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Why do fumigants remain in soils and ground water for decades?

By Brij L. Sawhney

In Connecticut, soil fumigants containing ethylene dibromide (EDB) and 1,2-dichloropropane (1,2-DCP) have been widely used to control nematodes in tobacco and strawberry fields. Their use was banned in 1984 because experiments with laboratory animals showed them to be carcinogenic. Despite their discontinuance, these chemicals have been detected in ground water near where they had been applied. The question to be answered is: how long do they last in the soil and hence, in the ground water?

These fumigants are liquids at room temperature, but when injected into the soil they evaporate and diffuse through the soil in all directions. A portion of the fumigant escapes into the atmosphere and is lost and the remaining fumigant is diluted as it diffuses laterally and downward; some is absorbed by soil particles and some dissolved in soil water. When soil is dry and the pores are filled with air, diffusion is rapid. In moist or wet soil, diffusion is slower. Rain can leach the fumigant through the soil to ground water; however, a small fraction would be retained by the soil during the downward transport of water and dissolved fumigant.

To better understand the movement of these fumigants in soil, Thomas Rathier and I turned to the lysimeters that were originally installed in 1929 at the Valley Laboratory of The Connecticut Agricultural Experiment Station in Windsor to study the movement of fertilizer through soil. The lysimeters consist of cylindrical open-top metal tanks 9, 18 and 27 in. deep and 20 in. in diameter, with tin-lined metal pipes at the bottom that lead to the interior of a collection chamber underground. We refurbished the lysimeters and extended the metal pipe, using copper tubing, to reach glass bottles containing 50 ml hexane to extract the fumigant in the leachates. The lysimeters were filled with two soils, Merrimac fine sandy loam and Birchwood fine sandy loam, in the same sequence of horizons as in the field. Soil horizons are distinct layers of soil, with unique physical and chemical characteristics, produced by physical, chemical and biological weathering of the soil. Thus, the 9 in. deep lysimeter had only the A horizon, the 18 in. deep lysimeter had A and B horizons and the 27 in. deep lysimeter had A, B and C horizons.

Table 2. Concentrations of 1,2-dichloropropane (ppb) remaining in soils after 18 months.

Depth, in.	Merrimac	Birchwood
	9 in. deep lysimeter	
0-3	57	89
3-6	110	58
6-9	66	245
	18 in. deep lysimeter	
0-3	44	51
3-6	84	75
6-9	82	64
9-12	53	36
12-15	36	34
15-18	32	33

A plastic cover was installed to prevent rainfall from reaching the lysimeters (as shown on the cover). The soils were fumigated with 1,2-DCP at four times the recommended application rate for analytical convenience. Leaching was begun after 3 days by applying small increments of water to the soil until liquid appeared in the collection bottles and then additional water was applied to obtain 1 liter of leachate. The hexane and leachates in the bottles were thoroughly mixed by vigorous shaking and 1,2-DCP that was extracted into the hexane was determined using gas chromatography. We leached the soils periodically for a period of 18 months.

Table 1 shows concentrations of 1,2-DCP in five successive leachates from the two soils during a 6-month period. As expected, concentrations of 1,2-DCP in the effluent from shallow soils were very high initially and decreased rapidly with further leaching. In contrast, concentrations in leachates from deeper soils were low in the first effluent sample, increased in the next two samples, and then continued to decrease. Apparently, the fumigant had not reached the lower depths in the deeper lysimeters before leaching was begun. Initial leaching transported the fumigant downward but a portion was retained by the soil in

Table 1. Concentrations of 1,2-dichloropropane (ppm) in leachates from Merrimac and Birchwood fine sandy loam soils.

		Merrimac Lysimeter depth (in.)			Birchwood Lysimeter depth (in.)		
Leaching treatment	Days after injection	9	18	27	9	18	27
1	3	414	9.1	1.4	180	3.4	0.1
2	25	301	114	4.3	93	24.1	0.8
3	45	171	152	7.6	47	21.0	2.0
4	157	3.1	13.8	0.7	1.1	2.0	0.2
5	190	0.6	2.2	0.5	0.2	0.2	0.1

the lower depths, reducing its concentration in the initial effluent. After the fifth leaching treatment, the concentrations in leachates from all lysimeters decreased a 1000-fold from parts per million (ppm) to parts per billion (ppb). However, traces of the chemical were detected in the effluents even after 18 months and 12 leaching treatments. Concentrations of 1,2-DCP in leachates from the Birchwood soil were lower than concentrations in the Merrimac soil. This may have resulted from greater retention of fumigant by the higher organic matter and silt content of the Birchwood soil.

