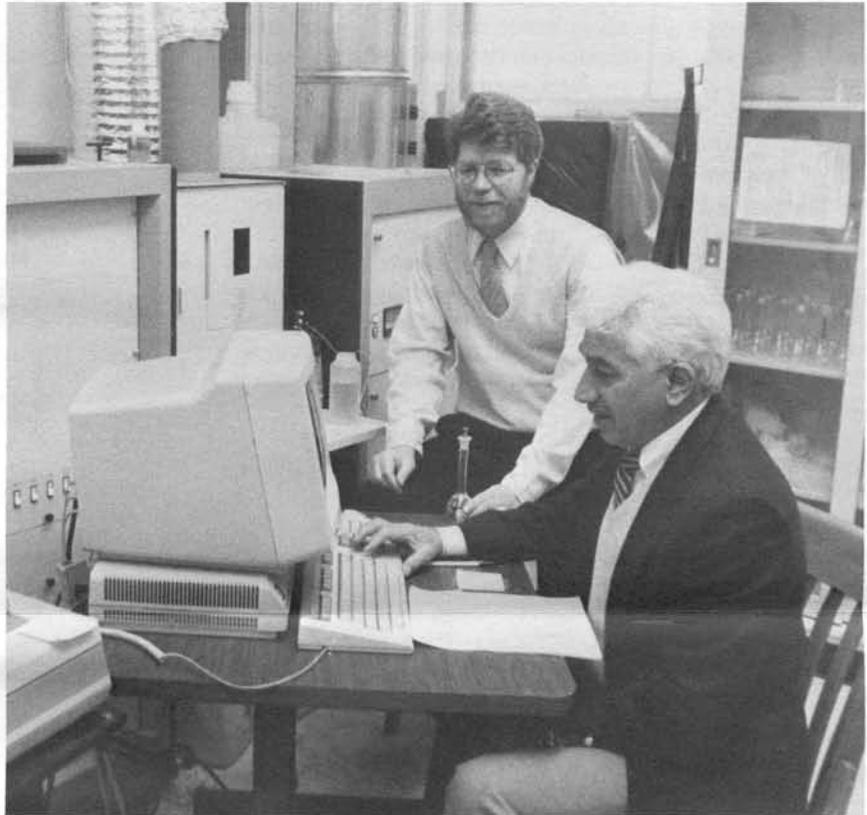# FRONTIERS of Plant Science

SPRING 1991
Volume 43 No. 2

*David Stilwell
and Brij Sawhney
at the ICP*

Do metals leach from wastes?

Warming will affect water supply

Chemicals sorb slowly in soil

Gypsy moth fungus strikes again

THE CONNECTICUT AGRICULTURAL EXPERIMENT STATION,

Do Heavy Metals in Wastes Leach to Ground Water?

By David E. Stilwell and Brij L. Sawhney

Connecticut is running out of landfill space for disposal of large amounts of solid wastes. Consequently, in addition to recycling, many municipalities have chosen to reduce the volume of their wastes by composting or incineration. The resulting compost and ash, however, need to be disposed in an environmentally safe manner. To determine whether heavy metals in these waste products would leach to contaminate ground water, we undertook to analyze waste leachates using state-of-the-art atomic spectroscopic instrumentation.

For these analyses, we primarily used the spectroscopic technique called inductively coupled plasma optical emission spectroscopy (ICP-OES). The metals analyzed were cadmium (Cd), chromium (Cr), copper (Cu), nickel (Ni), lead (Pb), and zinc (Zn). The ICP-OES was not sensitive enough to measure small amounts of cadmium and lead in the leachate from the wastes; hence we analyzed these metals by a more sensitive technique called graphite furnace atomic absorption (GFAA) spectroscopy.

We collected the ash residues from municipal refuse incinerators in Bridgeport, Bristol, Hartford, New Canaan, Wallingford, and Windham, and the compost samples from Fairfield and Greenwich. Starting materials for these composts were leaves, sewage sludge, street sweepings, and wood chips. To determine the amounts of heavy metals initially present in the wastes, we digested them in nitric acid and analyzed the solution using ICP-OES. The results (Table 1) show that the concentrations of heavy metals vary over a wide range in both the ash and compost. Furthermore, the ash residues contain much higher amounts of heavy metals than the composts.

