N concentrations measured under heavy residues were less than under light residues. Differences in soil nutrient status were thus possibly responsible for the effect (Horricks 1969). Similar studies using rape straw and chaff residue at 8,970 kg ha^{-1} showed reduced emergence of bromegrass and alfalfa, and reduced growth of barley, bromegrass, and alfalfa, but reductions were not significantly different than in controls using wheat straw (Waddington 1978; Waddington and Bowren 1978). The effect was ameliorated by applying inorganic nitrogen fertilizer; however, subsequent studies indicate that nitrogen limitations do not fully explain the inhibition (Mason-Sedun and Jessop 1988; Mason-Sedun et al. 1986).

Many variables contribute to differences in phytotoxicity. The *Brassica* species or cultivar may control the level of phytotoxicity (Mason-Sedun et al. 1986), although differences are not always dramatic (Vera et al. 1987) and may be influenced by the plant growth stage. Fresher plant tissues are more effective inhibitors than straw or stubble that has been stored or left after harvest. Aqueous extracts of fresh wild mustard (*B. campestris*) tissues produce a stronger inhibition of growth than those from aged tissues (Jiménez-Orsornio and Gliessman 1987). Green *Brassica* herbage reduced stand establishment more than *Brassica* straw and chaff, which caused only sporadic reductions (Vera et al. 1987). Rape stubble

residues were less or no more effective than pea or wheat residues in inhibiting wheat germination and growth (Jessop and Stewart 1983). The greatest inhibition of wheat occurred with freshly dried *Brassica* residues, an effect that declined with older residues (Mason-Sedun et al. 1986). Microbial degradation of the tissues may produce compounds apart from glucosinolates that are associated with plant inhibition or stimulation, further complicating data interpretation (Harper and Lynch 1982; Lovett and Duffield 1981; Lovett and Jackson 1980). The target plant species also vary in tolerance to the allelochemicals (Kasting et al. 1974; Oleszek 1987). Tomatoes planted in cabbage-amended soil seem particularly sensitive, wilting within 24 h (Ramirez-Villapudua and Munnecke 1988). Suppression of germination may in part be related to seed size, with smaller seeds being more susceptible (Vera et al. 1987).

Many studies concerning the effects of glucosinolate-containing plant tissues on plant growth have focused on water-soluble compounds as the responsible agents. Aqueous extracts of various *Brassica* and *Camelina* reduce seedling growth or inhibit germination (Table 2). Negative effects are not consistent in all species, and some plants show no change or are actually stimulated. There are not always correlations between germination inhibition and growth inhibition. Aqueous extracts had little effect on tomato germination, but severely inhibited growth just after germination (Gressel and Holm 1964). Depending on plant part, growth stage, or other conditions, extracts from the same plant species may be inhibitory or stimulatory to the target species (Jiménez-Orsornio and Gliessman 1987).

Intact glucosinolates are water soluble, but of several that have been tested for biological effects, only 3-indolylmethyl glucosinolate has produced inhibition of plant growth (Bialy et al. 1990; Kutacek 1964). High concentrations of 3-indolylmethyl glucosinolate in woad may be responsible for its inhibition of other plants, possibly by converting some of this glucosinolate to auxins (Andersen and Muir 1966; Elliott and Stowe 1971; Kutacek 1964; Stewart 1939). Ascorbigen, another possible water-soluble degradation product of this glucosinolate, inhibited germination and growth of clover, but only at relatively high concentrations (10^{-2}-10^{-3} M) (Kutacek 1964).

The water-soluble glucosinolate degradation product most studied in relation to plant growth and herbicidal potential is SCN^-. The herbicidal formulation amitrole-T consists of a mixture of amino-1,2,4-triazole and NH_4SCN. Thiocyanate salts such as KSCN and NH_4SCN can be used as selective herbicides and defoliants by varying the concentrations. Oxalis and spurge in lawns are killed at SCN^- concentrations between 1.7-14 g L^{-1} (0.17-1.4%), and about 11.2 kg ha^{-1} is used to defoliate cotton (Beekhuis 1975). At 112 kg ha^{-1} control of poison ivy, poison sumac, and poison oak is at least as favorable as control by 2,4-D or sodium arsenite. At 897 kg ha^{-1} SCN^- is a temporary soil sterilant (Beekhuis 1975). SCN^- is produced by *B. napus* and *S. alba* meals and thus it is of possible importance in pest control. SCN^- is not expected to be a signficant product from *B. juncea* meal.

At rates closer to what might be encountered in natural situations (500 μM SCN^-), percent germination of 39 different species and cultivars did not differ from controls, but growth of 22 species was adversely affected (Stiehl and Bible 1989). Early growth inhibition of some plants was also observed in bioassays by Park et al. (1983), while in hydroponic cultures Ju

et al. (1983) found complete kill of tobacco at < 5 μg mL^{-1} and of beans at concentrations over 25 μg mL^{-1}. Cabbage growth was severely inhibited, though not completely killed, at 100 μg mL^{-1}. SCN^- accumulated in plant tissues and toxicity positively correlated with tissue SCN^- concentrations (Stiehl and Bible 1989; Ju et al. 1983). Squash seedlings had low SCN^- concentrations in their tissues, suggesting that some plants may degrade or do not readily take up the anion (Stiehl and Bible 1989). Wu and Bassler (1969) found that SCN^- inactivates cotton chloroplasts by inhibiting O_2 release. Ionic thiocyanate-induced chlorosis may be related to SCN^- interactions with iron (Ju et al. 1983). Additional interesting effects of SCN^- on plants include increased yield (6%–15%) when seed potatoes are coated with 0.02% SCN^- and induced apple reddening by SCN^- sprays (Beekhuis 1975; Dustman and Duncan 1940).

Other water-soluble glucosinolate degradation products likely play important roles in altering seed germination and plant growth. Water soluble compounds from *B. napus* defatted seed meal severely inhibited lettuce seed germination and those from *B. napus* leaf tissue completely inhibited germination (Brown and Morra 1995, 1996). In contrast, aqueous extracts of root tissue had only a minor influence on germination. Several organic water soluble glucosinolate degradation products from the tissues were found by back-extracting aqueous extracts of the seed meal with CH_2Cl_2 and a $CaCl_2$ solution. Water-soluble products were particularly high in the seed meal and included 5-vinyl OZT, 5-propenyl OZT, 1-cyano-3-butene, 3,4-epithiobutyl CN, 2-hydroxy-3,4-epithiobutyl CN, 4-methylsulfinylbutyl ITC, and 5-methylsulfinylpentyl ITC. In addition, SCN^- is found in water extracts of seed meal and is an expected product in other tissues in lesser amounts (Brown and Morra 1991; Brown et al. 1991). These water-soluble glucosinolate products are probably involved in the inhibition of germination by seed meal tissue. However, inhibition of lettuce seed germination by water-soluble compounds from leaf and stem tissues could not be explained entirely by the total amount of identified glucosinolate degradation products (Brown and Morra 1996). This suggests either high toxicity for specific nonvolatile ITCs found in leaf and stem tissues or the participation of unidentified compounds.

Plant tissue extract phytotoxicity correlates with tissue amendment phytotoxicity, but residues are generally more effective inhibitors of seed germination than aqueous extracts (Mason-Sedun and Jessop 1988; Mason-Sedun et al. 1986). The greater inhibitory effect of residues suggests that something other than water-soluble toxins influences germination. Volatile ITCs are probably the major allelochemicals responsible for inhibitory effects on plants, although some have disputed the practical significance of these compounds *in vivo* (Bell and Muller 1973; Choesin and Boerner 1991).

Plant toxicity is illustrated by methyl ITC, often studied because of its use as a commercial soil fumigant. Methyl ITC is usually generated *in situ* from a precursor (e.g. dithiocarbamate), but may be applied directly (Miller 1988). The fumigant Vapam, which releases methyl ITC, was the only one of four soil fumigants found to be toxic to strawberry plants when applied as a drench (Eide 1959). Residues of methyl ITC must be degraded before planting commences because of phytotoxicity (Sirons 1973). Methyl ITC inhibits growth and germination of weeds such as pigweed, dandelion, lambsquarter, bermuda grass,

purslane, crabgrass, quackgrass, spurge, fleabane, barnyard grass, fall panicum, common ragweed, stinkgrass, henbit, and carpetweed (Beekhuis 1975; Teasdale and Taylorson 1986).

Many weed seeds are killed while dormant, a capability distinguishing ITCs from other herbicides. Activity in the gas phase for propenyl ITC as well as methyl ITC was demonstrated by complete or severe germination inhibition of corn, soybeans, wheat, rapeseed, cucumber, carrot, alfalfa, dandelion, redroot pigweed, and barnyard grass at concentrations of 1 ppm in the headspace of airtight containers (Vaughn and Boydston 1995). Although exact mechanisms of germination inhibition by ITCs are not known, evidence suggests interference with protein synthesis and possibly processes involved in the formation of phosphorylated sugars (Leblová-Svobodová and Koštír 1962). Benzyl ITC is a potent inhibitor of plant enzyme activity (Lykkesfeldt and Møller 1993).

ITCs express variable phytotoxicities, a property related to the remainder of the molecular structure. Benzyl ITC inhibits germination and growth of several weeds (Dale 1986; Powell and Spencer 1988; Wolf et al. 1984) at a rate lower than methyl ITC (Teasdale and Taylorson 1986). Two extremes of effectiveness were observed in wheat bioassays at ITC concentrations of 500 ppm; butyl ITC had no effect on germination, shoot, or root growth while phenylethyl ITC completely inhibited germination (Bialy et al. 1990). Propenyl, methyl, ethyl, phenyl, and benzyl ITCs were intermediate with respect to inhibition.

In addition to studies with pure compounds, organic solvent extracts of papaya shown to contain benzyl ITC inhibited velvetleaf, but not corn, at $4x10^{-4}$ M (Wolf et al. 1984). Similarly, $CHCl_3$ extracts of mustard inhibited seedling growth of barley, rye, broccoli, and radish (Jiménez-Orsornio and Gliessman 1987). Barley and rye were most affected; inhibition of radish was not statistically significant. Ethyl acetate extracts of *Rorippa indica* contained 8-methylsulfinyloctyl, 9-methylsulfinylnonyl, 10-methylsulfinyldecyl, and the corresponding sulfonyl ITCs and inhibited lettuce germination by 90% (Yamane et al. 1992). Only 10-methylsulfonyldecyl ITC was without activity toward germination and growth.

Inhibitory effects with pure compounds and organic extracts also occur in studies involving volatiles from glucosinolate-containing plant tissues. Volatiles produced from *Brassica* tissues were shown to inhibit germination and growth of lettuce, wheat, and barnyard grass (*Echinochloa crusgalli*) (Oleszek 1987). In a separate study, 22 volatile glucosinolate products consisting of ITCs and nitriles were identified in the headspace of chambers containing *B. napus* seed meal, root, and leaf and stem tissues (Brown and Morra 1995, 1996). Tissues producing those volatiles inhibited germination in bioassays, whereas no inhibition was observed when the same tissues were treated to hydrolyze glucosinolates and remove volatile glucosinolate products before bioassays were initiated. Comparison of headspace volatiles and extracts from the intact and hydrolyzed tissues revealed that ITCs were the most abundant products of intact tissues. The presence of other, nonglucosinolate derived volatiles could not explain inhibition since the same compounds were present in the headspace of intact and hydrolyzed tissues. Some volatile glucosinolate products have also been observed in the headspace of vessels containing *B. campestris* (1-methylpropyl and 4-pentenyl ITC), *B. juncea* (1-methylpropyl and propenyl ITC), *B. nigra* (propenyl ITC), and *S. alba* (3-butenyl ITC and phenylethyl CN) (Tollsten and Bergström 1988). Propenyl ITC has

been detected in headspace of cabbage (Chin and Lindsay 1993) and methyl thiocyanate as a volatile product from broccoli (Hansen et al. 1992).

The effects of volatile ITCs are short-lived. Benzyl ITC was very effective at inhibiting weed germination if the seeds were placed on fresh media; however, if seeds were placed on media two days old, very little difference was observed from the control (Dale 1986). In seed germination bioassays, 50 % of the methyl ITC disappeared within 1-2 d and the remainder was almost completely gone in 5-7 d (Teasdale and Taylorson 1986).

Many of the overall effects on crop plants can be considered beneficial. Tarahumara Indians in northern Mexico claim that there are fewer weeds in plots after mustard is grown (Jimenez-Orsornio and Gliessman 1987). Ramirez-Villapudua and Munnecke (1987) noted that plots treated with cabbage amendments and solar heating were weed free for months. Potato yield was increased and weed biomass was reduced 50%-96 % after rapeseed was incorporated into the test plots (Boydston and Hang 1995). Palouse wheat farmers of the northwestern United States have claimed higher yields after rapeseed was included in the rotation. In Australia, Kirkegaard et al. (1994) measured greater wheat yields following *Brassica* crops compared to other break crops. Other beneficial effects may result from penetration of the soil by large taproots and suppression of pathogens. However, one potential benefit of glucosinolate-containing plants is weed control by inhibiting seed germination and seedling growth. To take advantage of allelochemic effects in weed suppression, we must consider the mechanisms of plant suppression, characterize the compounds and chemistry involved in this suppression, target weed species, and avoid negative effects on the crop. We must especially consider the potential negative consequences of phytoxicity when targeting pests of horticultural crops.

B. Fungicidal and Bactericidal Activities

Glucosinolate products may greatly influence fungal and bacterial populations. Although products were not identified, in the presence of myrosinase several alkyl and aryl glucosinolates were cytotoxic to *Salmonella typhimurium* (Tiedink et al. 1991). ITCs are among the most potent products and are suspected to be the major inhibitors of microbial activity. Benzyl ITC is sometimes used as an antibiotic to treat infections of the respiratory and urinary tracts (Mennicke et al. 1988). Bacteriostatic, bactericidal, and fungicidal effects of many ITCs are well documented (Table 3).

In many cases, microorganisms are differentially inhibited by the same ITC. For example, although methyl ITC is active against a broad range of organisms, dose responses vary tremendously among species. Munnecke et al. (1962) estimated the range of toxicity to *Rhizoctonia* as 110-1500 µg methyl ITC generated h^{-1}; *Myrothecium*, 20-490 µg h^{-1}; and *Pythium*, 10-24 µg h^{-1}. In general, gram-negative bacteria are less susceptible than gram-positive bacteria to ITCs; some microorganisms avoid toxicity by degrading the inhibitory compound (Fenwick et al. 1983; Smelt et al. 1989).

The toxicity and range of activity also vary with changes in the ITC R-group. Greater toxicity is often related to increased volatility (Lewis and Papavizas 1971; Munnecke and Martin 1964). Substituents in the R-group govern solubility, which in general is negatively correlated with activity (Drobnica et al. 1967a, 1967b); however, reasons for differences in toxicity are not always clear. Recent studies of Manici et al. (2000) indicate that ITCs produced from thiofunctionalized glucosinolates such as glucoiberin and glucoerucin are more fungitoxic against *Pythium irregulare* and *Rhizoctonia solani* than alkenyl glucosinolate products such as propenyl ITC. This research group proposes that species such as *Eruca sativa*, *Iberis amara*, and *Rapistrum rugosum* may be more effective in controlling fungal pathogens because they contain thiofunctionalized glucosinolates.

Glucosinolate products with nitrile character are biologically active, but effects are more limited than for ITCs. The yeast *Nematospora sinecaula* is inhibited by butyl thiocyanate at 40 $\mu g\ mL^{-1}$ (Holley and Jones 1985) and modified thiocyanates are used to control slime mold in the paper industry (Beekhuis 1975; Wood 1975). However, tests against various microorganisms showed that 2-200 times as much thiocyanate was required to obtain equivalent growth inhibition compared to the corresponding ITC (Virtanen 1965; Walker et al. 1937). Propenyl CN did not inhibit *Peronospora* at concentrations > 1000 $\mu g\ mL^{-1}$ (Greenhalgh and Mitchell 1976). A propenyl cyanide concentration approximately 40 times that of propenyl ITC was required for equivalent inhibition, but benzyl CN inhibited *Nematospora* at < 50 $\mu g\ mL^{-1}$ (Holley and Jones 1985). Solutions of propenyl glucosinolate with myrosinase were more effective at inhibiting *Leptosphaeria maculans* at pH 7 (where ITC should be the dominate product) than at pH 4 (where the proportion of nitrile product is increased) (Mithen et al. 1986). The same authors showed mild inhibitory effects of 3-indolylacetonitrile to *L. maculans*. 3-Indolylacetonitrile completely inhibited growth of *Penicillium chrysogenum* at 200 $\mu g\ g^{-1}$ (Smissman et al. 1961).