Following the leaching treatments, the lysimeters were excavated in 3-in. deep sections and the soils analyzed for 1,2-DCP. Analyses of the soils from 9 and 18 in. deep lysimeters (Table 2) clearly demonstrate that the soils retained small concentrations of the fumigant even after 18 months. In general, soil at the surface contained greater concentrations than the soil at the lower depths. Higher organic matter content in the surface is likely responsible for the greater retention of the fumigant.

Analyses of soil samples from a field plot fumigated with 1,2-DCP further attest to its persistence. Data in Figure 1 show that 2 weeks after application, the surface soil contained 210 ppb 1,2-DCP which decreased during the next 4 weeks to about 60 ppb. Thereafter, only slight changes occurred. Thus, we have found that some of the fumigant is held strongly by the soil and is released only slowly, providing a potential source of ground water contamination. Earlier, we had found that small concentrations of EDB persisted in the soil for more than two decades after application despite its high volatility, water solubility and weak adsorption to soil particles. These observations, therefore, offer an explanation for why soil fumigants, such as 1,2-DCP and EDB, are found in soils and ground water years after their application to nearby soils.

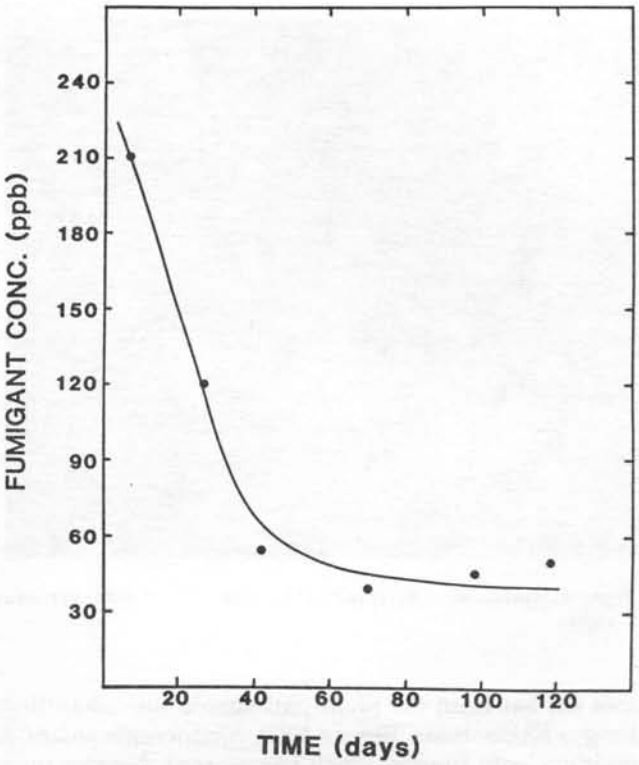

Figure 1. Concentration of fumigant remaining in soil for 4 months following application.

Further Reading

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Plant parasitic nematodes and fungi are an unhealthy alliance against strawberries

By James A. LaMondia and S. Bruce Martin

Black root rot is a seriously debilitating disease of strawberry in Connecticut. Its symptoms include a rotting of perennial roots and the death and deterioration of small feeder roots (Figure 1). This reduction in the root system results in declining plant vigor and lowered productivity.

Attempts to breed for disease resistance and develop chemical controls for use on living plants have failed. Black root rot is currently controlled by removing plants, fumigating the soil and then replanting strawberry crowns into the fumigated soil. This method of control is costly and removes strawberries from production for a minimum of a year.

It has generally been accepted that black root rot does not have one specific cause. Indeed, numerous microorganisms can be recovered from diseased roots and many have been shown to cause some level of disease on strawberry. Since this disease was first described in the early 1900s, many fungi (over 25 genera), the lesion nematode (*Pratylenchus penetrans*), and environmental conditions such as flooding, freezing and poor soil aeration have all been suggested as possible causes. The basis for this apparent confusion was an underlying inability to consistently reproduce the disease with a single pathogen or condition.