To test the leachability of heavy metals in these samples, we carried out both laboratory and field experiments. In the laboratory, we used cylindrical glass columns (45 cm x 2.4 cm) filled with ash residues or composts. We then leached them continuously by pumping distilled water through the column for 3 weeks and collecting the leachate that percolated through daily. In the field, G.J. Bugbee and C.R. Frink grew perennial flowers under irrigation in pots containing media with compost in varying proportions. Water percolating through the containers was collected biweekly for 12 weeks. We analyzed leachates from both the laboratory and field experiments for heavy metals.

In the laboratory experiments, heavy metal concentrations in leachates from ash residues were initially high during the first 2-3 days. Thereafter, metals continued to leach at low concentrations, generally below the public drinking water standards adopted by the Connecticut Department of Health Services (Table 2). Concentrations of heavy metals in leachates from ash residues after 2 days leaching are given in Table 2.
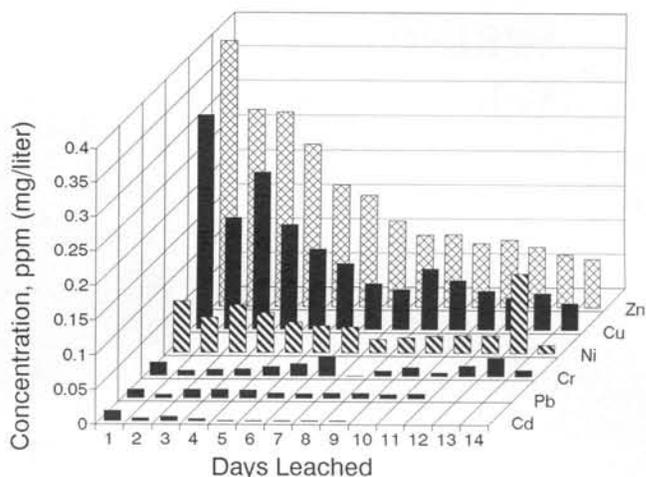

Figure 1. Heavy metals leached from Greenwich compost.

Concentrations of heavy metals in leachates from the compost also decreased with time. With the exception of Cu, all leachates from compost were below the drinking water standards from the outset. Figure 1 illustrates the leaching of different metals from Greenwich compost over a 2-week period.

In the field experiments, concentrations of heavy metals leached from pots containing compost remained low for the entire 12-week study. With the exception of lead, all metals remained below the drinking water standards. Concentrations of heavy metals leached over the 12-week period from the 100% compost are given in Table 2. Heavy metals in leachates from growth media containing smaller proportions of compost tended to be correspondingly lower.

While the heavy metals in leachates from incinerator ashes and composts in our experiments were below the drinking water standards after a few days, they continued to leach slowly out of the wastes. Only about 5% of the total metals present were leached during these experiments.

We are now developing procedures using different extractants that should help predict not only the leachability of metals from wastes applied to soil but also help understand the retention and movement of these metals through soils to ground water. In addition, these procedures may permit recovery of heavy metals from wastes prior to their disposal, thus keeping potentially toxic materials out of the environment while producing a valuable by-product.

Table 1. Range in concentration in parts per million of total heavy metals in incinerator ash and compost.

Sample	Cd	Cr	Cu	Ni	Pb	Zn
Ash Residues	12-91	60-799	370-8,500	100-1,200	850-5,300	1,733-6,400
Composts	4-7	100-150	200-475	100-350	115-210	300-800

Table 2. Range in concentration in parts per billion of heavy metals in leachates from incinerator ash residues and composts.

Sample	Cd	Cr	Cu	Ni	Pb	Zn
			Laboratory columns			
Ash Residues	0.5-5	<4	40-400	10-60	5-16	—
Composts	0.1-3	10-60	20-1,500	10-80	<5-16	10-1,700
			Field Containers			
100% Compost	<0.14-5	<10-40	40-700	<7-100	<5-100	10-1,000
			Public Drinking Water Standards			
	10	50	1,000	—	50	—

Warming would affect Connecticut through its water supply

By Paul E. Waggoner

For more than a century scientists have understood the principle of greenhouse warming. Some gases in the air transmit the solar rays that warm the planet but absorb the outgoing rays that cool it. Fact rather than principle, however, causes the recent anxiety over the possibility of greenhouse warming. About a decade ago observations spanning 30 years showed beyond doubt that the air was becoming richer in the greenhouse gas carbon dioxide. Recently, enrichment by other greenhouse gases has been seen.