Similarly, other products inhibit microbial activity and growth, though not to the extent of ITCs. OZTs have little effect on the growth of propionic bacteria (Rutkowski et al. 1972) and the fungal pathogen *L. maculans* (Mithen et al. 1986), but express some activity against *Phoma lingam* (Schnug and Ceynowa 1990) and *Aphanomyces euteiches* f. *pisi* (Smolinska et al. 1997a). 3-Indolylmethanol is quite inhibitory to *L. maculans,* but ascorbigen and diindolylmethane are only mildly inhibitory (Mithen et al. 1986).

Like OZTs, SCN^- has little effect on propionic bacteria (Rutkowski et al. 1972) and the fungal pathogen *L. maculans* (Mithen et al. 1986). Ammonium thiocyanate inhibits bacterial growth in soil but stimulates fungi at concentrations >250 $\mu g\ g^{-1}$ (Smith et al. 1945). SCN^- inhibits nitrite forming organisms (Smith et al. 1945) and SCN^--containing amitrole-T inhibits nitrification (Van Schreven et al. 1970). Although the effects of SCN^- are limited, SCN^- often works synergistically with other chemicals. For example, use with certain peroxides produces bacteriocidal solutions, although neither is effective alone (Beekhuis 1975). Similarly, SCN^- was more efficient in lysing cells when combined with other anions or lysozymes than when any agent was used alone at the same concentrations (Pollack et al. 1983).

Activity of aqueous plant extracts against pathogens or other organisms has been observed. Aqueous extracts of mustard (*B. campestris*) inhibited *Verticillium chlamydosporium* (Owino et al. 1993) and those of cabbage root inhibited *Glomus mosseae* spore germination (Vierheilig and Ocampo 1990). *B. napus* seed meal extracts inhibited *A. euteiches* (Smolinska et al. 1997a), but slightly enhanced growth of a *Propionibacterium* (Rutkowski et al. 1972). Buffered seed homogenates of *Brassica hirta* (*S. alba*) inhibited growth of *Nematospora* by more than 99% (Holley and Jones 1985). Glucosinolates extracted from *Brassica kaber* and hydrolyzed in aqueous solution with myrosinase inhibited *Glomus intraradices* (Schreiner and Koide 1993b).

Suppression appears to be related, at least in part, to the solubility of compounds produced by glucosinolates in the tissue. 4-Hydroxybenzyl ITC has greater solubility than many ITCs and would be the most prominent glucosinolate product expected in *B. hirta* and *B. kaber* extracts. Several water-soluble glucosinolate products present in aqueous extracts of *B. napus* were inhibitory to *A. euteiches* (Smolinska et al. 1997a). In contrast, water extracts of cabbage tissues did not suppress *Aphanomyces* root rot of peas (Papavizas 1966). The dominant ITC in this tissue has low water solubility.

Volatiles from tissues or organic solvent extracts are often highly inhibitory toward microorganisms. These fractions are also most likely to contain highly active ITCs. Extracts of *B. juncea* (in which propenyl ITC is the most prominent product) made with 70% ethanol and added to growth media at 0.025%-0.8% were in several cases more inhibitory to bacteria than equivalent amounts of propenyl ITC (Kanemaru and Miyamoto 1990). Smaller amounts of other ITCs were also present in the extracts, possibly accounting for the greater toxicity. The authors suggest using mustard as a food preservative. Extracts ($CHCl_3$) of *B. kaber* roots expressed antifungal activity toward *Cladosporium cucumerinum* and *Glomus etunicatum* (Schreiner and Koide 1993a). Volatiles from *B. kaber* were not inhibitory to *G. intraradices*, most likely because relatively nonvolatile 4-hydroxybenzyl ITC is the major glucosinolate product in these tissues. As might be expected from its glucosinolate profile, *B. nigra* volatiles were inhibitory toward this organism (Schreiner and Koide 1993b). Volatiles from *B. nigra* and *B. juncea* tissues severely inhibited *Fusarium sambucinum* (Mayton et al. 1996), from *B. napus* and *B. juncea* roots suppressed *Gaeumannomyces graminis* (Angus et al. 1994), and from *B. napus* meal completely inhibited *A. euteiches* (Smolinska 1997b). In all cases, volatile ITCs were implicated as the responsible agents. This effect of volatiles from plant tissues on microorganisms has been termed "biofumigation" (Angus et al. 1994; Kirkegaard et al. 1993).

Studies of pathogen inhibition by glucosinolate-derived allelochemicals have also been described for soils. Cabbage vapors passed through soil columns reduced *Rhizoctonia solani* contained within that soil (Lewis and Papavizas 1974). Volatiles emanating from cabbage-amended soil that were passed through tubes containing *Pythium ultimum* and *Sclerotium rolfsii* cultures inhibited growth of the cultures, especially when warmed to 38°C (Gamliel and Stapleton 1993). Approximately one-third the incidence of *Fusarium* infection of oat crowns was observed when soils were covered with heavy *B. campestris* residue compared to light residue applications (Horricks 1969). Sealed vessels containing soil amended with leaf and stem tissue of nine cruciferous species markedly reduced populations of *Fusarium*

oxysporum compared to untreated soil and soil amended with alfalfa, wheat straw, chicken manure, or steer manure (Ramirez-Villapudua and Munnecke 1988). Inhibition of *Fusarium* was diminished or not detectable when cabbage-amended soils were left uncovered, but tissue amendment in combination with solarization was more effective than either solarization or amendment alone (Ramirez-Villapudua and Munnecke 1987).

Detailed investigations of the toxicities of individual isothiocyanates to growth stages of *Fusarium oxysporum* pathogens in forest nurseries have been conducted in the laboratory. Bioassays with four *F. oxysporum* isolates were conducted using sealed containers in which 0.3 µL of 2-propenyl, ethyl, buty, phenylethyl, benzyl, or phenyl isothiocyanate was allowed to volatilize. Propenyl and ethyl isothiocyanates were the most fungistatic of those compounds tested to mycelial growth. Sporulation and conidia viability were not affected by any of the isothiocyanates. However, the same concentrations of propenyl and ethyl isothiocyanates that only inhibited mycelial growth, completely suppressed conidia and chlamydospore germination of all isolates. Other glucosinolates releasing ethyl, benzyl, and phenethyl isothiocyanates were also fungitoxic to *F. oxysporum* conidia and chlamydospores. Changes in populations of the pathogen resulting from a green manure crop will only be achievable if conidia and chlamydospores are targeted, since decreased populations resulting from the direct inhibition of *F. oxysporum* mycelial growth seem unlikely. We concluded that the pathogenic *F. oxysporum* isolates typically infesting nursery soils in northern Idaho will be most suppressed by species of plants containing glucosinolates that release the highest concentrations of propenyl isothiocyanate such as *Brassica carinata*, *B. nigra*, and *B. juncea* (Smolinska et al., 2003).

Although the allelochemicals from glucosinolates are inhibitory to many organisms, incorporated organic matter may simultaneously stimulate microbial populations by providing increased amounts of carbon substrate. Incorporated *B. napus* residues were less stimulatory than corn residues to *Fusarium* root diseases in a forest nursery (James, personal communication 2002), but resulted in more disease than fallow treatments (James et al. 1996). This is a major obstacle to using meal amendments to control fungal pathogens in soil. Formulation technologies or amendment strategies must be developed to ensure that pathogen populations are not stimulated.

One of the more thoroughly studied pest inhibition systems includes the use of cruciferous amendments to control *Aphanomyces* root rot of peas and beans. The results indicate the successes and difficulties commonly encountered in research concerning the biological activity of glucosinolate-containing crops toward plant pests. In greenhouse studies of soils infested with the fungus, Papavizas (1966) tested leaf and stem amendments of several cruciferous plants, of which cabbage was the most effective. Controls contained no amendments. About 70% of the control plant roots were infected with *Aphanomyces;* soils amended with as little as 0.5% dried cabbage leaves showed approximately a tenfold reduction in root infection. The effects were still observed on plantings made 15 weeks after amendment. Interestingly, although *Aphanomyces* root rot was clearly suppressed, some amended soils actually had increases in *Rhizoctonia* root rot.

We suspected that volatile components were the responsible agents, so we tried to analyze headspace vapors above amended soils using aqueous trapping reagents and GC (Lewis and Papavizas 1970). No ITCs were detected in this case, but in contrast to decomposing corn, the vapors included CH_3SH (thiomethane), $(CH_3)_2S$ (dimethyl sulfide), and $(CH_3)_2S_2$ (dimethyl disulfide). Bioassays showed that these vapors were toxic to *Aphanomyces*, though much less so than ITC vapors which in some cases were 1000 times more inhibitory. Furthermore, these vapors could be trapped in aqueous solutions, which suppressed root rot only slightly (Lewis and Papavizas 1971; Papavizas and Lewis 1971).

Additional studies of microbial inhibition focused on conditions encountered in the field. In containerized plantings both inside and outside greenhouses, amendments of Brassicaceae tissues significantly reduced *Aphanomyces* root rot disease beyond fallow and wheat-amended treatments by 32%-38% (Chan and Close 1987). When Brassicaceae crops were grown in soil instead of being introduced as amendments, reductions averaged 41%. Davis (1988) found in field studies that wheat in rotation had very little effect on *Aphanomyces*, and that a greater reduction was observed when rapeseed varieties were used. However, neither cropping with rapeseed nor amending with rapeseed tissues resulted in reductions more significant than with oats. In other field studies, similar disease reductions to those observed with rapeseed also occurred with oats and corn (Papavizas and Lewis 1971; Parke and Rand 1989). Root rot severity was reduced in field tests using a white mustard (*S. alba*) green manure but no difference in yield was observed compared to fallow, perhaps because of reduced pea emergence in white mustard treated plots (Muehlchen et al. 1990). However, continuing a second cycle of peas and white mustard resulted in reduced root rot severity and increased yield in spite of a similar reduction in pea emergence. Careful study of the variables influencing allelochemical efficacy is needed to consistently and effectively control pests.

B. napus meal has been used for pest control in a limited number of studies. Anti-fungal activity against *Cylindrocladium parasiticum* has been reported (Bhardwaj et al. 1996). The investigators applied 1, 2, or 3 t ha^{-1} of *B. napus* meal to soil and compared *C. parasiticum* control in peanuts to control by Vapam. The University of Idaho supplied the meal to the investigators. All three rapeseed meal rates reduced disease incidence of Cylindrocladium black rot of peanuts. A maximum 70% reduction in disease incidence (compared to an untreated control) occurred in the 3 t ha^{-1} treatment of peanut cultivar susceptible to the disease. Although glucosinolate concentration of the meal was not mentioned, the concentration was likely less than 50 μmol g^{-1} and thus substantially below what is contained in mustard meals.

Attempts have been made to control other fungal pathogens using meal. Dandurand et al. (2000) used *B. napus* cv. "Dwarf Essex" meal in laboratory experiments to control *Sclerotinia sclerotiorum* and *A. euteiches*. A 100% reduction in carpogenic germination and a 33% reduction of myceliogenic germination of *S. sclerotiorum* occurred in soil amended with Dwarf Essex meal. A low glucosinolate *B. napus* meal (Stonewall) reduced carpogenic germination by 44% and had no effect on myceliogenic germination, indicating that glucosinolate hydrolysis products were critical to suppression. *A. euteiches* root rot of pea was reduced 77% by Dwarf Essex meal and was unaffected by low glucosinolate Stonewall

meal. In all experiments meal was not homogeneously incorporated into the soil, but was placed on the bottom of the bioassay container and separated from the overlying soil by sterile fiberglass cloth.

In summary, fungal and bacterial pathogens can likely be controlled by glucosinolate-containing meals. Previous research was conducted most often with *B. napus* meal containing glucosinolate concentrations less than 50 μmol g^{-1} tissue. Higher concentration glucosinolate meals will be more effective. Experimentation must be conducted to determine whether the additional carbon contributed from the meal exerts a growth-promoting effect on the fungal pathogens, thereby decreasing the pesticidal efficacy of the meal. Amendment techniques or formulations must be optimized to decrease growth promotion of the pathogen.

C. Allelochemical Effects on Insects and Other Invertebrates

As with other organisms, organic extracts of glucosinolate-containing plant tissues have marked effects on insects. Usually extracts are placed on a medium such as filter paper and the solvent is evaporated (controls contain solvent only). Lichtenstein et al. (1964) found root extracts of Brussels sprouts to be very toxic to *Drosophila melanogaster*, as demonstrated by 50% mortality in 10 min. Macerated root tissue was quite toxic also; 50% mortality in 3 h for *Drosophila* and 50% mortality in 24 h for the common housefly *Musca domestica*. Toxicity was in most cases strongly correlated with phenylethyl ITC content. Tissues that produced mortalities but did not possess phenylethyl ITC produce other ITCs.

Insecticidal activity of several ITCs has been demonstrated, especially for aromatic compounds (Åhman 1986; Borek et al. 1995b; Chew 1988a; Lichtenstein et al. 1962, 1964; Seo and Tang 1982; Wadleigh and Yu 1988). Borek et al. (1995b) tested the toxicities of six commercially available ITCs to eggs of the black vine weevil (*Otiorhynchus sulcatus* (F.)) and concluded that aromatic ITCs were most toxic. Later the same group of investigators showed using an expanded set of 12 ITCs and QSAR relationships that ITC polarity was most important in explaining observed toxicities (Borek et al. 1998). Using a linear-structure-activity relationship they predicted that the highest contact toxicities of ITCs to black vine weevil eggs will occur from glucosinolates producing ITCs with higher numbers of carbon atoms or those bearing sulfinyl, thio, or aromatic moieties.

Whitefringed weevil larvae (*Naupactus leucoloma*) were used as bioassay organisms to test the toxicity of volatile and nonvolatile glucosinolate hydrolysis products (Matthiessen and Shackleton 2000). Comparisons of the toxicity of two pure ITCs in the headspace of sealed containers showed that methyl ITC vapors were more toxic than phenylethyl ITC across a temperature range of 5°-20°C. The toxicity of volatiles from *B. juncea* meal (assumed to be propenyl ITC) were more toxic than those from *B. napus* meal when equal weights of the tissues were compared. Water-soluble products displayed no toxicity to weevil larvae.

In screening products to protect seedling corn from injury by southern corn root worm (*Diabrotica undecimpunctata howardi*), propenyl ITC killed the worm but also prevented the corn seeds from germinating (Landis and Gould 1988). Methyl ITC is mainly used to control

various fungi that cause damping off and root rot, but is also used to control insects such as wireworms and symphilids, and nematodes (Beekhuis 1975; Mullins and Kirkbright 1987; Sirons 1973; Toba 1984; Worthing 1987). Propenyl ITC was the most effective of 57 volatile compounds tested against the wireworms *Limonius californicus* and *Limonius canus*, with an LC_{50} of 2.33 µg mL^{-1} (Lehman 1942). Rapeseed meal amended (3% on a weight basis) to soil repelled wireworms (*L. californicus*), but in uncovered containers did not kill them (Brown et al. 1991). Maximum total ITC content of 301 nmol g^{-1} soil decreased rapidly. Subsequent testing using propenyl ITC in the same soil showed that wireworms were killed in lower but similar concentrations in capped vials (LC_{50} range 211-238 nmol g^{-1} soil) and that propenyl ITC added to soil was more persistent than ITC produced from the rapeseed meal-amended soil in the previous test (Williams et al. 1993). However, glucosinolate products like ITCs are not always toxic to insects at concentrations found in plant tissues. In fact, ITCs can act as cues or even attractants influencing the behavior of certain insects (Finch and Skinner 1982; Pivnick et al. 1991; Rodman and Chew 1980; Traynier and Truscott 1991).

Other glucosinolate hydrolysis products have insecticidal properties as well. Organic thiocyanates have been used in insecticides to control weevils in grain and to produce quick knockdown of flying insects such as flies, and have a relatively low impact on mammals (Beekhuis 1975; Wood 1975). 3-Indolylacetonitrile, known more for its auxin-like activity on plants, also inhibits growth of insects (Smissman et al. 1961). SCN^- is ineffective when used alone, but is insecticidal in combination with other chemicals (Beekhuis 1975). SCN^- was toxic to wireworms only at concentrations much higher than observed in rapeseed meal-amended soil (McCaffrey et al. 1995).