The pathogen most commonly associated with black

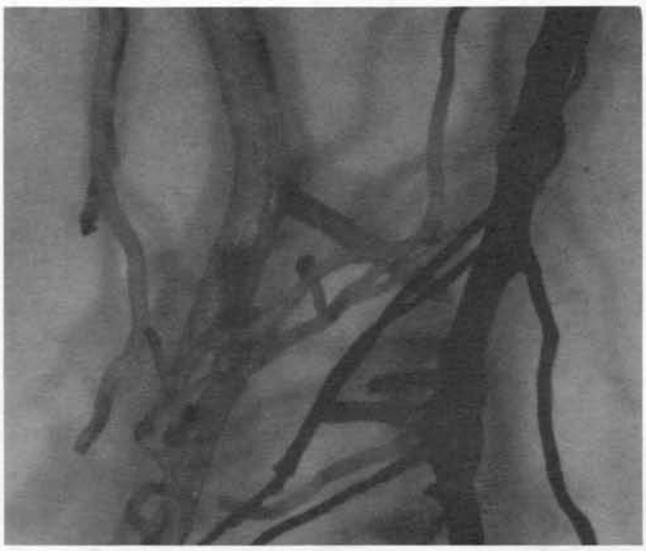

Figure 1. Healthy strawberry root. at left and root-rot diseased root at right.

root rot has been the plant pathogenic soil-inhabiting fungus *Rhizoctonia*. Before 1960, *Rhizoctonia solani*, a multinucleate fungus which causes root diseases on a large number of plants, was named as the cause of black root rot of strawberry. However, in 1967, the *Rhizoctonia* attacking strawberry was found to be binucleate, having only two nuclei per hyphal cell, and distinctly different from *R. solani*. This fungus was named *R. fragariae*, after the scientific name for strawberry (*Fragaria x annassa*).

Researchers in Japan have recently further differentiated binucleate *Rhizoctonia* into subcategories based on anastomosis, or fusion, of the vegetative fungal strands (hyphae). They identified at least 15 anastomosis groups (AG). Each AG consists of related fungi which are more similar to each other than to different AG for many traits, including pathogenicity and host specialization.

Almost all field-grown strawberry plants have roots extensively colonized by *R. fragariae*. The amount of disease which results from this infection depends on the ability of each isolate to cause disease, environmental conditions, and the presence of other pathogens. Plant parasitic nematodes increase the severity of several fungal diseases, and the lesion nematode has been circumstantially associated with black root rot of strawberries.

We designed a series of experiments to determine which pathogens were responsible for causing black root rot in Connecticut. First, we surveyed five pick-your-own strawberry farms growing seven cultivars. We isolated *R. fragariae* from almost all plants with black root rot symptoms, but found *R. solani* infrequently. We identified three AG of *R. fragariae*, AG-A, AG-I and AG-G by determining hyphal fusion to known AG standards obtained from Japan. When we made isolations from different roots of the same plant, 77% of the plants had only one AG colonizing the entire root system.

Most *Rhizoctonia* isolates obtained in the survey were pathogenic when inoculated to the strawberry cultivar 'Honeoye'. They caused feeder roots to rot off at the point of attachment to perennial roots and caused sunken dark lesions in the cortex of the perennial roots. Fungi identical to those inoculated were readily reisolated from the diseased tissue.

Disease severity after 4 weeks in these experiments ranged from 0.6-10% root rot at 25-30C, and 1.8-60% root rot at 15C. Although the ability of specific isolates to cause disease varied in each AG, AG-I was consistently more pathogenic than AG-A or AG-G.

Our survey indicated that almost all roots (over 70%) contained *Rhizoctonia*, with a great range in pathogenicity among the isolates collected. Some isolates of *Rhizoctonia* had colonized strawberry roots without causing disease.

The survey also indicated that lesion nematodes are common in strawberry fields in Connecticut. The nematodes cause elliptical reddish-brown lesions on strawberry roots that are distinct from black root rot symptoms. These nematodes are microscopic worms that are less than 1 mm long and 10 microns (about 1/2,500th of an inch) in diameter. They cut through root cells with their spear-like stylets during feeding (Figure 2). We often associated severely affected areas of fields with plant parasitic nematode populations of 60 to 120 per gm of plant root. In adjacent healthy areas numbers of nematodes were very low or undetectable (0 to 8 per