Despite computational power at hand beyond the imaginings of the last century, scientists still disagree about how much warmer, wetter or drier the climate will be where we live. So, calculating the effects of greenhouse warming on Connecticut from specific scenarios of future climate and sea level is naive and perhaps even misleading.

Still, if people are either fearful of the unknown or content with the present—or both, they will lean toward playing it safe. They will lean to stopping the enrichment of the air. In the case of one greenhouse gas, CFCs, nations are doing just that. Although we can use energy more efficiently, the cost and impracticality of international reduction in CO_2 emissions
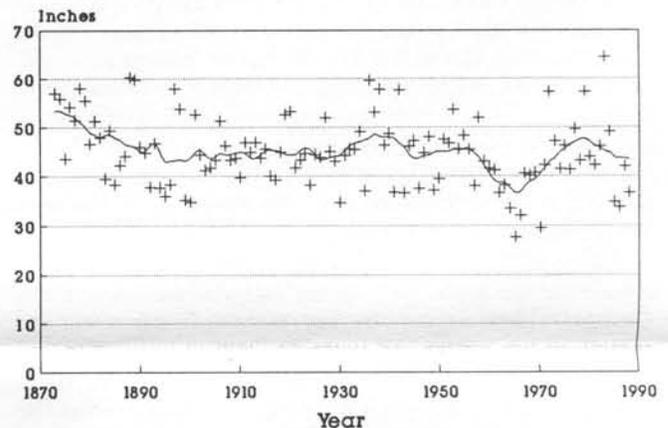

Figure 1. Paul E. Waggoner in the laboratory.

Figure 2. The 10-year moving average for precipitation at New Haven.

boggles the mind. So, in the end playing it safe includes getting ready to cope with a different climate. Different—but with an uncertain difference.

Although people often lament how little is known about environmental matters, they actually know a great deal about the sensitivity of land and water to climate. Differences today among climates, landscapes and water show them. Today, the difference from Norwalk to Norfolk is an average 8 F in January and 5 F in July, which resembles before and after the heralded greenhouse warming. The landscape is about the same in Norwalk and Norfolk, implying little sensitivity to climate.

Between coastal Connecticut and coastal southern California is also 8 F, but between Norwalk here and San Luis Obispo there, rain makes maples vs. chaparral. At 21 and 23 inches, the average rains for the winter are much the same. But, for the summer, the averages differ from 3 to 22 inches.

Further, as much as 45 inches of precipitation falls in some winters in California. That much never falls in a Connecticut winter.

In brief, the predicted greenhouse warming of the global average is no more than we can now experience in our small state by driving from Norwalk north to Norfolk in the summer
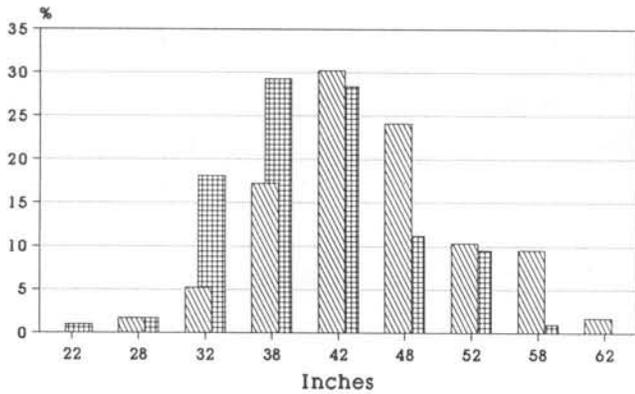
Figure 3. Past annual precipitation and 10% less.

or from Norfolk to Norwalk in the winter. But climate is more than average global temperature.

Although concentrating is good strategy, perspective is prudent. We must remember that the period until climate changes is long, akin to that from Woodrow Wilson until now. In that period California has raised its farming to preeminence by managing its water. Such changes will occur while we are trying to adapt our land and water to uncertain climate. During the coming century changes in countless factors will burden us and Nature. Common sense says we should weigh them and work mostly on the heaviest.

The sensitivity is on the margin more than in the middle of zones like the Corn Belt or the Appalachian oak forest. Changes will be wrought by, say, more or less frequent and severe droughts rather than subtly changing averages.