Invertebrate plant pests other than insects are also potential targets. Winkler and Otto (1980) found that rotational plantings of rape or mustard in strawberries checked the spread of some nematodes, particularly *Pratylenchus penetrans*. Leguminosae, potato, or grass rotations did not alter nematode populations, although green manure applications of Leguminosae (peas, beans and vetch), rape, or mustard reduced nematode numbers. Similarly, growing rapeseed in soil and incorporating the tissue as a green manure significantly reduced populations of *Meloidogyne chitwoodi* compared to fallow (Mojtahedi et al. 1991), although results were not as clear in a study involving *Meloidogyne incognita* and *Meloidogyne javanica* (Johnson et al. 1992). In the presence of myrosinase, glucosinolates are toxic to *Heterodera schachtii* at concentrations of 0.5-5.0 mg mL^{-1} (Lazzeri et al. 1993). Some varieties of *Brassica* crops are being offered commercially as "trap crops" for nematodes. Rather than killing the nematodes, *Brassica* plants interfere with nematode reproductive cycles. Biochemical mechanisms responsible for nematode resistance and suppression, although not well understood (Lazzeri et al. 1993), deserve further attention.

Rapeseed meal has been used as a soil amendment in an attempt to control nematodes. Investigators applied 1, 2, or 3 t ha^{-1} of *B. napus* meal to soil and compared control of the soybean cyst nematode *(Heterodera glycines* Ichinohe*)* in soybean to chemical control by aldicarb (Bhardwaj et al. 1966). The University of Idaho supplied the meal to the investigators. The results were ambiguous, and acceptable control was not achieved. Higher glucosinolate concentration meals are thus necessary to control this plant pest.

IV. Management Considerations

The evidence strongly supports the idea that glucosinolate degradation products are biologically active and have considerable potential for use in pest control strategies. However, many factors must be considered when these strategies are implemented if we are to take full advantage of this natural pesticidal activity. Release efficiency and release rate from plant tissues, susceptibility of the target species, effectiveness of the particular glucosinolate degradation product, soil texture, organic matter, pH, moisture content, and effectiveness of the products in the aqueous and vapor phases all contribute to pesticide efficacy.

Understanding the processes and fates of the allelochemicals in soil is crucial for maximizing potential benefits in pest control and minimizing potential negative environmental impacts. Soils and soil/plant interactions may influence which products are formed and their effectiveness in the soil environment. Although additional work is necessary in this area, enough data have been collected to make some observations and generalizations concerning the behavior of several glucosinolate products in soil.

A. Product Formation

Conditions affecting product formation during glucosinolate degradation have most often been examined in isolated plant tissue systems. For pest control, however, we are particularly interested in what happens in soil. As discussed in previous sections, the plant's glucosinolate profile and characteristics of the solution in which hydrolysis takes place control qualitative aspects of product formation. When plant tissues are incorporated into soil, the soil's influence on product formation may be linked as much to its moisture content as other soil characteristics. Under drier conditions little soil solution is available to influence the reaction, and the effects of pH and metal ions on product formation could be determined solely by the reaction microenvironment of the plant tissue. However under more moist or wet conditions, the soil solution and soil colloids are much more likely to participate in reactions that alter product formation.

Glucosinolate products such as ITCs, SCN^-, OZTs, and to a lesser extent nitriles are produced in soil amended with plant tissue (Brown et al. 1991, 1994). Nine glucosinolate degradation products—five ITCs, three nitriles, and one OZT—were identified in field soils extracted after a *B. napus* plow-down (Gardiner et al. 1999). The most abundant products were 2-phenylethyl ITC and benzenepropanitrile. ITCs have also been collected in the rhizospheres of a few plants (Tang and Takenaka 1983; Yamane et al. 1992), including *B. napus* (Kirkegaard et al., 2001).

A model system using propenyl glucosinolate and myrosinase amendments was used to investigate product formation in six soils at two moisture contents of field capacity (0.033 MPa) and saturation. Propenyl ITC was produced as the dominant product regardless of soil characteristics (Borek et al. 1994). Only minor amounts of propenyl CN were detected.

Sinigrin and myrosinase added to unbuffered aqueous soil extracts resulted in greater proportions of nitrile, and in some cases nitrile became the dominant product. Glucosinolate hydrolysis produces H^+, decreasing solution pH as the reaction proceeds. Although this enhances nitrile formation in unbuffered extracts, soils provide a large buffering capacity that in effect prevents nitrile formation. None of these soils were more than moderately acidic (pH of 5.65-8.3), so glucosinolate hydrolysis in wet acidic soils (pH < 5) may result in more nitrile formation. Conditions favoring production of ITCs could be advantageous for pest control since these are typically the most biologically active products.

Additionally, product release rates and efficiencies must be considered. Although lower in total glucosinolate content, root and shoot tissues of *B. napus* realeased volatile products more efficiently than did meal tissue (Brown and Morra 1995, 1996). The condition of the tissue is also important. Fresh tissues may release products more slowly than those physically disrupted before amendment by tissue crushing, air drying, freeze drying, or grinding. Lower maximum concentrations are thus likely to be produced from fresh tissue, but the period of release is potentially extended. Recent investigations indicate that maceration of green tissues is indeed necessary to maximize ITC release (Morra and Kirkegaard 2002). Such a limitation does not exist when using meal amendments as soil additives since the seed crushing procedure has resulted in extensive cellular disruption.

B. Product Activity and Fate

1. Lifetimes

Lifetimes of glucosinolate products in the environment are generally short, an advantage when considering environmental impact. ITCs remain in soil for a few days to a few weeks. Even in gas-tight containers, half-lives of methyl ITC in several soils were 0.5-50 d at 15^{o}C (Smelt et al. 1989). Concentrations of methyl ITC in greenhouse air, where soil had been amended with metham-sodium, were reduced to less than 0.2% of the original amount by the third day (Van Den Berg et al. 1992). One week after a major spill of metham-sodium into the Sacramento River of California, neither metham-sodium nor the methyl ITC hydrolysis product was detectable (del Rosario et al. 1994). In a germination test 80% of the inhibitory capacity of propenyl ITC in soil was gone after 2 weeks (Bell and Muller 1973). Other research showed that the half-life of propenyl ITC in six soils was 20-60 h; propenyl CN had a longer half-life of 80-100 h. The average half-life in all six soils was 48 h for propenyl ITC and 96 h for propenyl CN (Borek et al. 1995a). Biological effects of volatile ITCs should be short-lived, especially in uncovered soils. The potential for negative environmental consequences is therefore quite small and is illustrated by the fact that no methyl ITC residues were detected in more than 200 surface water samples (Hogendoorn et al. 1992). However, a short residence time places limits on achieving effective pest control and may contribute to the variability observed in the suppression of soil-borne plant pests.

Lifetimes of allelochemicals produced *in situ* in plant tissue-amended soil differ from those of the respective pure chemicals amended to soil without plant tissue. Ninety percent of the maximum ITC in rapeseed meal-amended soil dissipated within 24 h (Brown et al. 1991),

whereas only 60% of propenyl ITC amended in the form of an aqueous phase mixture to the same soil was lost in 24 h (Williams et al. 1993). This is consistent with the finding that an average of 30% propenyl ITC, when added in pure form, was lost in six soils during a 24 h period (Borek et al. 1995a). Accelerated dissipation of ITC thus occurs in the presence of plant tissue amendments, most likely because of sorption to the additional organic carbon.

Lifetime of SCN^- in soil is also relatively short. Losses of SCN^- in four soils were 40%-95% over a six-day period (Brown and Morra 1993). In contrast to ITC, however, SCN^- produced *in situ* in rapeseed meal-amended soil dissipates more slowly, having an extended lifetime in the presence of such tissues (Brown and Morra 1993; Brown et al. 1991). Adding propenyl ITC along with solutions of SCN^- to soil inhibited SCN^- loss, demonstrating that combinations of glucosinolate products may alter the behavior of individual products in soil. In this case, propenyl ITC most likely inhibited microbial activity and the corresponding microbial degradation of SCN^-.

2. Volatilization

ITC disappears via many routes; volatile losses are one major route. Unsealed bottles had much greater losses of methyl ITC than sealed bottles (Ashley et al. 1963). Thirty-four percent of the methyl ITC in spiked soil was recovered in an air stream passing through it, and nearly all of that within 10 h (Munnecke et al. 1962). Vapor pressures for methyl ITC have been reported as 13 and 20.7 mm Hg at 20°C, relatively low values for a fumigant (Sirons 1973; Smelt and Leistra 1974); thus, volatile losses may be less of a problem for ITCs than for some commercial products. However, volatilization is important for even distribution of fumigants in soil. Vapor pressures of various ITCs and nitriles vary widely, so large differences in soil fumigation resulting from glucosinolate hydrolysis products are expected.

Loss of ITC into the atmosphere is not desirable, since that amount of product is not available for pest inhibition. Volatile losses could also be of concern for health and environmental reasons. Photodissociation by sunlight appears to be one rapid and effective pathway for removing methyl ITC from the atmosphere, taking about 41 h (Alvarez and Moore 1994). This process would likely apply to other ITCs; however, questions remain as to the fate and impact of dissociation products (Geddes et al. 1995).

3. Organic Matter

Many fumigants are less effective in soil than in nonsoil systems. This is particularly true of ITCs. Propenyl ITC was about 193 times more toxic to wireworms than CS_2 (carbon disulfide) in air, but was only about 29 times more toxic in a silt-loam soil (Lehman 1942). Similar results were found with methyl ITC compared to CS_2 and other fumigants (Matthiesson et al. 1996). Phytotoxicity to wheat from *Brassica* residues or extracts was generally greater when wheat was grown in sand than in soil (Mason-Sedun and Jessop 1988).

Sorption of ITCs to soil constituents is an important mechanism that decreases ITC effectiveness. Sorption of methyl ITC to soil increases with increasing organic matter content (Munnecke and Martin 1964; Smelt and Leistra 1974). As a result, much less methyl ITC is extractable from organic muck soils than from mineral soils (Sirons 1973). Although Ashley et al. (1963) determined that the disappearance of extractable methyl ITC was slowest in a peat soil amended with metham-sodium, amounts of extractable ITC could have been controlled by metham-sodium hydrolysis rates instead of ITC sorption. As generally observed for methyl ITC, increased propenyl ITC disappearance from soil is correlated with greater organic carbon contents and typically greater nitrogen contents (Borek et al. 1995a). This trend was not apparent for the corresponding nitrile. Faster ITC disappearance likely results from greater reactivity with nucleophilic groups commonly found in soil organic matter such as alcohols, phenols, thiols, carboxylic acids, and amines. These types of reactions may also explain reduced efficiency of volatile ITCs released from seed meal tissue compared to other plant tissues (Brown and Morra 1996). Amino groups in protein, contained in high concentration in rapeseed meal, readily react with ITCs (Björkman 1973; Kawakishi and Kaneko 1987) and reduce measured volatile concentrations.

4. Temperature

Methyl ITC sorption to soil is not greatly enhanced by increasing the temperature from 4^{o} to 30^{o} C (Matthiessen et al. 1996), although elevated temperatures are correlated with increased amounts of ITC in the vapor phase and faster rates of disappearance from soil (Ashley et al. 1963; Borek et al. 1995a; Turner and Corden 1963). Increased temperature was also associated with a greater inhibitory effect toward pathogenic fungi in a covered cabbage-amended soil (Gamliel and Stapleton 1993), probably because of more thorough fumigation. Greater concentrations of volatile thiomethane, dimethyl sulfide, and propenyl ITC were observed at elevated temperatures. Temperature influences the fate of nonvolatile products as well. For example, higher temperature generally increased disappearance rates of SCN^{-} in soil (Brown and Morra 1993).

5. Water

Aqueous solubilities control ITC partitioning in the three-phase soil system. Methyl ITC has reported solubilities in water of 7.6 mg mL^{-1} (Sirons 1973) and 8.9 mg mL^{-1} (Smelt and Leistra 1974) at 20^{o}C. Estimates of methyl ITC distribution between the vapor, aqueous, and solid phases of soil indicate that most of the ITC is in the aqueous phase under moist conditions, with a substantial amount retained in the solid phase (Smelt and Leistra 1974). Although ITC in solution still has biological activity, uneven distribution in soil is likely caused by localized concentrations and reduced diffusion (Leistra et al. 1974). This heterogeneity could contribute to variations in effectiveness. We do not know whether ITCs such as 4-hydroxybenzyl ITC with greater water solubility would have greater pesticidal activity than more volatile and less soluble ITCs under wet conditions. Methyl ITC was susceptible to leaching with high moisture in sandy soil (Frick et al. 1995), therefore, other ITCs may leach in permeable soils subjected to large water inputs. Henry's constants must therefore be determined for the ITCs of interest to better predict partitioning within the three-phase S soil environment.

Increased water content increases ITC longevity in soil. More methyl ITC was measured in headspace of soils with lower water contents and rates of disappearance were more rapid (Turner and Corden 1963). Although 30% of applied methyl ITC was lost by volatilization under a drier moisture regime, very little vapor phase methyl ITC was lost during a wet regime (Frick et al. 1995). Increased water content increased the half-life of propenyl ITC (Borek et al. 1995a). Thus continually wet conditions, especially when combined with cold temperatures, could result in increased ITC lifetimes and perhaps increased potential for pest inhibition resulting from longer exposure times. This could also extend the risks of residual effects on subsequent plantings.

In contrast to ITC, increased soil moisture content accelerates the disappearance of propenyl CN (Borek et al. 1995a). The fates of ITCs and organic nitriles in soil, at least in the case of propenyl derivatives, appear to be controlled by different mechanisms. Propenyl CN is sorbed or reacts more quickly at the water phase than at the gas phase, which may indicate that the overall reaction rate for nitriles is controlled by the gas/water phase partition coefficient.

6. Soil Texture

Volatile losses are greatest from coarse textured soils, but texture is less important than factors such as organic carbon content. In a comparison of three soils, volatile loss of methyl ITC was greatest from a sandy loam (0.67% organic matter, 8% clay); least volatilization occurred from a loam with more clay but also greater organic matter (2.03% organic matter, 25% clay). The finest textured soil, a clay loam (0.55% organic matter, 40% clay), had intermediate losses of methyl ITC compared to the other two soils (Munnecke and Martin 1964). Extractable concentrations of methyl ITC obtained from sandy, clay, and loam soils amended with metham-sodium are similar for the first few hundred hours (Ashley et al. 1963). As such, evidence suggests that sorption to soil clay is not a major mechanism of disappearance for ITCs. In contrast, sorption to or degradative catalysis by inorganic soil constituents may play a role in SCN^- disappearance from soil, particularly at higher temperatures (Brown and Morra 1993).

7. pH

Soil pH influences the formation and disappearance of glucosinolate hydrolysis products, although effects on disappearance are not dramatic. Greater amounts of methyl ITC were trapped in headspace from soils adjusted to a higher than to a lower pH (Munnecke and Martin 1964), and additing lime to three soils tended to shorten residence times of methyl ITC in soil (Ashley et al. 1963). No correlation between soil pH and propenyl ITC or propenyl CN disappearance was observed for six soils ranging in pH from 4.35 to 9.10 (Borek et al. 1995a). Typical pH values of agricultural soils are thus not expected to greatly alter allelochemical residence times.

8. Microbial Activity

Microbial degradation may also be responsible for the disappearance of glucosinolate hydrolysis products. Soil sterilized with heat and soil extracts sterilized by filtration or heating slowed the disappearance of methyl ITC in sealed bottles (Ashley et al. 1963). Accelerated loss of methyl ITC after successive soil applications has been demonstrated in field and laboratory studies (Smelt et al. 1989).

Although microbial degradation is suggested by these data, this is not a consistent observation. For example, attempts to sterilize soil by autoclaving or ethyleneoxide treatment did not change disappearance rates of propenyl ITC (Borek et al. 1995a). The same soil treatments increased propenyl CN half-life only slightly. In contrast to soils that appear to have enhanced degradation, a second treatment of fumigant to soil did not enhance ITC disappearance (Ashley et al. 1963) and two soils treated at least 13 times showed no increase in the ITC disappearance rate (Smelt et al. 1989). Similarly, five additions of propenyl ITC or propenyl CN during a period of 10 d failed to alter the half-lives of these chemicals (Borek et al. 1995a). No clear evidence demonstrates that biotic transformation controls the fate of ITCs in soil. The relative importance of microbial activity in the degradation of organic nitriles is also unclear, although biotic degradation is probable. Numerous microorganisms have been isolated that degrade aliphatic nitriles and a few that degrade aromatic nitriles (Nawaz et al. 1991, 1992).

Several bacteria have been identified that degrade SCN^- (Betts et al. 1979; Happold et al. 1958; Katayama and Kuraishi 1978; Putilina 1961; Smith and Kelly 1988; Stafford and Callely 1969). SCN^- is rapidly broken down, and a flush of growth after breakdown results from the added nitrogen source (especially for NH_4SCN). Even after temporary sterilization with 897 kg NH_4SCN ha^{-1} marked stimulation of plant growth began to occur after 69 d (Beekhuis 1975). Other investigations showed that autoclaving soils before incubation and adding NaN_3 or propenyl ITC slowed SCN^- disappearance (Brown and Morra 1993). Disappearance of SCN^- was correlated with organic carbon content of soils when temperatures were at or below 30°C. This suggests that SCN^- losses are related to the amount of carbon available to support microbial activity rather than SCN^- sorption to the organic carbon fraction of the soil.

Results for methyl ITC and propenyl ITC discussed throughout this section are not necessarily the same as for other ITCs because of the influence of the R group chemistry. Different R groups affect volatility and solubility, resulting in altered biological activities. As a consequence, individuals involved in efforts to develop plant varieties for pest control should consider glucosinolate type as well as total glucosinolate concentration.

C. Additional Allelochemicals

Numerous other S-containing compounds, mainly volatiles, have been identified as secondary products of glucosinolates in cruciferous tissues. Methanethiol, dimethyl sulfide, and dimethyl disulfide are produced in cabbage-amended soils (Gamliel and Stapleton 1993). Although these compounds possess lower toxicities than ITCs (ITCs > thiols ≅ thiocyanates > sulfides), they are produced in larger amounts and for much longer periods than propenyl ITC (Gamliel and Stapleton 1993; Lewis and Papavizas 1971; Virtanen 1965; Walker et al. 1937). Greater total amounts and longer production times may compensate for lower toxicities, increasing the potential importance of these compounds in pest inhibition.

Several of these S-containing compounds may result from abiotic or biotic degradation of primary glucosinolate hydrolysis products. Two water soluble degradation products of 4-methylthio-3-butenyl ITC, one identified as 2-thioxo-3-pyrrolidinecarbaldehyde, were fungicidal (Uda et al. 1993). Some smaller molecular weight products might be explained by the simple loss of a part of the molecule such as methanethiol from thioalkyl ITC (Uda et al. 1990). Other compounds, including COS, H_2S, and CS_2 are formed from ITCs by a series of hydrolysis reactions (Bailey et al. 1961; Challenger 1959; Dateo et al. 1957). Alternatively, H_2S so generated might react with CO_2 and produce COS (Shaw et al. 1980). Aerated and waterlogged soils amended with SCN^- produced COS via an unknown mechanism (Minami and Fukushi 1981). Only COS was produced in a waterlogged soil amended with SCN^-, although samples were monitored for H_2S, CH_3SH, CH_3SCH_3, CS_2, and CH_3SSCH_3 (Minami 1982). Bending and Lincoln (1999) suggest with respect to fresh tissues that other volatile S compounds were likely to be as important in pest control as ITCs. Further information regarding reaction pathways would enhance our ability to predict and optimize pest control efficiency.

Other compounds besides products of glucosinolate degradation may be biologically active and thus contribute to pest inhibition. For example, S-containing indole compounds found in *B. campestris* and *B. oleracea* are not derived from glucosinolates and act as phytoalexins (Monde et al. 1991; Takasugi et al. 1988). In addition, phenolic compounds are sometimes suspected as biologically active agents in cruciferous plants (Kutácek 1964), a possibility since seed meals of some *Brassica* contain relatively higher phenolic compound concentrations than other sources (Shahidi and Naczk 1992). Given the ubiquitous nature of phenolics, biological activity may be related more to quality than quantity (Levin 1971; Singleton and Kratzser 1973). Although phenolics are often suggested to participate in plant defenses against infection, little work appears to have been done on the potential pesticidal activity of specific phenolics in *Brassica* seed meals.

Additional inhibitory compounds may be produced by breakdown of the S-containing amino acids methionine and cysteine. Compounds such as methanethiol, dimethyl disulfide, and dimethyl trisulfide are derived from the non-protein amino acid *S*-methyl-1-cysteinesulfoxide (SMCSO) via a methyl methanethiosulfinate intermediate (Chin and Lindsay 1994; Marks et al. 1992; Maruyama 1970; Ostermayer and Tarbell 1960). The intermediate is produced

either enzymatically by cysteine sulfoxide lyase or nonenzymatically under acidic conditions. SMCSO constitutes 0.25%-2% (dry weight) of the tissue in *Brassica* plants (Gosden 1979; Marks et al. 1992), which indicates that contributions to pesticidal activity could be significant. Ensiled forage rape (*B. napus*) contained approximately 83% of the original SMCSO content, but only one-tenth the original glucosinolate content (Fales et al. 1987), suggesting SMCSO may be less susceptible to rapid degradation and thus remain available for longer time periods.

In some cases, methanethiosulfinate is proposed to react with H_2S to form thiols and sulfides (Chin and Lindsay 1994). Any H_2S produced from ITCs could thus react with SMCSO products to form yet additional allelochemicals. Optimal pest inhibition may require combined interactions of glucosinolate products, SMCSO products, and additional compounds produced by reactions between components of these two pools. Various products could be formed simultaneously or sequentially, with one suite of biologically active compounds replacing another during an extended period. Effects on nematodes have been observed to last several weeks (Santos and Mojtehedi, personal communication) suggesting the involvement of other compounds beyond the active lifetime of volatile ITCs.

D. Glucosinolate Concentrations

Yield data for many plant/soil/pest systems suggest that glucosinolate concentrations are, or border on being, sufficient for pest control. Efforts to develop plants with high glucosinolate levels for pest control are worthwhile. Since the traditional approach of plant breeders has been to select for reduced concentrations of glucosinolates, concentration increases are likely. Eventually perhaps, particular strains of plants with specific glucosinolate profiles could be developed for specific targets susceptible to the respective glucosinolate products.

Breeding may not be the only means to increase product concentration. Some limited increases in resistance have been achieved by applying synthetic ITC precursors to *Brassica* plants (Dawson et al. 1993; Griffiths et al. 1989). Methyl jasmonate and salicylic acid, other compounds that occur naturally, have been associated with increased levels of certain glucosinolates in leaves when applied to those tissues (Doughty et al. 1995; Kiddle et al. 1994). Perhaps glucosinolates could be applied to plant surfaces in a resistance strategy or to the soil (combined with myrosinase) for pest suppression. Although synthetic inputs would not be eliminated, reductions might be achieved by supplementing plowed-under plant tissues with low levels of commercial ITC-producing fumigants.

Although data are limited, we can look quantitatively at the question of glucosinolate concentrations and the potential to control plant pests. The amount of methyl ITC recommended for soil applications using sodium N-methyldithiocarbamate can be estimated by assuming a 15.2 cm depth of incorporation, soil bulk density of 1.4 g cm^{-3}, and 100% conversion to methyl ITC (Brown et al. 1991). Calculated values were 517-1294 nmol methyl ITC g^{-1} soil depending on the crop and type of control required. These are higher than the amount of ITC (301 nmol g^{-1} soil) observed in soil amended with rapeseed meal-amended at a rate of 3% (w:w) (Brown et al. 1991). To kill 50% of wireworms (*L.*

californicus), rapeseed meal had to be amended at a rate of 114 g kg^{-1} soil (Elberson et al. 1996), too high to be useful. However, the same level of control for black vine weevil (*Otiorhynchus sulcatus*) required only 19 g rapeseed seed meal kg^{-1} soil (Borek et al. 1996b).

The previous studies were performed with rapeseed meal having a glucosinolate concentration near 40-50 µmol g^{-1} tissue. Complete release of glucosinolate to ITC has not been observed (Brown et al. 1991; Brown and Morra 1995). Instead, the data indicate that a maximum of 20% of the glucosinolate will be released as ITC from rapeseed meal (Brown et al. 1991). If we now assume similar release efficiencies for mustard meals that contain glucosinolate concentrations of 250 µmol g^{-1} tissue, we can estimate the amount of meal necessary to approach the recommendations application rates for commercially available ITC fumigants (517-1294 nmol methyl ITC g^{-1} soil). A 1% (w:w) meal amendment to soil of a meal containing 250 µmol glucosinolate g^{-1} tissue would result in the release of 500 nmol ITC g^{-1} soil. We are now at the lower limit of what is considered necessary for soil sterilization. Doubling the amendment rate to 2% (w:w) would increase predicted ITC release to 1000 nmol g^{-1} soil and thus achieve a concentration considered near the upper limit of that recommended for commercial fumigants. Thus, meals with glucosinolate concentrations in excess of 200 µmol g^{-1} tissue may indeed be effective in pest control at practical tissue amendment rates.

E. Timing

Length of exposure to the allelochemical is one variable associated with timing. Lewis and Papavizas (1971) showed in sealed containers that concentrations failing to kill microorganisms in 2 d might kill them in 4-6 d. Evidence indicates similar results with insects and seeds (Lichtenstein et al. 1962, 1964; Pieczarka and Warren 1960). Dormant seeds making up the seed bank in soil and exposed to root exudates over a period of time could be more susceptible to inhibition than introduced seeds exposed to root exudates for only a short time.

Another important variable is the time when initial exposure occurs; in other words, the time when the target organism is introduced to the glucosinolate-containing tissue. Pea seeds planted immediately after soil amendment with cabbage did not germinate. Peas planted 3 weeks later showed some reduction of growth if fresh leaves were used, but not if air-dried leaves were used. Plantings after 7 weeks showed no growth reduction or slight growth enhancement (Papavizas 1966). Only fresh cabbage juice inhibited lactic acid (*Leuconostoc mesenteroides*) bacterial growth (Kyung and Fleming 1994). Inhibition of germination and plant growth by ITCs was most effective when the chemicals were applied to seeds or applied within the first 3 d of the germination period (Leblová-Svobodová and Koštír 1962).

Timing maximal glucosinolate product formation with a susceptible life stage of the target organism may be necessary. Glucosinolate concentrations in plants usually start out low, climb with fluctuations to some maximum, then drop off near the time of plant senescence (Freer et al. 1989; Griffiths et al. 1991; Macfarlane-Smith and Griffiths 1988). Aqueous extracts of wild mustard were most effective at inhibiting growth when extracts were made

during the bolting and flowering stage (Jiménez-Orsornio and Gliessman 1987). Coplantings of *Brassica* plants with other plants do not inhibit seed germination or plant growth (Bell and Muller 1973; Choesin and Boerner 1991), perhaps because plant stages susceptible to inhibition are past by the time sufficient glucosinolate products are present. In the case of coplanting with two *Brassica* species, planting wild mustard with broccoli resulted in higher broccoli yields, but wild mustard planted before broccoli inhibited broccoli yield (Jiménez-Orsornio and Gliessman 1987). In a consistent fashion, insects and microorganisms may be more susceptible at certain stages in their life cycle. Relatively sudden releases and higher concentrations of products from amendments timed to susceptible stages of an organism's life cycle would be most effective.

F. Additional Benefits

Other benefits may be obtained by using glucosinolate-containing plants in pest control strategies. For example, soil structure is improved by use of organic amendments and high root development like that in oilradish and mustard is important to prevent soil erosion and nitrate leaching. Reports in the literature also indicate that *B. napus* is efficient at absorbing phosphorus from deficient soils (Grinsted et al. 1982; Hedley et al. 1982b). In addition, plant tissue amendments can serve as nutrient sources and high protein-containing rapeseed meal may be used as a supplementary nitrogen source (Johansson and Ascard 1994; Kücke 1993). Carbon to nitrogen ratios of *B. juncea*, *S. alba*, and *B. napus* meals range from 7 to 10 (Morra and Johnson-Maynard 2003). Mineralizing the meal will thus provide a substantial amount of plant available N and no immobilization. Biofumigating compost with seed meal would thus add nitrogen to the mix and simultaneously reduce unwanted weed seeds and disease pathogens.

V. Crushing and Extraction Technology

Current methods of cold pressing the meal result in residual oil of 5%-10% on a weight basis. Residual oil may help trap hydrophobic ITCs, prevent volatile losses, and increase pesticidal effectiveness. However, residual oil may also decrease the release efficiency of ITC from the meal into the soil and decrease its effectiveness. The overall impact of residual oil in the meal will vary with the ITC and its respective hydrophobicity. The effect of the oil on pest control has never been determined.

Commercial crushing facilities produce temperatures in the seed and seed meal that may deactivate myrosinase. Temperatures are increased on purpose to maximize oil extraction or unintentionally if an extrusion process follows crushing. The maximum temperature at which myrosinase integrity is maintained during a commercial crushing procedure has not been determined.

Current research is focused on using the meal as a carrier for the pesticide. The meal will also provide plant nutrients in addition producing ITC for pesticide control. However, the meal will also provide a carbon source for fungi and potentially increase pathogen problems. Extracting the ITC before soil application may circumvent this problem.

Techniques have been developed for extracting propenyl isothiocyanate from *B. juncea* meal using a commercially available unit. A commercial enterprise has been started by Mr. Peter Fergeson (Peter_I.M. Ferguson@eol.ieaust.org.au) in NSW Australia to extract propenyl ITC using a unit built by Flavourtech (33 Lenehan Rd., Griffith, NSW 2680, Australia). The ITC is then marketed to Japanese companies that use it as a food additive. Using a similar approach for producing pesticides seems feasible.

VI. Allergenic Reactions

Although the compounds are produced by plants, human and animal toxicity is still a concern if alternative pest control strategies are to be implemented. Do natural toxic substances in plants have advantages over synthetic pesticides? In contrast to a new synthetic pesticide, much information about the toxicology of these products is already known because of the importance of cruciferous crops in human nutrition and animal diets.

When used as a primary food source, glucosinolate-containing plant material clearly has deleterious effects. Feeding kale to livestock can reduce fertility and induce goiter (Johnston and Jones 1966). Diets of crambe meal caused early death to rats (Daxenbichler et al. 1966), and in separate tests, rats fed crambe meal and rapeseed meal exhibited symptoms similar to rats with nitriles in their rations (Van Etten and Tookey 1979). Livestock poisoning has been commonly reported when animals are fed excessive cruciferous plant material (Kingsbury 1964).

ITCs are general biocides whose activity results from interaction with proteins. They interact nonspecifically and irreversibly with proteins and amino acids to form stable products by reacting with sulfhydryl groups (Fenwick et al. 1983; Kawakishi and Kaneko 1985; Ware 1983), disulfide bonds (Kawakishi et al. 1983), and amines (Kawakishi and Kaneko 1987; Wood 1975). Reaction with terminal amino groups is the basis of the well-known Edman degradation for amino acid sequencing of proteins. ITCs inactivate enzymes *in vitro*, but the actual effects *in vivo* may be controlled by accessibility (Wood 1975).

Numerous studies concerning ITC toxicities have been performed. Contact of ITCs with skin and mucous membranes (respiratory tract) cause irritation, and many are considered lachrimators. At 20-50 mg kg^{-1} body weight propenyl ITC produced epithelial hyperplasia, stomach ulcers, and minor inflammatory foci in the livers of dogs, but did not show similar effects in rats even at 500 mg kg^{-1} body weight (Hall 1973). Antithyroid effects are attributed to ITCs, although this may be caused by metabolic conversion of the ITCs to SCN^-. An oral LD_{50} in rats for methyl ITC is listed as 175 mg kg^{-1} (Worthing 1987) and 339 mg kg^{-1} for propenyl ITC (Wood 1975). Subcutaneous LD_{50} values are considerably lower at 50 mg kg^{-1} for methyl ITC and 80 mg kg^{-1} for propenyl ITC (Wood 1975). The LC_{50} of methyl ITC at 96 h is 0.13 mg L^{-1} for bluegill and 0.37 mg L^{-1} for trout and carp (Worthing 1987).

Mammalian systems metabolize and eliminate ITCs fairly rapidly. Less than 5% of a dose of propenyl ITC was retained by rats and mice 24 h after administration (Ioannou et al. 1984). ITCs administered both orally and by injection in rats and mice are primarily detoxified by glutathione and excreted as *S*-(*N*-methylthiocarbamoyl)mercapturic acids (Lam et al. 1993; Ioannou et al. 1984; Mennicke et al. 1983). Detoxification and excretion of benzyl ITC in humans is similar (Mennicke et al. 1988).

ITC attack of DNA and cancer cell induction seem to be unimportant in describing the mode of toxicity. Mutagenicity tests are sometimes positive, but often negative (Fenwick et al.