The distinction between a forest and a crop is the smart farmer who changes and adapts to climate and a lot more. The shade-tobacco industry of Connecticut was built in a couple of decades. The Experiment Station is vigorously searching for new crops and varieties for Connecticut. If climate must change, the adaptability of farmers is encouraging news.

The Appalachian oak forest stretches nearly from Atlanta in the South to Portland, ME in the North. Climate warming could shift this zone northward hundreds of miles. The zone would no longer encompass Carolina but would reach New Brunswick in Canada. Being well inside the oak forest, we are unlikely to see great changes.

In the past, abnormal weather such as spring droughts rather than changes in averages made changed forests. Altered extremes are the harm or help of a climate change. Trees that disperse their seed widely will cope best with climate change. Climate change will not deal the coup de grâce to a tree. Instead unfavorable climate may weaken it, and then a pest, wind or fire kill it. Or, climate change may help a tree resist a killer. Finally, impacts will lag for decades, be hard to detect and be hard to blame on climate change.

The crosses in Fig. 2 show the varying annual rain in southern Connecticut from 1870 on the left to 1989 on the right. Although the average was 45 inches, reality lay between the minimum of 28 inches during the dry 1960s and the maximum of 64 inches in 1983.

To capture the variability, I show the frequency distribution of annual amounts in Fig. 3. The diagonally hatched bars are the actual past frequencies. The most frequent amounts

and so the tallest diagonally hatched bars are near 42 inches at the center, but the range is 28 to 64.

Although the new climate could as easily bring more rain, take the example of 10% less. The darker, checkered bars are the frequency distribution I made by cutting each past year to 90% of what it really was. A new minimum appears in the class centered on 22 inches. The frequencies near 32 and 38 inches shoot up. And high amounts are less frequent. After such a climate change, people might not sense the fall from 45 to 40.5 inches average, but they would feel more frequent droughts and less frequent floods.

Runoff is the critical matter for water supply. So, I reckoned the runoffs and put them in the frequency distribution in Fig. 4. Subtracting from each rain a reasonable 25 inches of evaporation leaves the runoff with the frequencies shown by the diagonally hatched bars. Runoff near 18 inches is most frequent, but some runoffs are near 2 and 38 inches.

The impact of climate change on runoff can be reckoned in two ways. Subtracting the past evaporation rate from the new, 90% rain cuts runoff 22%. On the other hand, if the new climate is warmer by a degree or two, evaporation will be more. When 10% more evaporation or 27 inches is subtracted from the new 10%-less rain, runoff is cut fully 35%.

The darker, checkered bars in Fig. 4 show the new runoff for 10% less rain and 10% more evaporation. Frequencies of runoff near 2, 8 and 12 inches jump up. For the new climate, the bars for rain in Fig. 3 jump less than the bars for runoff on the right of Fig. 4. A small change in climate levers a big rise or fall in runoff and supply.

But finding the lever, what do we do? Regional predictions of rain conflict. Decades will pass before the message of change is detectable above the noise of annual variability. We have plenty of other pressing needs today for the attention and money we might spend on an uncertain change in water supply decades from now.

The strategic measures for water supply are those with a payoff certain and soon rather than uncertain and late. I think of two:

1. Improve the security of our present water supply in the present, variable climate. The methods can range from rules and construction to conservation and prices. And
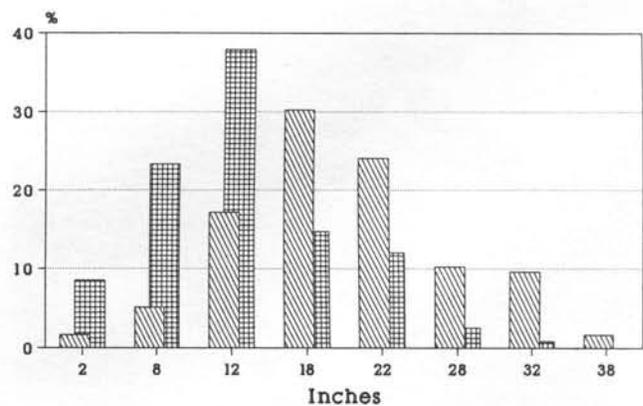

Figure 4. Runoff past and runoff changed by 10% less precipitation and 2 inches more evaporation.

making water systems robust for coping with present variability makes them robust for coping with climate change, too.