1983; Ioannou et al. 1984; Musk and Johnson 1993). Chronic administration of propenyl ITC to rats and mice caused papillary growths in bladders of male rats only (related to more concentrated metabolite excretion), but did not cause tumors (Ioannou et al. 1984). There is in fact evidence that ITCs are anticarcinogenic (Mossoba et al. 1989; Fimognari et al. 2004). Glucosinolate-containing cruciferous vegetables such as cabbage, broccoli, and Brussels sprouts are correlated with reduced incidence of cancer (Graham et al. 1978). Tumors were inhibited in mice and rats that were given ITCs both before and after administering known carcinogens (Fenwick et al. 1983; Wattenberg 1977, 1981). Short-term chemical mechanisms appear to be involved in the suppression, such as high toxicity toward cancer cells (Nastruzzi et al. 1996), but longer term induction of enzyme systems that fight cancer in the body are also implicated (Institute of Food Technologists 1993). A potent inducer of protective enzymes is 4-methylsulfinylbutyl ITC found in broccoli (Zhang, et al. 1992, 1994). Thus, if ITC is consumed in normal dietary levels, it may be more beneficial than harmful.

Toxicological implications of glucosinolate hydrolysis must also include the possibility of OZT formation. The most common OZT, 5-vinyl-2-oxazolidinethione, is often referred to as "goitrin" because of its ability to induce goiter in the thyroid gland. High-protein rapeseed meal has limited use as a cattle feed, in part because the glucosinolate precursor of goitrin is present in large amounts. Other information on biological activity is relatively scarce, although OZTs interfere with a few enzymatic processes. For example, OZTs prevent the oxidation of trimethylamine (Fenwick et al. 1983) and goitrin moderately inhibits dopamine β-hydroxylase (Zenker et al. 1988). OZT toxicities to mice reported in the form of LD_{50} values range from 1260 to 1415 mg kg^{-1} (Van Etten and Tookey 1979). There is some susceptibility to nitrosation in the presence of nitrite (Lüthy et al. 1984), suggesting the possible formation of carcinogenic compounds under conditions encountered in the stomach. General toxicity appears to be relatively low, but further investigation of OZT toxicities seems appropriate.

Toxicity of other organic products, including nitriles, epithionitriles, and thiocyanates is likely related to the cyano group. Cyanide salts and gas inactivate certain enzyme systems, especially those involved in cellular respiration such as cytochrome oxidase (Johnston 1987; Sittig 1985). Similarities in the metabolism of organic nitriles and cyanide include increased urinary excretion of SCN^-, detection of CN^- in tissues, and depressed cytochrome oxidase activity (Duncan 1991). Toxicities of organic nitriles vary but are generally lower than cyanide salts and hydrogen cyanide. Toxicity seems particularly pronounced towards the liver (hepatotoxic) and kidney (Dietz et al. 1991; Duncan 1991; Fenwick et al. 1983; Van Etten et al. 1969). The LD_{50} in rats for ethyl CN (propanenitrile) is 50-100 mg kg^{-1} (Sittig 1985); for 1-cyano-2-hydroxy-3-butene, values of 170 mg kg^{-1} and 200 mg kg^{-1} have been reported (Fenwick et al. 1983; Tookey et al. 1980). Unsaturated nitriles appear to be less toxic than saturated nitriles. For example, rat oral LD_{50}'s exceeded 600 mg kg^{-1} for 3-butenyl CN (4-pentenenitrile) and 720 mg kg^{-1} for benzonitrile, although acetonitrile (methyl CN) is an exception with a reported oral LD_{50} in rats of 3030-6500 mg kg^{-1} (Dietz et al. 1991; Smiley 1979).

Thiocyanate and epithionitrile toxicities appear similar to nitrile toxicities. Low molecular weight thiocyanates, including benzyl and phenyl, respond to the same antidotes for poisoning as does cyanide (Wood 1975). Alkyl thiocyanates are generally more active than aromatic thiocyanate, and toxicity decreases with increasing molecular weight (Wood 1975). For 1-cyano-3,4 epithiobutane, mortality in rats occurred after ingestion of 180 mg kg^{-1} (Dietz et al. 1991) and an LD_{50} of 109 mg kg^{-1} has been reported (Fenwick et al. 1983). An LD_{50} range of 178-240 mg kg^{-1} was estimated for 1-cyano-2-hydroxy-3,4 epithiobutane (Van Etten et al. 1969).

Although the LD_{50} reported for 3-indolylacetonitrile in rats is 255 mg kg^{-1}, indolyl products such as 3-indolylmethanol stimulate enzymatic systems involved in detoxification of xenobiotics and the inhibition of cancer (Loub et al. 1975). Protective activity, however, is less dramatic than with ITCs. Results of several experiments are somewhat mixed depending on the system examined and the specific conditions (McDanell et al. 1988), making it difficult to assess actual impact. In one study conducted with trout, 3-indolylmethanol administered after exposure to aflatoxin B_1 actually enhanced carcinogenesis. However, 3-indolylmethanol, as well as several ITCs, OZTs, and nitriles, were not teratogenic in rats (Fenwick at al. 1983).

SCN^- is generally less toxic than either ITCs or organic cyano compounds. In fact, biological systems often metabolically detoxify cyanides by rhodanese-catalyzed conversion to SCN^-, which is then readily excreted (exogenous sulfur is needed and thus thiosulfate is administered as part of the antidote for cyanide poisoning). Rhodanese is widely distributed in nature (Tabatabai and Singh 1976). As a result, SCN^- was considered nontoxic and was used for a time as a drug to reduce blood pressure. However, side effects of SCN^- caused its use to be dropped.

SCN^- toxicity to rats is similar to benzonitrile with a reported LD_{50} for NaSCN of 765 mg kg^{-1}. Dogs are more susceptible than rats or mice to SCN^- (Wood 1975). The process of cyanide conversion to SCN^- is apparently in metabolic equilibrium, and adding SCN^- to biological systems produces cyanide. However, this alone does not account for its acute toxicity (Wood 1975). SCN^- interacts with proteins, and is listed as the most effective anion in the Hofmeister series for destabilizing protein structure (Voet and Voet 1990; Wood 1975). It may act as a noncompetitive inhibitor with many enzymes, and penetrates cell membranes (Wood 1975). SCN^- is a pseudohalogen that acts as a competitor with iodine and thus may cause goiter. Unlike goiter caused by OZT, goiter resulting from SCN^- can be corrected by adding iodine to the diet.

Effects of specific glucosinolate degradation products on individual organisms vary and are not always known. In sufficient quantity many of these compounds are highly toxic. Even with plant tissues, irritation of skin from excessive handling or a negative respiratory reaction might occur. However, exposure to amounts encountered in pest control strategies with plant tissues is likely to be minimal. The action of the toxins is direct and "up front." There do not appear to be serious, more subtle, negative long-term impacts on human health such as cancer or birth defects. Indeed, we have probably ingested many of these compounds in low levels for thousands of years, most of the time presumably without detriment.

VII. Registration

Products derived from mustard meal or meal-containing glucosinolates have been registered for a variety of purposes (Table 4). EPA has granted an "Exemption From the Requirement of Tolerance to Isothiocyanate as a Component of Food Grade Oil of Mustard" (Federal Register 1966). The most relevant products in the current discussion include mustard meal (*B. juncea*), currently marketed in Australia as a snail and slug killer and meadowfoam (*Limnanthes alba*) meal marketed in the United States as a soil amendment in horticulture. Meadowfoam meal is marketed by Natural Plant Products as Limnax™, AlbaGro™, and AlbaAide™. EPA approved pesticides containing propenyl ITC as an active ingredient are marketed by Champon Natural Products (Champon Millenium Chemicals, Inc. 11112 Split Rail Lane, Fairfax Station, VA 22039; Phone: 703-426-8424; E-mail: champon@ix.netcom.com; website: www.champon.com). A number of other products containing propenyl isothiocyanate as an active ingredient have been approved by the EPA for various pests (Table 4). Thus, the precedent for EPA approval of products containing propenyl ITC as an active ingredient has been set. Additional ITCs contained in other meals other than *B. juncea* most likely will require greater testing before it can be approved by the EPA.

VII. Genetics and Interspecific Hybridization

Canola or rapeseed (*Brassica napus* L.) is a member of the *Brassicaceae* family. Canola is the term used to describe *Brassicaceae* cultivars that contain erucic acid less than 2% of the total fatty acid content and less than 30 μmol per gram of total glucosinolates in oil-free meal (Arnoldo et al. 1992). Rapeseed is used to describe oilseed *B.* napus with high (>40%) erucic acid content in the oil. Traditionally rapeseed cultivars also contained high (80-120 μmol per gram of total glucosinolates in oil-free meal) glucosinolate content in the seed meal, although new rapeseed cultivars have seed meal comparable to canola.

Early records indicate that canola (rapeseed) was cultivated in India more than 3,000 years ago. It was later introduced to China and Japan (Shahidi 1990). The exact center of origin for *B. napus* is uncertain; however, it may have had multiple areas of origin in Europe within overlapping ranges of the diploid parental taxa (*B. rapa* and *B. oleracea*) (Warwick and Francis 1994). The main phytogeographical zones for *B. napus* are the Euro-Siberian, and the Irano-Turanian regions (Warwick and Francis 1994). The main regions of canola cultivation are parts of Asia (China, India, Indonesia), Europe, the Americas (mainly Canada), parts of Africa, and Australasia.

A. Taxonomy, Genomic Constitutions, and Relationships

The origins of amphidiploid *B. napus*, *B. carinata*, and *B. juncea* were suggested by U (1935), based on interspecific hybridizations and chromosome counts (Figure 3). This triangle arrangement of species indicates that cultivated canola, *B. napus* (n = 19, AACC genome), originated as a result of natural hybridization between *B. oleracea* (n = 9, CC genome) and *B. rapa* (n = 10, AA genome) (U 1935; McNaughton 1976). This has been confirmed by later studies using different techniques, including flavonoid composition (Dass and Nybom 1967) and seed protein serology (Vaughan 1977). Song et al. (1988) used RFLPs to study the genomic constitution of diploid and amphidiploid species, and concluded that amphidiploid *B. napus* has evolved through different combinations of the diploid morphotypes (*B. rapa* and *B. oleracea*) and that phylogenetic origins may be common mechanisms for the natural occurrence of amphidiploids in *Brassica*, which confirmed that *B. napus* is an interspecific hybrid derived from *B. rapa* and *B. oleracea*. The authors suggested that the C genome component is larger in the cultivated *B. napus* lines, since these plants were closer to the C genome than the A genome in the phylogenetic tree.

B. Oil and Seed Meal Characteristics and Inheritance

The major fatty acids of *Brassica* species oil are palmitic (16:0), stearic (18:0), oleic (18:1), linoleic (18:2), linolenic (18:3), eicosenoic (20:1) and erucic acids (22:1). Some mustard species also have relatively high concentrations of nervonic acid (24:1). Canola oil must, by definition, not exceed more than 2% erucic acid content. In contrast, industrial rapeseed oil is usually very high (40%-50%) in erucic acid content. Laboratory animals that eat diets with a high proportion of oil containing high erucic acid levels perform poorly. Also, high erucic acid levels in human

diets can cause abnormality of fat utilization in the heart and skeletal muscles, with undesirable changes in the tissue of the myocardium (Roine et al. 1960). Other reports from Canada and Europe have confirmed these changes and have shown that they do not occur with diets containing canola type oil with a low erucic acid content (Abdellatif et al. 1970). In canola, reduced erucic acid content is almost always associated with high oleic acid content, which is almost as effective in reducing cardiovascular risk as is the long-touted polyunsaturated linoleic acid (Ackman 1990).

Linolenic acid is very unstable and is easily oxidized to give unpleasant smelling substances. Canola oil contains 8%-12% linolenic acid, although cultivars can be developed with reduced levels (DeBonte 1994). In contrast, a high percentage of linoleic acid in edible oil is desirable (Scarisbrick and Daniels 1986). Canola oil is relatively low in this nutritionally valuable fatty acid, and an increase would improve its dietary value (Holmes 1980). Nutritionally, linoleic acid (vitamin F) is an important and essential polyunsaturated fatty acid that also reduces cholesterol content in the blood and is an essential component of cell membranes (Scarisbrick and Daniels 1986).

Yellow mustard (*S. alba*) contains considerably higher erucic acid levels than are suitable as an edible oil. Also, yellow mustard does not produce high enough erucic acid levels to be valuable for industrial purposes (Carlson and Van Dyne 1992). In addition, yellow mustard is low in linoleic acid and has higher linolenic acid than would be desirable in edible oil.

Since the early 1960s, many researchers have investigated the inheritance of erucic acid content in several *Brassica* species. In *B. napus*, erucic and eicosenoic acid content are controlled by the genotype of the developing embryo and not by the sporophyte (Dorrel and Downey 1964; Harvey and Downey 1964; Kondra and Stefansson 1965; Stefansson and Hougen 1964). Erucic acid content in *B. napus* is controlled by a two gene-pair-system acting in an additive manner (Downey and Craig 1964; Kondra and Stefansson 1965; Stefansson and Hougen 1964). Jönsson (1977a, 1977b) found that erucic acid content in *B. napus* is controlled by a series of multiple alleles. Levels of 5%-10%, 20%-35%, and more than 35% erucic acid content are controlled by alleles at one, one or two, and two loci, respectively.

Very few studies have been carried out to examine the inheritance of fatty acid profiles in *S. alba* (Rafiullah 1994). Rafiullah used a 4x4 half diallel cross to determine the inheritance of fatty acid profile as quantitative characteristics. The results indicated that erucic and oleic acids had greater additive genetic variation than dominant genetic variation, and that erucic acid was controlled by additive and nonadditive genes with some degree of linkage and or epistasis in *S. alba*. However, these studies were conducted by chemically analyzing field open pollinated seed. This could add serious bias to the results because of outcrossing. Tang et al. (1995) found that erucic acid content in yellow mustard has a large quantitative component with a few major dominant alleles.

Traditional rapeseed cultivars (where canola cultivars were derived) all had relatively high concentrations of glucosinolates in the seed that adversely affected the quality of the meal as livestock feed. When glucosinolate compounds are enzymatically degraded, they produce toxic compounds that can cause metabolic disturbances when fed to nonruminant livestock (Kondra

and Stefansson 1970). High glucosinolate levels needed therefore to be reduced in rapeseed cultivars to avoid these detrimental effects on animals consuming the meal (Josefsson 1972).

A tremendous breeding effort was made to develop low-glucosinolate rapeseed (canola). The cultivar "Bronowsky" was the original, and only, source of low glucosinolates in *B. napus* and *B. rapa*. The genes that affect the early stages of biosynthesis of the major glucosinolates apparently control biosynthesis of glucosinolates in Bronowsky. This cultivar had low levels of glucosinolates in 1968 but was unadapted (Jönsson 1977a; Josefsson and Appelqvist 1968; Kondra and Downey 1969; Kondra and Stefansson 1970). However, the cultivars "Tower" and "Erglu" were developed relatively quickly by a backcross procedure to combine low levels of glucosinolates with low levels of erucic acid (Stefansson and Kondra 1975).

In contrast to canola, yellow mustard seed has traditionally been selected for condiment mustard powders. Mustard pungency is associated with high content of glucosinolates and their hydrolysis products (Holmes 1980). Therefore, past breeding efforts in this species have been aimed at increasing glucosinolate levels rather than making any attempt to reduce the content of glucosinolates in the seed.

Very few studies have examined the inheritance of glucosinolates in yellow mustard. This is mainly because very little genetic variation has been found for this trait within the species. Glucosinolate content of *S. alba* seeds produced from the same parent from both self- and cross-pollinations were similar, showing that inheritance of glucosinolates is maternally controlled (Kondra and Stefansson 1970; Love et al. 1990). F_2 seed of reciprocal crosses contained both 2-propenyl and 3-butenyl glucosinolates, indicated nuclear genes controlled their formation. Love et al. (1990) also concluded that the synthesis of both 2-propenyl and 3-butenyl glucosinolates were controlled by multiple additive alleles at the same loci. More recently a single recessive allele has been identified (Brown et al. 2002) that completely blocked 3-hydroxybenzyl glucosinolate in yellow mustard seed meal.

C. Interspecific and Intergeneric Crosses in Brassicaceae

Substantial literature discusses intergeneric cross compatibility within the family Brassicacae. *B. napus* has been combined with several species of *Diplotaxis* and *Eruca* by sexual crosses and embryo rescue (Batra et al. 1990; Ringdahl et al. 1987), and with various other *Brassica* species (Glimelius et al. 1990; Jourdan et al. 1989a; Sjodin and Glimelius 1989). Other intergeneric *Brassica* hybrids produced include various combinations of *B. juncea*, *B. campestris*, *Diplotaxis*, *Eruca*, *Raphanus*, *Moricandia*, and *Trachystoma* (e.g. Agnihotri et al. 1990a, 1990b; Bing et al. 1996; Chevre et al. 1997; Kirti et al. 1992; Metz et al. 1997; Sikdar et al. 1990; Takahata and Takeda 1990; Toriyama et al. 1987a, 1987b). These hybrids generally showed some degree of fertility in crosses and have a range of chromosome numbers in their progeny.

Agnihotri et al. (1990a, 1990b) reported on the production of *B. napus* × *Raphanobrassica* and *B. napus* × *Eruca* using controlled crossing followed by embryo rescue. Lefol and Darmency (1993) studied spontaneous and manual interspecfic and intergeneric crosses between *B. napus* and two weedy relatives, *B. adpressa* and *R. raphanistrum*. They were

able to obtain hybrids that showed superior vegetative development compared to the weed parent; the backcrosses to the parents also produced seed. In their studies on interspecific crosses, Nishiyama et al. (1991) found that many of these crosses produced wrinkled or empty seed because of poor endosperm development. However, crosses between *B. napus* and *B. campestris* and between *B. napus* and *B. nigra* spontaneously produced a few true F_1 seeds (Nishiyama et al. 1991). Sucessful intergeneric hybridization between *B. napus* and *S. alba* have recently been reported (Brown et al. 1994, 1997). The result of this latter hybrid combination prompted further investigation of *B. napus* x *S. alba* hybrids with elevated glucosinolate content for use as biofumigants.

Kerlan et al. (1992) studied the potential for interspecific hybrid production between *B. napus* and five related species (*B. oleracea* L. var *capitate*, *B. oleracea* L. var *acephala*, *B. nigra* L. Koch, *B. adpressa* L., *R. raphanistrum* L., and *S. arvensis*). Under optimal conditions with *in vitro* ovary culture, hybrid plants were obtained in all species cross combinations and more hybrids were obtained when canola was used as the female.

Eber et al. (1994) reported that spontaneous hybridization between male sterile *B. napus* and *B. adpressa* and *R. raphanistrum* where the pollen fertility of hybrids was 0%-30%.

In a study involving six *B. napus* and four *S. arvensis* lines (Bing et al. 1995), no hybrids were obtained from any cross. When ovule culture was used, one hybrid from *B. napus* × *S. arvensis* was obtained but was highly sterile. The authors concluded that the crossing between and transfer of genes from *B. napus* to *S. arvensis* would be remote even under favorable conditions.

IX. Recommendations

Meals with isothiocyanate-producing glucosinolate concentrations in excess of 200 μmol g^{-1} tissue will most effectively control a wide variety of plant pests. The target is to produce in excess of 100 nmol ITC g^{-1} soil to approach commercially recommended rates for synthetic ITC pesticides. This should be possible assuming glucosinolate to ITC release efficiencies of 20%. Consideration should be given to increasing the release efficiency of the ITC from the meal using physical methods of processing the meal or through the addition of adjuvants. Absolute ITC amounts and release efficiencies must be determined for the meals of interest to confirm that we indeed are producing ITC in excess of 100 nmol g^{-1} soil. Meals must be tested against specific target organisms and phytotoxic effects on the crop plant must be determined. Fungal pathogens will be the most difficult to control because carbon added to the soil in the form of meal may enhance growth of the pathogen. Insects, nematodes, and weeds will be more easily controlled, and commercialization of a final product with acceptable efficacy is likely. Different ITCs express different toxicities as a result of direct effects on the plant pest as well as differential sorption and reaction with soil colloids. Bioassay results obtained in the absence of soil must therefore be confirmed within the soil environment. Predictions of ITC pesticidal activity should be approached in the same fashion as commercial pesticides by determining organic carbon partition coefficients, Henry's constants, and half-lives. These parameters will vary with the ITC, and pesticidal activity can be optimized by selecting ITCs with the greatest potential for efficacy. The potential to introduce thiofunctionalized glucosinolates into species by way of breeding efforts may improve pesticidal efficacy of the meal. Additional benefits from the meal such as N release may increase the advantages of using meal amendments in cropping strategies. Effort should be devoted to quantifying the nutrient benefits of meal amendment since such benefits may be just as important to the consumer as pesticidal activity.

X. LITERATURE CITED

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Table 1. Naturally Occurring Glucosinolates

R=	trivial name	plant	part[a]	Reference.
methyl CH_3	glucocapparin	various *Capparis*	s	Kjaer and Thomsen 1963a
		various *Cleome*	s	Kjaer et al. 1955
			s	Kjaer and Thomsen 1963a
ethyl CH_3CH_2	glucolepdiin	*Lepidium menziesii*	s	Kjaer and Larsen 1954
2-methylethyl (isopropyl) $(CH_3)_2CH$	glucoputranjivin	*Brassica napobrassica*	r	Shaw et al. 1989
		Cochlearia officinalis	s	Kjaer and Conti 1953
		Lunaria biennis	s	Kjaer and Conti 1953
		Moringa peregrina	s	Kjaer et al. 1979
propyl $CH_3CH_2CH_2$		*Brassica oleraceae*	l	MacLeod and Nussbaum 1977
1-methylpropyl $CH_3CH_2(CH_3)CH$	glucocochlearin	*Brassica napobrassica*	r	Shaw et al. 1989
		Brassica campestris (*B. rapa)*	l,r	Carlson et al. 1987
		Dentaria pinnata	r	Delaveau and Kjaer 1963
2-methylpropyl $CH_3(CH_3)CHCH_2$		*Armoracia lapathifolia*	r	Grob and Matile 1980
			r	Gilbert and Nursten 1972
		Brassica napus	s	Brown and Morra 1995
		Conringia orientalis	l	Underhill and Kirkland 1972
		Moringa peregrina	s	Kjaer et al. 1979
butyl $CH_3(CH_2)_3$		*Armoracia lapathifolia*	r	Grob and Matile 1980
		Capparis flexuosa	l	Kjaer and Schuster 1971
2-methylbutyl $CH_3CH_2(CH_3)CHCH_2$		*Armoracia lapathifolia*	r	Grob and Matile 1980
		Dentaria pinnata	r	Delaveau and Kjaer 1963
3-methylbutyl $CH_3(CH_3)CHCH_2CH_2$		*Armoracia lapathifolia*	r	Grob and Matile 1980
pentyl $CH_3(CH_2)_4$		*Armoracia lapathifolia*	r	Grob and Matile 1980
		Brassica rapa	l	Itoh et al. 1984

4-methylpentyl $CH_3(CH_3)CH(CH_2)_3$		*Armoracia lapathifolia*	r	Grob and Matile 1980
		Brassica napus	l,s,r	Brown and Morra 1995, 1996
		Raphanus sativus	r	Kjaer et al. 1978
hexyl $CH_3(CH_2)_5$		*Brassica napus*	s	Kondo et al. 1985
		Raphanus sativus	r	Kjaer et al. 1978
5-methylhexyl $CH_3(CH_3)CH(CH_2)_4$		*Armoracia lapathifolia*	r	Grob and Matile 1980
		Brassica napus	l,s,r	Brown and Morra 1996
allyl CH_2CHCH_2	sinigrin	*Armoracia lapathifolia*	r	Grob and Matile 1980
			r	Birch et al. 1992
			l	Shaw et al. 1989
		Brassica carinata	s	Nastruzzi et al. 1996
			s	Röbbelen and Thies 1980
		Brassica juncea	s	Hanley et al. 1983
			l, s, r	Sang et al. 1984
		Brassica napus	s	Elfakir et al. 1992
			r	Birch et al. 1992
		Brassica oleraceae	s	Minchinton et al. 1982
			l	Hill et al. 1987
			l,r	Josefsson 1967a,b
2-methyl-2-propenyl $CH_2(CH_3)CCH_2$		*Peltaria alliacea*	s	Daxenbichler et al. 1991
3-butenyl $CH_2CHCH_2CH_2$	gluconapin	*Brassica campestris (B. rapa)*	s	Hanley et al. 1983
			l,r	Carlson et al. 1987
		Brassica oleraceae	l	Shaw et al. 1989
			r	Birch et al. 1992
			s	Minchinton et al. 1982
		Brassica napus	s	Elfakir et al. 1992
			l	Koritsas et al. 1989
			l, s	Sang et al. 1984
			r	Birch et al. 1992
		Brassica napobrassica	r	Shaw et al. 1989
3-methyl-3-butenyl $CH_2(CH_3)CCH_2CH_2$		*Capparis linearis*	l	Kjaer and Wagnières 1965

4-pentenyl $CH_2CH(CH_2)_3$	glucobrassicanapin	*Armoracia lapathifolia*	r	Grob and Matile 1980
			r	Gilbert and Nursten 1972
		Brassica campestris (B. rapa)	l,r	Carlson et al. 1987
		Brassica oleraceae	s	Minchinton et al. 1982
		Brassica napus	s	Quinsac et al. 1991
			l	Koritsas et al. 1989
			l, s	Sang et al. 1984
			r	Birch et al. 1992
		Brassica napobrassica	r	Shaw et al. 1989
5-hexenyl $CH_2CH(CH_2)_4$		*Armoracia lapathifolia*	r	Grob and Matile 1980
		Brassica napus	s	Kondo et al. 1985
		Raphanus sativus	r	Kjaer et al. 1978
2-hydroxypropyl $CH_3(OH)CHCH_2$		*Armoracia lapathifolia*	r	Grob and Matile 1980
3-hydroxypropyl $HOCH_2(CH_2)_2$		*Arabidopsis thaliana*	s	Hogge et al. 1988
3-hydroxybutyl $CH_3(OH)CH(CH_2)_2$		*Armoracia lapathifolia*	r	Grob and Matile 1980
		Capparis flexuosa	l	Kjaer and Schuster 1971
4-hydroxybutyl $HOCH_2(CH_2)_3$		*Arabidopsis thaliana*	s	Hogge et al. 1988
		Capparis flexuosa	l	Kjaer and Schuster 1971
2-hydroxypentyl $CH_3(CH_2)_2(OH)CHCH_2$		*Armoracia lapathifolia*	r	Grob and Matile 1980
1-methyl-2-hydroxyethyl $HOCH_2(CH_3)CH$	glucosysimbrin	*Coluteocarpus vesicaria*	s	Al-Shehbaz, Al-Shammary 1987
		Dentaria laciniata	s	Daxenbichler et al. 1991
		Euclidium syriacum	s	Al-Shehbaz, Al-Shammary 1987
		Torularia torulosa	s	Al-Shehbaz, Al-Shammary 1987
1-hydroxymethylpropyl $CH_3CH_2(OHCH_2)CH$		*Coluteocarpus vesicaria*	s	Al-Shehbaz, Al-Shammary 1987
1-ethyl-2-hydroxyethyl $HOCH_2(CH_3CH_2)CH$	glucosisautricin	*Cleome diandra*	s	Daxenbichler et al. 1991
		Sisymbrium austriacum	s	Kjaer and Christensen 1962a
2-hydroxy-2-methylpropyl $CH_3(OH)(CH_3)CCH_2$	glucoconringiin	*Cochlearia officinalis*	s	Challenger 1959
		Conringia orientalis	s	Challenger 1959

			l	Underhill and Kirkland 1972
		not spec		Eagles et al. 1981
		Erysimum orientale	s	Kjaer 1960
2-hydroxy-2-methylbutyl $CH_3CH_2(OH)(CH_3)CCH_2$	glucocleomin	*Cleome spinosa*	s	Kjaer and Thomsen 1962
		Dentaria laciniata	s	Daxenbichler et al. 1991
4,5,6,7-tetrahydroxydecyl $CH_3(CH_2)_2(CH_2OH)_4(CH_2)_3$		*Capparis grandis*	r	Gaind et al. 1975
R-2-hydroxy-3-butenyl $CH_2CH(OH)CHCH_2$	progoitrin (glucorapiferin)	*Brassica campestris (B. rapa)*	s	Soluski and Dabrowski 1984
			l,r	Carlson et al. 1987
		Brassica napobrassica	r	Shaw et al. 1989
		Brassica napus	s	Quinsac et al. 1991
			l	Koritsas et al. 1989
			l, s, r	Sang et al. 1984
			s	Daun 1986
			r	Birch et al. 1992
		Brassica oleraceae	s	Minchinton et al. 1982
			l	Shaw et al. 1989
			r	Birch et al. 1992
S-2-hydroxy-3-butenyl $CH_2CH(OH)CHCH_2$	epiprogoitrin	*Crambe abyssinica*	s	Hanley et al. 1983
			s	Wetter and Dyck 1973
			s	Bartlet et al. 1994
		Brassica napus	s	Daun 1986
2-hydroxy-4-pentenyl $CH_2CHCH_2(OH)CHCH_2$	gluconapoleiferin	*Brassica napobrassica*	r	Shaw et al. 1989
		Brassica napus	s	Elfakir et al. 1992
			l	Koritsas et al. 1989
			l, s, r	Sang et al. 1984
			r	Birch et al. 1992
		Brassica oleraceae	r	Birch et al. 1992
3-hydroxy-4-pentenyl $CH_2CH(OH)CHCH_2CH_2$		*Armoracia lapathifolia*	r	Grob and Matile 1980
4-oxoheptyl $CH_3(CH_2)_2CO(CH_2)_3$	glucocapangulin	*Capparis angulata*	s	Kjaer and Thomsen 1963a
		not spec.		Ettlinger and Kjaer 1968
5-oxoheptyl $CH_3CH_2CO(CH_2)_4$	gluconorcappasalin	*Capparis salicifolia*	s	Kjaer and Thomsen 1963b

5-oxooctyl $CH_3(CH_2)_2CO(CH_2)_4$	glucocappasalin	*Capparis salicifolia*	s	Kjaer and Thomsen 1963a
3-methoxycarbonylpropyl $CH_3OCO(CH_2)_3$	glucoerypestrin	*Erysimum aucherianum*	s	Al-Shehbaz, Al-Shammary 1987
		Erysimum filifolium	s	Al-Shehbaz, Al-Shammary 1987
		Erysimum rupestre	s	Kjaer 1960
			l	Chisholm 1973
2-methylthioethyl $CH_3S(CH_2)_2$		*Armoracia lapathifolia* (*Cochlearia armoracia*)	r	Grob and Matile 1980
3-methylthiopropyl $CH_3S(CH_2)_3$	glucoibervirin	*Arabidopsis thaliana*	s	Hogge et al. 1988
		Brassica napus	s	Minchinton et al. 1982
		Brassica oleraceae	s	Minchinton et al. 1982
			l	Shaw et al. 1989
4-methylthiobutyl $CH_3S(CH_2)_4$	glucoerucin	*Arabidopsis thaliana*	l,s	Hogge et al. 1988
		Brassica campestris (B. rapa)	r	Carlson et al. 1987
		Brassica napus	r	Sang et al. 1984
			r	Birch et al. 1992
		Brassica oleraceae	s	Minchinton et al. 1982
			r	Birch et al. 1992
		Eruca sativa	s	Kjaer and Gmelin 1955
			s	Nastruzzi et al. 1996
		Raphanus sativus	r	Kjaer et al. 1978
		Sinapis alba (B. hirta)	r	Brown and Morra, unp.
5-methylthiopentyl $CH_3S(CH_2)_5$	glucoberteroin	*Arabidopsis thaliana*	s	Hogge et al. 1988
		Brassica naporbrassica	r	Shaw et al. 1989
		Brassica campestris (B. rapa)	r	Carlson et al. 1987
		Raphanus sativus	r	Kjaer et al. 1978
6-methylthiohexyl $CH_3S(CH_2)_6$	glucolesquerellin	*Arabidopsis thaliana*	s	Hogge et al. 1988
		*Ochthodium aegyptiacum*r	s	Al-Shehbaz, Al-Shammary 1987
7-methylthioheptyl $CH_3S(CH_2)_7$		*Arabis laxa*	s	Al-Shehbaz, Al-Shammary 1987
		Arabidopsis thaliana	s	Hogge et al. 1988
8-methylthiooctyl $CH_3S(CH_2)_8$		*Arabidopsis thaliana*	l,s	Hogge et al. 1988