2. Invent and have at hand ways of rapidly and surely adapting water supply and management. The ways can range from building footings or reserving land to preparing for fast construction and for emergency measures. These permit postponing expensive action safely and thus shorten the time between investing in adaptation and the payoff of actual need.

Talk of climate change centers on an average global warming. But reality is a panoply of elements and their timing and variability in a real place like Connecticut. During the coming decades, we shall adapt to any change in climate and change in other ways that may obscure or enhance the impacts of climate change.

Our landscape of hardwoods that regrew from the clearing of earlier centuries may be changed again by climate—but not much because it is well within the zone of the Appalachian oak forest. Farmers will rapidly adapt to any climate change.

It is with water supply that climate change will lever practical affairs in Connecticut.

Pesticides and other chemicals sorb slowly in soil

By Joseph J. Pignatello

There is a growing interest in the detailed behavior of pesticides and other synthetic organic chemicals in soil and ground water. Soil and environmental chemists have long known that most of these chemicals bind (sorb) to soil particles, either by *adsorption* (binding to surfaces) or *absorption* (penetration into the particles). Sorption is studied by adding the compound to a well-mixed suspension of soil in water and measuring its distribution between the water and the soil after allowing for equilibrium to be reached. The use of soil-water suspensions is appropriate because, under most circumstances, soil in the field contains enough moisture to coat all particles with water.

The ratio between the sorbed concentration and the solution concentration at equilibrium is usually expressed as a distribution constant, K_d. For example, for equal amounts of soil and water, if the ratio is 1, half of the molecules are bound to the soil and half are dissolved in solution. K_d is specific to a given chemical and soil, but predictions are possible from correlations with soil and chemical properties. The driving force for sorption of most organic compounds seems to be
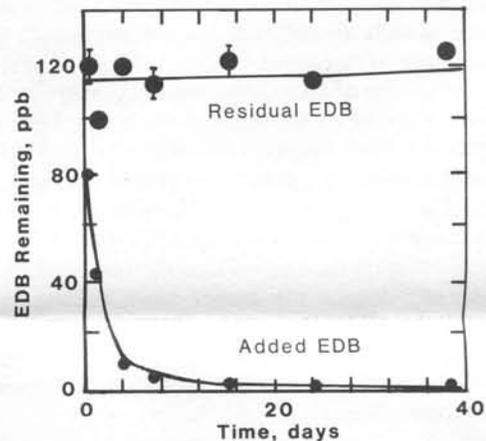

Figure 2. Biodegradation of EDB by soil bacteria in a field soil from Lockwood Farm in Hamden showing the stability of residual EDB present in the sample compared to rapid degradation of freshly-added EDB.

primarily their repulsion from water. Sorption occurs mainly to the natural organic matter fraction of the soil, which consists of decomposed microorganism, plant, and animal material. Water content in this organic matter is diminished.

Sorption strongly influences the fate of chemicals in the soil. The rate of leaching from soil or the rate of transport in ground water is affected by the extent of sorption, since sorbed molecules do not move with the flowing liquid. Moreover, there is strong evidence that molecules in solution are much more available than sorbed molecules for uptake and biodegradation by soil microorganisms. Consequently, K_d is a key parameter in any mathematical model of the fate and transport of contaminants.

The assumption that K_d is a constant is valid only when the sorption process is rapid with respect to degradation or movement in the soil water; usually this means equilibrium must be reached within several hours to perhaps 2 days, since contaminants don't move or degrade much in that time.

Figure 1. Joseph J. Pignatello preparing a sample for analysis.

Table 1. Residual of some contaminants in an agricultural soil after sorption from water solution for 1 day followed by purge-desorption for 4 days.

Compound	Major use	Residual as % of initial sorbed
Trichloroethylene	solvent	4.8
Tetrachloroethylene	solvent	1.8
1,3-dichloropropene	soil fumigant	10
DBCP	soil fumigant	1.7
1,2-dibromopropane	research	2.7
EDB	soil fumigant	3.4
carbon tetrachloride	solvent	1.9
1,1,1-trichloroethane	solvent	1.5

Nearly all sorption studies use a 24-hour period. Further, sorption must be reversible, meaning that desorption occurs with incoming cleaner water. All current fate models for organic compounds operate under these assumptions.

I have been interested in the kinetics (rates) of sorption and desorption in soils. In 1986 I began collecting data showing the assumption of rapid reversibility to be false, and that, at least for a fraction of chemical, sorption/desorption equilibrium times could be on the order of months and even years.