9-methylthiononyl $CH_3S(CH_2)_9$		*Arabis hirsuta*	s	Daxenbichler et al. 1991
10-methylthiodecyl $CH_3S(CH_2)_{10}$		*Arabis amplexicaulis*	s	Daxenbichler et al. 1991
4-methylthio-3-butenyl $CH_3SCHCH(CH_2)_2$	glucodehydroerucin	*Raphanus sativus*	s r	Daxenbichler et al. 1991 Visentin et al. 1992
3-hydroxy-5-methylthiopentyl $CH_3S(CH_2)_2(OH)CH(CH_2)_2$		*Erysimum hieracifolium* *Armoracia lapathifolia*	s r	Kjaer and Schuster 1970 Grob and Matile 1980
3-hydroxy-6-methylthiohexyl $CH_3S(CH_2)_3(OH)CH(CH_2)_2$		*Erysimum rhaeticum*	s	Kjaer and Schuster 1973
3-oxo-8-methylthiooctyl $CH_3S(CH_2)_5CO(CH_2)_2$		*Arabis hirsuta*	s	Kjaer and Schuster 1972
3-methylsulfinylpropyl $CH_3SO(CH_2)_3$	glucoiberin	*Arabidopsis thaliana* *Brassica napus* *Brassica oleracea*	l s r l	Hogge et al. 1988 Daun 1986 Birch et al. 1992 Hansen et al. 1995
4-methylsulfinylbutyl $CH_3SO(CH_2)_4$	glucoraphanin (sulphoraphane)	*Arabidopsis thaliana* *Brassica napus* *Brassica oleracea*	l,s s l l	Hogge et al. 1988 Daun 1986 Hansen et al. 1995 Hill et al. 1987
5-methylsulfinylpentyl $CH_3SO(CH_2)_5$	glucoalyssin	*Alyssum argenteum* *Arabidopsis thaliana* *Berteroa incana*	s l,s s	Kjaer and Gmelin 1956 Hogge et al. 1988 Kjaer and Gmelin 1956
6-methylsulfinylhexyl $CH_3SO(CH_2)_6$	glucohesperin	*Arabidopsis thaliana* *Euclidium syriacum* *Notoceras bicorne*	l,s s s	Hogge et al. 1988 Al-Shehbaz, Al-Shammary 1987 Al-Shehbaz, Al-Shammary 1987
7-methylsulfinylheptyl $CH_3SO(CH_2)_7$	glucosiberin	*Arabis laxa* *Arabidopsis thaliana*	s l,s	Al-Shehbaz, Al-Shammary 1987 Hogge et al. 1988
8-methylsulfinyloctyl $CH_3SO(CH_2)_8$	glucohirsutin	*Aethionema arabicum* *Arabidopsis thaliana*	s l,s	Al-Shehbaz, Al-Shammary 1987 Hogge et al. 1988

9-methylsulfinylnonyl $CH_3SO(CH_2)_9$	glucoarabin	*Arabis alpina*	s	Challenger 1959
		Arabis nova	s	Al-Shehbaz, Al-Shammary 1987
		Drabopsis nuda	s	Al-Shehbaz, Al-Shammary 1987
10-methylsulfinyldecyl $CH_3SO(CH_2)_{10}$	glucocamelinin	various *Camelina*	s	Kjaer et al. 1956b
11-methylsulfinylundecyl $CH_3SO(CH_2)_{11}$		*Camelina microcarpa*	s	Daxenbichler et al. 1991
4-methylsulfinyl-3-butenyl $CH_3SOCHCH(CH_2)_2$	glucoraphenin	*Brassica napus*	s	Daun 1986
			r	Birch et al. 1992
		Raphanus sativus	s	Sang et al. 1984
			s	Nastruzzi et al. 1996
3-hydroxy-5-methylsulfinylpentyl $CH_3SO(CH_2)_2(OH)CH(CH_2)_2$		*Erysimum hieracifolium*[b]	s	Kjaer and Schuster 1970
3-hydroxy-6-methylsulfinylhexyl $CH_3SO(CH_2)_3(OH)CH(CH_2)_2$		*Erysimum rhaeticum*	s	Kjaer and Schuster 1973
3-oxo-8-methylsulfinyloctyl $CH_3SO(CH_2)_5CO(CH_2)_2$		*Arabis hirsuta*	s	Kjaer and Schuster 1972
3-methylsulfonylpropyl $CH_3SO_2(CH_2)_3$	glucocheirolin	*Brassica oleraceae*	l	Shaw et al. 1989
		Cheiranthus cheiri		Challenger 1959
			s	Nastruzzi et al. 1996
4-methylsulfonylbutyl $CH_3SO_2(CH_2)_4$	glucoerysolin	*Cheiranthus cheiri*		Challenger 1959
		Erysimum perofskianum	s	Kjaer and Conti 1954
		not spec		Eagles et al. 1981
6-methylsulfonylhexyl $CH_3SO_2(CH_2)_6$		*Euclidium syriacum*	s	Al-Shehbaz, Al-Shammary 1987
8-methylsulfonyloctyl $CH_3SO_2(CH_2)_8$		*Heliophila amplexicaulis*	s	Daxenbichler et al. 1991
9-methylsulfonylnonyl $CH_3SO_2(CH_2)_9$		*Arabis turrita*	s	Daxenbichler et al. 1991
		Heliophila amplexicaulis	s	Daxenbichler et al. 1991
10-methylsulfonyldecyl $CH_3SO_2(CH_2)_{10}$		*Arabis turrita*	s	Daxenbichler et al. 1991
4-methylsulphonyl-3-butenyl $CH_3SO_2CHCH(CH_2)_2$		*Raphanus sativus*	s	Cole 1980

3-hydroxy-5-methylsulfonylpentyl $CH_3SO_2(CH_2)_2(OH)CH(CH_2)_2$		*Erysimum hieracifolium*[b]	s	Kjaer and Schuster 1970
6-methylsulfonyl-3-hydroxyhexyl $CH_3SO_2(CH_2)_3(OH)CH(CH_2)_2$		*Erysimum rhaeticum*	s	Kjaer and Schuster 1973
Benzyl $C_6H_5CH_2$	glucotropaeolin	*Carica papaya*	c	Hanley et al. 1983
		Lepidium sativum	s	Hanley et al. 1983
			s	Hasapis and MacLeod 1982
		Reseda media	s,l	Olsen and Sørenson 1980
		Sinapis alba (B. hirta)	l,r	Brown and Morra, unp
			l	Cole 1976
		Tropaeolum majus	s,l	Lykkesfeldt and Møller 1993
			l	Underhill and Wetter 1969
2-hydroxybenzyl 2-$OHC_6H_5CH_2$[c]		*Reseda odorata*		Olsen and Sørensen 1979
3-hydroxybenzyl 3-$OHC_6H_5CH_2$	glucolepigramin	*Lepidium vesicarium*	s	Daxenbichler et al. 1991
		Reseda media	s,l	Olsen and Sørenson 1980
4-hydroxybenzyl 4-$OHC_6H_5CH_2$	glucosinalbin	*Brassica napus*	s	Quinsac et al. 1991
			s	Elfakir et al. 1992
		Sinapis alba (B. hirta)	s	Minchinton et al. 1982
			s	Nastruzzi et al. 1996
			l,r	Brown and Morra, unp
		Sinapis arvensis	s	Al-Shehbaz, Al-Shammary 1987
3,4-dihydroxybenzyl 3,4$(OH)_2C_6H_5CH_2$				Kjaer and Larsen 1973
3-methoxybenzyl 3-$CH_3OC_6H_5CH_2$		*Limnanthes douglasii*	s	Kjaer 1960
		not spec.		Ettlinger and Kjaer 1968
4-methoxybenzyl 4-$CH_3OC_6H_5CH_2$	glucoaubrietin	*Aubrietia hybrida*	l,s	Kjaer et al. 1956a
3,4-dimethoxybenzyl 3,4-$(CH_3O)_2C_6H_5CH_2$		*Heliophila longifolia*	s	Daxenbichler et al. 1991
3,4,5-trimethoxybenzyl 3,4,5-$(CH_3O)_3C_6H_5CH_2$		*Coronopus squamatus*	s	Daxenbichler et al. 1991
2-benzoyloxyethyl $C_6H_5COO(CH_2)_2$		*Moricandia arvensis*	s	Daxenbichler et al. 1991

1-methyl-2-benzoyloxyethyl $C_6H_5COOCH_2(CH_3)CH_2$	glucobenzosisymbrin	*Sisymbrium austriacum*	s	Daxenbichler et al. 1991
1-ethyl-2-benzoyloxyethyl $C_6H_5COOCH_2(CH_3CH_2)CH_2$	glucobenzsisaustricin	*Sisymbrium austriacum*	s	Kjaer and Christensen 1962b
3-benzoyloxypropyl $C_6H_5COO(CH_2)_3$	glucomalcomiin	*Arabidopsis thaliana*	l,s	Hogge et al. 1988
		Malcolmis maritima	s	Kjaer 1960
		not spec.		Challenger 1959
4-benzoyloxybutyl $C_6H_5COO(CH_2)_4$		*Arabidopsis thaliana*	l,s	Hogge et al. 1988
			s	Eagles et al. 1981
5-benzoyloxypentyl $C_6H_5COO(CH_2)_5$		*Arabidopsis thaliana*	l,s	Hogge et al. 1988
6-benzoyloxyhexyl $C_6H_5COO(CH_2)_6$		*Arabidopsis thaliana*	l,s	Hogge et al. 1988
2-(L-rhamnopyranosyloxy)benzyl 2-$[(OH)_3C_6H_8O]OC_6H_4CH_2$		*Reseda odorata*	f	Olsen and Sorensen 1979
4-(L-rhamnopyranosyloxy)benzyl 4-$[(OH)_3C_6H_8O]OC_6H_4CH_2$		*Thlaspi perfoliatum*	s	Al-Shehbaz, Al-Shammary 1987
4-(4'-O-acetyl-L-rhamnosyloxy)benzyl 4-$[(4'\text{-}CH_3CO)(OH)_2C_6H_8O]OC_6H_4CH_2$		*Moringa peregrina*	s	Kjaer et al. 1979
2-phenylethyl $C_6H_5(CH_2)_2$	gluconasturtiin	*Armoracia lapathifolia*	r	Grob and Matile 1980
			r	Gilbert and Nursten 1972
		Brassica campestris (*B. rapa*)	r	Carlson et al. 1987
		Brassica juncea	l, s, r	Sang et al. 1984
		Brassica oleraceae	s	Minchinton et al. 1982
			r	Birch et al. 1992
		Brassica napobrassica	r	Shaw,et al. 1989
		Brassica napus	s	Elfakir et al. 1992
			l	Koritsas et al. 1989
			l, s, r	Sang et al. 1984
			r	Birch et al. 1992
		Reseda media	s,l	Olsen and Sørenson 1980
		Sinapis alba (B. hirta)	r	Brown and Morra, unp.
3-phenylpropyl $C_6H_5(CH_2)_3$		*Armoracia lapathifolia*	r	Grob and Matile 1980

4-phenylbutyl $C_6H_5(CH_2)_4$		*Armoracia lapathifolia*	r	Grob and Matile 1980
2-hydroxy-2-phenylethyl $C_6H_5(OH)CHCH_2$	glucobarbarin	*Barbaria vulgaris*	s	Daxenbichler et al. 1991 Ettlinger and Kjaer 1968
2-(4-methoxyphenyl)-2-hydroxyethyl $[4\text{-}CH_3OC_6H_4](OH)CHCH_2$		*Arabis hirsuta*	s s	Daxenbichler et al. 1991 Kjaer and Schuster 1972
2,2-dimethyl-2-(4-methoxyphenyl)ethyl $[4\text{-}CH_3OC_6H_4](CH_3)_2CCH_2$		*Pentadiplandra brazzeana*	r	Migirab et al. 1977
2-(L-arabinopyranosyloxy)-2-phenylethyl $C_6H_5[(OH)_3C_5H_6O]CHCH_2$		*Sesamoides canescens*	l	Olsen et al. 1981
3-indolylmethyl $C_8H_6NCH_2$	glucobrassicin	*Brassica campestris (B. rapa)*	s	Sosulski and Dabrowski 1984
			l,r	Carlson et al. 1987
			l	Hansen et al. 1995
		Brassica napobrassica	r	Shaw et al. 1989
		Brassica napus	s	Quinsac et al. 1991
			l	Macfarlane-Smith et al. 1991
			l, s, r	Sang et al. 1984
			r	Birch et al. 1992
		Brassica oleraceae	l	Hanley et al. 1983
			r	Birch et al. 1992
		Camelina alyssum	s	Bäuerle et al. 1986
		Lepidium graminifolium	s	Bäuerle et al. 1986
		Raphanus sativus	l	Sang et al. 1984
4-hydroxy-3-indolylmethyl $4\text{-}OHC_8H_5NCH_2$	4-hydroxyglucobrassicin	*Brassica napobrassica*	r	Shaw et al. 1989
		Brassica napus	s	Quinsac, et al. 1991
			l, s, r	Sang etal. 1984
			r	Birch et al. 1992
		Brassica oleraceae	s	Shaw et al. 1989
			r	Birch et al. 1992
1-methoxy-3-indolylmethyl $1\text{-}(CH_3O)C_8H_5NCH_2$	neoglucobrassicin	*Brassica campestris (B. rapa)*	s	Sosulski and Dabrowski 1984
		Brassica napobrassica	r	Truscott et al. 1983
		Brassica napus	l	Macfarlane-Smith et al. 1991

			s	Elfakir et al. 1992
			r	Sang et al. 1984
			r	Birch et al. 1992
		Brassica oleraceae	l	Hanley et al. 1983
			r	Birch et al. 1992
		Cochlearia officianalis	s	Bäuerle et al. 1986
4-methoxy-3-indolylmethyl 4-(CH_3O)$C_8H_5NCH_2$	4-methoxyglucobrassicin	*Brassica napobrassica*	r	Shaw et al. 1989
		Brassica napus	l	Koritsas et al. 1989
			l, r	Sang et al. 1984
			r	Birch et al. 1992
		Brassica oleraceae	l	Shaw et al. 1989
			r	Birch et al. 1992
		Lepidium sativum	s	Bäuerle et al. 1986
1-acetyl-3-indolylmethyl 1-(CH_3CO)$C_8H_5NCH_2$		*Tovaria pendula*	s	Schraudolf and Bauerle 1986
1-sulphonate-3-indolylmethyl 1-(OSO_3)$C_8H_5NCH_2$	glucobrassicin-1-sulfonate	*Isatis tinctoria*	s	Elliott and Stowe 1970

[a] s = seed, young seedling, or inflorescence, l = leaf and/or stem, r = root, [b] identification changed to *E. virgatum* Roth (Kjaer and Schuster 1973), [c] tentative identification.

Table 2. Effects of Aqueous Extracts from Glucosinolate-Containing Tissues on Other Plants

Plant	Inhibition	Stimulation or no effect
	Seedling growth	
Brassica campestris	barley (*Hordeum vulgare*)	
	vetch (*Vicia* sp.)	
	radish (*Raphanus sativus*)	
	wheat (*Triticum aestivum*)	
Brassica juncea	wheat	
(seed tissue)	tomato (*Lycopersicum*	
	esculentum)	
Brassica napus	velvetleaf (*Abutilon theophrasti*)	wild mustard (*Brassica kaber*)
	morningglory (*Ipomoea*	
	purpurea)	
	wheat	
Brassica nigra	*Bromus rigidus*	
	Bromus mollis	
	Avena fatua	
	wheat	
Brassica oleracea	radish	lettuce
	lettuce (*Lactuca sativa*)	
	wheat	
Camelina sativa	flax (*Linium usitatissimum*)	
	Seed germination	
Brassica juncea	alfalfa (*Medicago sativa*)	carrot (*Daucus carota*)
(seed tissue)		
(seed tissue)	cabbage (*Brassica oleracea*)	pepper (*Capsicum frutescens*)

(seed tissue)	radish	timothy (*Phleum pratense*)
(seed tissue)	turnip (*Brassica rapa*)	tomato
Brassica oleracea	wheat	

References: Mason-Sedun and Jessop 1988; Jimenez-Orsornio and Gleissman 1987; Mason-Sedun et al. 1986; Leather 1983; Bell and Muller 1973; Kutacek 1964; Gressel and Holm 1964; Patrick et al. 1963; Grummer and Beyer 1960.

Table 3. Influence of Naturally Occurring Isothiocyanates on Microorganisms

Organism[a]	Concentration		Evaluation criterion
	µg mL^{-1}	[M]	
	Methyl ITC		
P. petersonii	20	$27x10^{-5}$	inhib. growth & prod.
	100	$68x10^{-5}$	biomass reduced 93%
P. shermanii	10	$14x10^{-5}$	inhib. growth & prod.
	100	$68x10^{-5}$	biomass reduced 90%
S. aureus	11	$15x10^{-5}$	minimum for inhibition
A. eutiches	0.1	$14x10^{-7}$	no zoospore formation
A. niger	23	$31x10^{-5}$	50% growth inhibition 4d
	50	$68x10^{-5}$	100% growth inhibition 4d
	110	$15x10^{-4}$	100% growth inhibition >14d
C. circinans	40	$55x10^{-5}$	100% growth inhibition
G. graminis	0.1	$10x10^{-7}$	minimum for inhibition in hs[b]
M. sitophila	<7	$<10x10^{-5}$	100% growth inhibition
P. glaucum	2	$27x10^{-6}$	minimum for inhibition
P. cyclopium	14	$19x10^{-5}$	50% growth inhibition 6d
	37	$51x10^{-5}$	100% growth inhibition 6d
	110	$15x10^{-4}$	100% growth inhibition >14d
R. oryzae	11	$15x10^{-5}$	50% growth inhibition 6d
	17	$23x10^{-5}$	100% growth inhibition 6d
	28	$38x10^{-5}$	100% growth inhibition >14d

	Ethyl ITC		
A. niger	17	$20x10^{-5}$	50% growth inhibition 4d
	122	$14x10^{-4}$	100% growth inhibition 4d
C. circinans	40	$46x10^{-5}$	no effect
P. cyclopium	>261	$>30x10^{-4}$	100% growth inhibition 14d
R. oryzae	261	$30x10^{-4}$	100% growth inhibition >14d
	Allyl ITC		
B. subtilis IFO-13722	0.11	$11x10^{-7}$	100% growth inhibition[b]
B. cereus IFO-13494	0.09	$91x10^{-8}$	100% growth inhibition [b]
E. coli	36	$36x10^{-5}$	delay growth 36 h[c]
E. coli JCM-1649	0.034	$34x10^{-8}$	100% growth inhibition[b]
P. aeruginosa	27	$27x10^{-5}$	delay growth 45 h
P. fragi	16	$16x10^{-5}$	delay growth 40 h
P. vulgaris	36	$36x10^{-5}$	delay growth 60 h
S. enteritidis JCM-1891	0.11	$11x10^{-7}$	100% growth inhibition[b]
S. aureus	1	$10x10^{-6}$	minimum for inhibition
	36	$36x10^{-5}$	delay growth 33 h
	0.11	$11x10^{-7}$	100% growth inhbition[b]
A. alliaceus	60	$61x10^{-5}$	biomass reduced 98%
	5	$51x10^{-6}$	100% growth inhibition
A. eutiches	0.1	$10x10^{-7}$	no zoospore formation
A. niger	6	$60x10^{-6}$	50% growth inhibition 4d
	65	$66x10^{-5}$	100% growth inhibition 4d
	5	$51x10^{-6}$	100% growth inhibition
	60	$61x10^{-5}$	biomass reduced 60%
B. allii	40	$40x10^{-5}$	100% growth inhibition

B. cinerea	600	$61x10^{-4}$	minimum for inhibition of germ.
C. circinans	5	$51x10^{-6}$	100% growth inhibition
Cytospora sp.	>99	$>10x10^{-4}$	100% inhibition of germ
Fusarium sp.	>99	$>10x10^{-4}$	100% growth inhibition
F. oxysporum NFRI-1011	0.022	$22x10^{-8}$	100% growth inhibition[b]
F. solani IFO-9425	0.034	$34x10^{-8}$	100% growth inhibition[b]
G. graminis	0.1	$10x10^{-7}$	min. for inhibition in hs
G. saubinetti	15	$15x10^{-5}$	100% growth inhibition
	1	$10x10^{-6}$	100% growth inhibition
M. laxa	300	$30x10^{-4}$	min. for inhibition of germ.
M. sitophila	<10	$<10x10^{-5}$	100% growth inhibition
M. piriformis	150	$15x10^{-4}$	minimum for inhibition of germ.
P. chrysogenum IFO-6223	0.062	$63x10^{-8}$	100% growth inhibiton[b]
P. cyclopium	9	$90x10^{-6}$	50% growth inhibition 6d
	22	$22x10^{-5}$	100% growth inhibition 6d
	151	$15x10^{-4}$	100% growth inhibition >14d
P. expansum	600	$61x10^{-4}$	minimum for inhibition of germ.
P. gluacum	9	$91x10^{-6}$	minimum for inhibition
R. oryzae	10	$10x10^{-5}$	50% growth inhibition 6d
	74	$75x10^{-5}$	100% growth inhibition 6d
R. stolonifer	600	$61x10^{-4}$	minimum for inhibition of germ.
	5-Methylthiopentyl ITC		
S. aureus	5	$29x10^{-6}$	minimum for inhibition
A. niger	17	$10x10^{-5}$	50% growth inhibition 4d
	35	$20x10^{-5}$	100% growth inhibition 4d
	66	$38x10^{-5}$	100% growth inhibition >14d

P. cyclopium	23	$13x10^{-5}$	50% growth inhibition 6d
	33	$19x10^{-5}$	100% growth inhibition 6d
	66	$38x10^{-5}$	100% growth inhibition >14d
P. gluacum	31	$18x10^{-5}$	minimum for inhibition

4-Methylsulfinyl-3-butenyl ITC

B. cinerea	230	$13x10^{-4}$	minimum for inhibition of germ.
M. laxa	20	$11x10^{-5}$	minimum for inhibition of germ.
M. piriformis	460	$26x10^{-4}$	minimum for inhibition of germ.
P. expansum	930	$53x10^{-4}$	minimum for inhibition of germ.
R. stolonifer	290	$17x10^{-4}$	minimum for inhibition of germ.

Benzyl ITC

E. coli	3	$21x10^{-6}$	minimum for inhibition
P. vulgaris	6	$42x10^{-6}$	minimum for inhibition
S. lutealis	1.5	$10x10^{-6}$	minimum for inhibition
S. aureus	2	$13x10^{-6}$	minimum for inhibition
A. eutiches	1	$67x10^{-7}$	no zoospore formation
A. niger	2	$16x10^{-6}$	50% growth inhibition 4d
	27	$18x10^{-5}$	100% growth inhibition 4d
	57	$38x10^{-5}$	100% growth inhibition >14d
Cytospora sp.	<75	$<50x10^{-5}$	100% growth inhibition
Fusarium sp.	<1.5	$<10x10^{-6}$	100% growth inhibition
M. sitophila	<1.5	$<10x10^{-6}$	100% growth inhibition
P. cyclopium	6	$40x10^{-6}$	50% growth inhibition 6d
	30	$20x10^{-5}$	100% growth inhibition 6d
	57	$38x10^{-5}$	100% growth inhibition >14d
P. gluacum	2	$13x10^{-6}$	minimum for inhibition

P. palmivora	1490	$10x10^{-3}$	lethal
R. oryzae	67	$45x10^{-5}$	50% growth inhibition 6d
	194	$13x10^{-4}$	100% growth inhibition 6d
	Phenylethyl ITC		
S. aureus	4	$25x10^{-6}$	minimum for inhibition
A. alliaceus	20	$12x10^{-5}$	100% growth inhibition
A. eutiches	1	$61x10^{-7}$	no zoospore formation
A. niger	2.6	$16x10^{-6}$	50% growth inhibition 4d
	3.5	$21x10^{-6}$	100% growth inhibition 4d
	12	$75x10^{-6}$	100% growth inhibition >14d
	3	$18x10^{-6}$	100% growth inhibition
C. circinans	5	$31x10^{-6}$	100% growth inhibition
Fusarium sp.	20	$12x10^{-5}$	100% growth inhibition
G. graminis	0.2	$10x10^{-7}$	minimum for inhibition in hs
G. saubinetii	2	$12x10^{-6}$	100% growth inhibition
P. cyclopium	8	$48x10^{-6}$	50% growth inhibition 6d
	12	$76x10^{-6}$	100% growth inhibition 6d
P. glaucum	5	$31x10^{-6}$	minimum for inhibition
R. oryzae	>122	$>75x10^{-5}$	50% growth inhibition 6d
	4-Hydroxybenzyl ITC		
B. cinerea	450	$27x10^{-4}$	minimum for inhibition of germ.
M. laxa	90	$55x10^{-5}$	minimum for inhibition of germ.
M. piriformis	220	$13x10^{-4}$	minimum for inhibition of germ.
P. expansum	90	$55x10^{-5}$	minimum for inhibition of germ.
P. glaucum	2000	$12x10^{-3}$	minimum for inhibition
R. stolonifer	1800	$11x10^{-3}$	minimum for inhibition of germ.

[a] Bacteria:

Bacillus subtilis

Bacillus cereus

Escherichia coli

Propionibacterium petersonii

Propionibacterium shermanii

Proteus vulgaris

Pseudomonas fragi

Pseudomonas aeruginosa

Salmonella enteritidis

Sarcina lutealis

Staphylococcus aureus

Fungi:

Aphanomyces eutiches

Aspergillus alliaceus

Aspergillus niger

Botrytis allii

Botrytis cinerea

Colletotrichum circinans

Cytospora

Fusarium

Fusarium oxysporum

Fusarium solani

Gaeumannomyces graminis

Gibberella saubinetii

Monila sitophila

Monilinia laxa

Mucor piriformis

Penicillium chrysogenum

Penicillium cyclopium

Penicillium expansum

Penicillium glaucum

Phytophthora palmivora

Rhizopus oryzae

Rhizopus stolonifer

[b] headspace concentration

[c] as compared to control

References: Angus et al. 1994; Iori et al. 1993; Isshiki et al. 1992; Kanemaru and Miyamoto 1990; Fenwick et al. 1983; Tang and Takenaka 1983; Rutkowski et al. 1972; Lewis and Papavizas 1971; Drobnica et al. 1967a; Virtanen 1965; Davis 1964; McKay et al. 1959; Hooker et al. 1943; Walker, et al. 1937.

Table 4. EPA Registrations for Various Isothiocyanates

EPA Registration Number	Type	Isothiocyanate
499-136	repellent-vertebrates	propenyl
499-137	repellent-vertebrates	propenyl
499-138	repellent-vertebrates	propenyl
731-15	repellent-vertebrates	propenyl
731-22	repellent-vertebrates	propenyl
2139-55	Fungicide, insecticide, miticide	methyl
2139-76	Fungicide, insecticide, miticide, nematicide, herbicide	methyl
3008-77	fungicide	methyl
5332-7	repellent vertebrates, herbicide	propenyl
5332-8	repellent, herbicide	propenyl
61966-4	insecticide, miticide, repellent	propenyl
61966-5	insecticide, miticide, repellent	propenyl
61966-7	repellent-vertebrates	propenyl
67064-3	repellent-vertebrates	propenyl
70160-1	insecticide, miticide, repellent	propenyl
70160-2	repellent-vertebrates	propenyl
70160-3	repellent-vertebrates	propenyl
70160-4	insecticide, miticide, repellent	propenyl

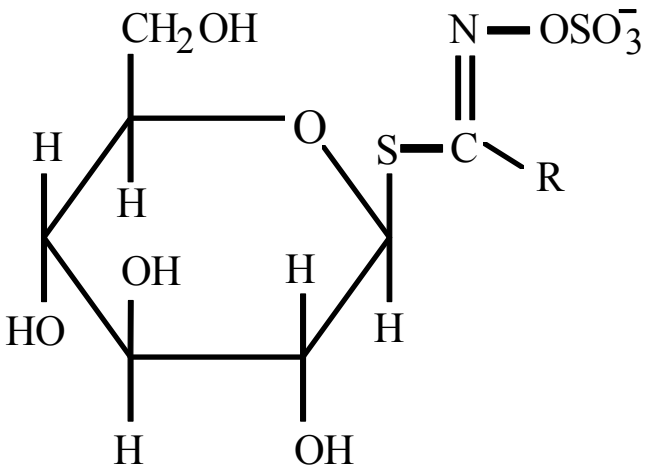

Figure 1. Generalized structure of glucosinolates

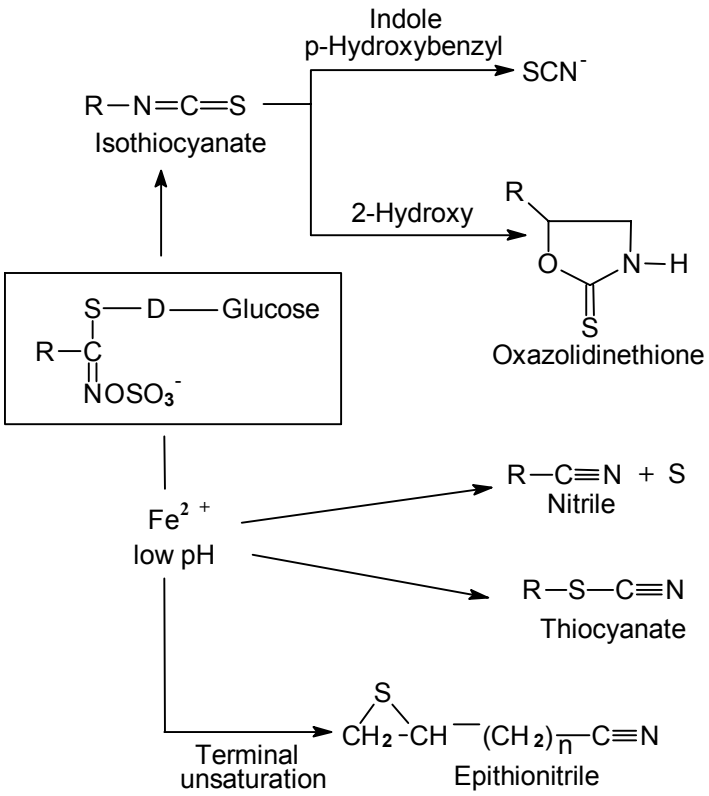

Figure 2. Glucosinolate degradation pathway[1]

[1] Enzymatic hydrolysis results in production of glucose followed by HSO_4^-. At least seven other products have been observed. Oxazolidinethione and SCN^- are thought to be formed from unstable R-N=C=S intermediates.

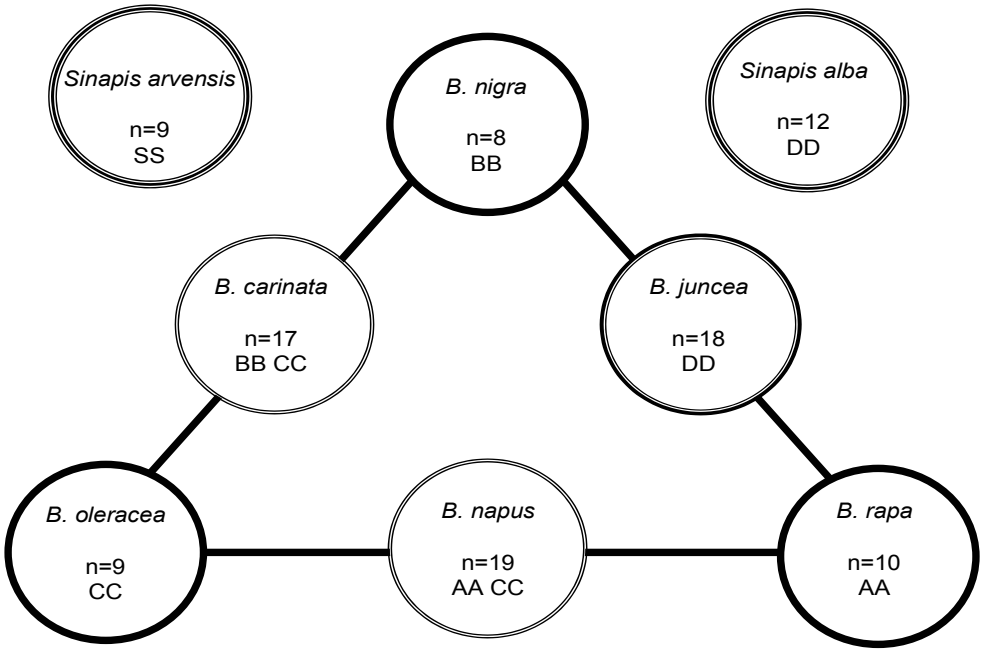

Figure 3. Relationship between *Brassica* species as described by U (1935)

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Plants may produce compounds that directly or indirectly affect their biological environment. These compounds fall within a broad category of compounds called allelochemicals, and are exclusive of food that influences growth, health, or behavior of other organisms (Whittaker and Feeney 1971). One reason for interest in allelochemicals is their potential for use in alternative pest management systems. Using plant-produced allelochemicals in agricultural and horticultural practices could minimize synthetic pesticide use, reduce the associated potential for environmental contamination, and contribute to a more sustainable agricultural system.

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