My initial studies involved ethylene dibromide (EDB), a soil fumigant used to control nematodes and other pests. Samples of soil collected from fields treated with EDB contained persistent residues, even up to 20 years after the last application, despite the known tendency of EDB to rapidly volatilize, and despite my earlier work showing it to be biodegraded by soil bacteria (*Frontiers,* Spring 1986). I sought explanations for this incongruity. I found that the field residues of EDB desorbed into water so slowly that years would be required to reach equilibrium. The apparent K_d's were more than 100 times greater than those measured in short-duration experiments with freshly added EDB. Also, to extract field EDB residues from the soil I had to use much harsher conditions than the classical methods for such compounds. By contrast, EDB freshly added to the soils behaved normally in every way. A remarkable consequence of this tenacious sorption is the stability of EDB to biodegradation by soil bacteria compared to the rapid degradation of radioactively-tagged EDB added to the same soils (Fig. 2).

Evidently, a fraction of the EDB originally applied to the soil in the field slowly made its way to sites on or in the particles that are remote from water that could leach it or bacteria that could degrade it. To ensure that this behavior was not unique to EDB, I have since carried out experiments on many other chemicals, including several soil fumigants and industrial chlorinated compounds (Table 1). I also examined soils from the field containing residues of herbicides. Most of these compounds are troublesome ground water contaminants.

In the laboratory, the compounds were allowed to sorb to the soil for periods ranging from 1 to 60 days. This was followed by desorption using two different methods. One involved repetitive 24-hour extractions with water over 3 weeks. The other involved continuous purging of the compound from solution as quickly as it desorbed from the soil over a period of 4 days.

Repetitive extraction confirmed that a small fraction of initial chemical sorbs much more strongly than the bulk. The apparent K_d at the end of each 24-hour extraction period gradually increased up to almost 200 times greater than the initial K_d. Yet these tightly held residues were not fixed irreversibly, since detectable amounts desorbed into the water during each extraction. With increasing sorption time, the residual in the soil increased in concentration and desorbed into solution more slowly.

The 4-day continuous purge desorption technique also revealed the formation of slow-desorbing residual fractions. Table 1 shows that this fraction was from 1.5 to 10% of the initial amount of chemical sorbed, depending on the compound, in a soil from an agricultural site. Smaller fractions (0.1 to 1%) were formed in a sample of subsoil taken from below the ground water table in an aquifer in Simsbury. The residual concentration increased with sorption time, which agreed with the results obtained in the repetitive extraction experiments. The residual also, not surprisingly, increased with the concentration that the soil was exposed to during the pre-purge sorption period.

Other experiments have provided insight into the underlying mechanisms of formation of these resistant residuals. Residuals were formed in different soils in proportion to the soil's natural organic matter content. Also, some residual was associated with undecomposed plant material. Very little was associated with the clays. These results indicate that the residuals are probably sorbed to the organic matter and not the clays or other mineral components, and moreover suggest that this type of sorption is probably no different in character than sorption of the bulk chemical. Extensive research on organic compounds indicates that they sorb by partitioning into the soil organic matter; in other words, by dissolving and distributing approximately evenly throughout the three-dimensional structure of the soil organic matter.

However, the soil mineral fraction seems to play an important secondary role. Pulverization of the soil liberated large amounts of residual, suggesting that some molecules of contaminant are trapped in bits of organic matter lodged among grains of particles which are cemented together in aggregates. This aggregation prevents rapid exchange of molecules with
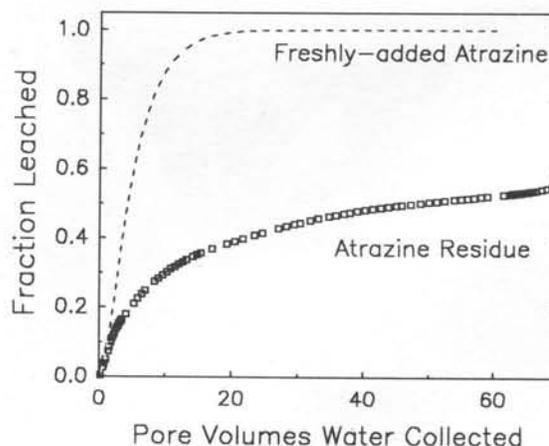

Figure 3. Leaching of residual atrazine compared to freshly-added atrazine from a field soil.

the bulk solution. Furthermore, acidification of the soil to a pH less than about 2 also promotes desorption. Iron and aluminum oxides, which can act as cementing agents for soil aggregates, begin to dissolve at those acid concentrations.

One consequence of the formation of resistant sorbed fractions is that the soil can act as a reservoir for a contaminant, keeping it stable to biodegradation and slowly releasing it to the infiltrating water. This prolongs the natural or deliberate cleansing of a contaminated system. To see whether this actually occurs in the field, we collected soil samples from farms around the state where two herbicides, atrazine and metolachlor, had been applied to the soil. Samples were collected 2-15 months after the last application. In all cases we found that a large fraction of the residual herbicide (60 to 94%) existed in a resistant sorbed state after suspension in water for 24 hours. Furthermore, the resistant fraction was greater with increasing length of time between the last application of the herbicide and collection of the sample; again, showing that more chemical diffuses into remote sites with time.

The most dramatic effects were seen when one of the soils was placed in a cylindrical glass column and water was passed through to simulate leaching in the field. Figure 3 shows the relative amount of atrazine leached as a function of the number of pore volumes of water (i.e., total volume of water in the column at any given time) that had passed through the column. After an initial slug, there was a prolonged "tailing,"

or bleeding, of atrazine from the column. Metolachlor behaved similarly.

After 4 months and 70 pore volumes of water, corresponding to more than 10 years of rainfall in Connecticut, only about 55% of the atrazine (45% of metolachlor) initially in the soil had been leached. Furthermore, both herbicides were evenly distributed along the column and not preferentially stripped from the soil closest to the water inlet. This clearly indicates that the rate of desorption of herbicide from individual soil particles occurred on a much slower time scale than passage of the water flowing through the column. Finally, the behavior of the resistant residue was not well simulated by fresh herbicide added to the column and leached under the same conditions in a separate experiment. By only 20 pore volumes, nearly all of the freshly added atrazine had leached (dashed curve, Fig. 3).

My conclusion is that when organic chemicals are added to soil they leave a resistant fraction that increases with time. This fraction is stable to biodegradation because the molecules are unavailable to the indigenous bacteria. The resistant molecules are unavailable most likely because they are buried within the soil organic matter; there is some evidence, however, that particle aggregation can be a further mechanism for entrapment. The resistant fraction can bleed out slowly, prolonging the time it takes to completely flush a contaminant from the soil. On the other hand, it is much less available for uptake and manifestation of toxic effects.

Many gypsy moth caterpillars destroyed by fungus for second year

By Ronald M. Weseloh and Theodore G. Andreadis

Last year we reported the discovery of a fungus called *Entomophaga maimaiga* that destroyed enormous numbers of gypsy moth caterpillars in 1989 (*Frontiers*, Spring 1990). We documented its impact on gypsy moths and showed that it was widespread throughout Connecticut and the Northeast. We also began to study this natural enemy in greater detail, because the more we know about it the better we will be able to predict its effects and use it efficiently. We report here the results of this extended study.

The gypsy moth was imported and accidently released in New England in 1869. The natural enemies that attack it in the Old World were not present in North America, which is the main reason the caterpillars became a problem here. Early in this century a program was begun to import natural enemies from both Europe and Asia. Twelve parasites and predators are now established, as well as a virus disease that can be very important in causing large populations to crash. However, outbreaks still occur, and we are constantly trying to find new, effective, and safe natural enemies.

In 1909, Dr. G.P. Clinton, who was the Botanist at our Experiment Station in Connecticut, was commissioned by Harvard University to bring back a fungus from Japan that was known to attack the gypsy moth there. At that time gypsy moths were almost non-existent in Connecticut, and so it would not have been possible to release any natural enemies

against the pest in our state. However, Massachusetts had a permanent infestation, and the fungus that Dr. Clinton imported was released there in 1911. This fungus was not recovered until 1989, when we found it killing large numbers of gypsy moths in Connecticut. Although it was not found for almost 90 years, its appearance in 1989 was evidently triggered by favorable wet weather and the presence of large numbers of gypsy moth caterpillars.

E. maimaiga overwinters as resting spores within dead caterpillars. In early spring these presumably germinate and infect young caterpillars. The fungus multiplies inside the body of the larva, and eventually produces either pear-shaped spores called conidia that can infect other larvae, or round resting spores that overwinter. Wet weather favors fungus growth and reproduction. Thus, heavy precipitation appears to be necessary for high fungal activity.

We began our detailed study by collecting fungal resting spores from dead caterpillars in the fall and winter of 1989-1990. These were placed on wet filter paper in Petri dishes and periodically examined for germination. Resting spores collected in March were the first ones that germinated. They produced germ tubes that formed conidial spores at their tips. These conidia were discharged into the air and infected caterpillars when they landed on them. The fact that resting spores did not germinate before March probably means they

Figure 1. Ronald M. Weseloh, left, and Theodore G. Andreadis, right, in the gypsy moth rearing laboratory.

All caterpillars that were infected with the fungus in May produced infective conidia only. Later, when larger and about to pupate, the caterpillars produced resting spores of the fungus that can overwinter.

To confirm the role of rain, we irrigated some plots and compared the impact of the fungus in these locations to that in adjacent, normal areas. Impact lawn sprinklers capable of watering circular areas 60 feet in diameter were placed in each of two plots. Garden hoses 200 feet long with timers attached supplied water to the sprinklers four times a day throughout May and June. Caterpillars were collected within these areas as well as in an adjacent, non-sprinkled area, and other larvae were exposed in cages. Results were mixed. No differences in fungal prevalence were noted in the larvae collected from the different areas, but more caged larvae from the sprinkled areas died from fungus than did those in the drier areas. The weather during May was probably too wet for differences to occur in the collected larvae, but the caged larvae showed that wetter areas did produce more infective conidia.

The link between high precipitation and fungal abundance seems clear, and we now know that precipitation in May is critical. We know that germination of resting spores begins early enough to infect hatching larvae, which then produce conidia that spread the disease to older larvae, with dramatic results. We also know that gypsy moth numbers have declined as the fungus continues to be abundant. There were 30 permanent sites in Connecticut where gypsy moth egg masses were found in 1990, but in 1991 the number of sites with egg masses dropped to 14. Indeed, the second year of heavy fungus activity has caused the gypsy moth to decline not only in Connecticut but throughout the Northeast. Our results clearly show that this pathogen has enormous potential for controlling the gypsy moth.
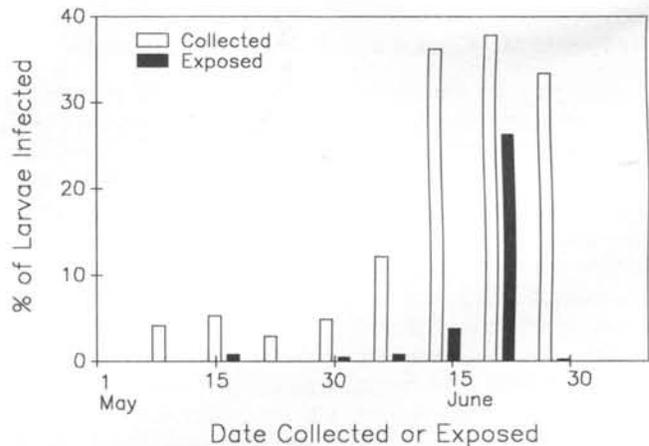
need to be exposed to a period of cold weather before they can become activated. The cold-treatment insures that spores will not germinate during a temporary warm spell in the middle of winter. Although they are capable of germinating in March, it is unlikely that many spores do so because temperatures are usually too low at that time of year. However, hatching caterpillars can become infected when the weather warms up in late spring.

To trace infection of caterpillars in the forest, we established plots in Bethel, Hamden, Monroe, Newtown, Sherman, Weston, Wilton, and Woodbury. In each plot, gypsy moth caterpillars were collected weekly, reared in the laboratory and examined daily for 2 weeks. We also exposed laboratory-reared larvae in small screen cages for several days per week in each plot. These caterpillars were retrieved and reared to determine how many had become infected.

Results from the collected and caged caterpillars were similar (Fig. 2). During May, some small caterpillars were infected with the fungus, but in June infections increased tremendously and enormous numbers of caterpillars died. May was unusually rainy in both 1989 and 1990, but June was much drier in 1990. The fact that the fungus was abundant both years means that abundant rainfall in May rather than June is critical for full development of the disease.

Figure 2. Prevalence of fungal infection in field-collected and cage-exposed larvae.