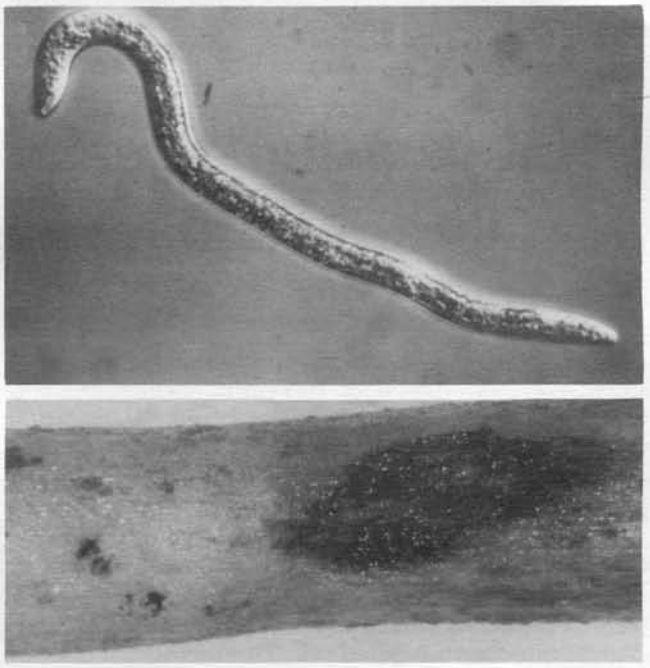

Figure 2. The root lesion nematode, *Pratylenchus penetrans*, and typical symptoms of nematode infection.

gm of root). Since we found plant roots were just as extensively colonized in both healthy and diseased areas by the same AG of *R. fragariae*, we concluded that the nematode was interacting with the fungus to cause increased disease.

We then devised an experiment to determine the interaction of *P. penetrans* and *R. fragariae* in root rot of strawberry. We inoculated 16-week-old strawberry runners (cultivar Honeoye) with three isolates of *R. fragariae*, (AG-A, AG-G, and AG-I) and *P. penetrans* in suspension at 0, 17 or 170 nematodes per cubic centimeter of previously fumigated soil. The plants and roots were incubated 8 weeks at 10 or 24C. In all cases, high nematode levels increased the amount of fungal rot caused by *Rhizoctonia*. The fungus alone caused 25-36% root rot at 10C and 30-38% at 24C. However, feeding by nematodes increased fungal root rot to 36-52% at 10C and 70-82% at 24C. Nematodes and fungi together reduced the length of main and lateral roots by up to 40% and feeder roots by up to 60%. This type of damage is typical of black root rot symptoms seen in strawberry fields and would decrease plant vigor and yield over time.

Reports from France and from West Virginia suggest that some *Rhizoctonia* isolates actually increase plant growth and yield by some, as yet, unknown mechanism. We found that a number of *Rhizoctonia* isolates taken from our test areas do not cause root disease, even in the presence of root lesion nematodes. We hope to colonize strawberry roots with these isolates to learn if this treatment will prevent pathogen invasion and subsequent root rot.

Estimating crop yield loss in the field caused by plant defoliation

By Francis J. Ferrandino

To establish guidelines for the prudent use of pesticides, it is important to determine how seriously the final yield of an agricultural crop will be affected by foliar injury caused by diseases or insects. This requires an understanding of the relationship between loss of leaf area, light interception and plant productivity.

Plants are living solar energy converters which, through the process of photosynthesis, convert carbon dioxide and water into carbohydrates. This process is powered by sunlight. Although the temperature of the air and soil and the availability of nutrients and water affect productivity, the rate at which a plant grows is limited by the amount of light it absorbs.

For a lone plant in the sun, the amount of light absorbed is simply proportional to the size of the plant. If damage due to disease or insects removes a portion of its leaves, the amount of light the plant can absorb will be reduced proportionately.

Agricultural crops are grown in closely planted rows, so individual plants shade one another as they grow. At maturity, there is enough leaf area in most agricultural crops to shade the ground five times over and many leaves are in partial shade. Thus, loss in yield is not simply proportional to the reduction in leaf area. In fact, a certain number of leaves can be removed with relatively little effect on total photosynthesis until light penetrates the plant canopy and is wasted on the ground. Because of this natural redundancy of leaves, plants can tolerate significant defoliation without a subsequent loss of yield.

I studied the effect of defoliation due to late blight on the yield of tubers from a field of potatoes (cv. "Superior") at Lockwood Farm in Mt. Carmel during the spring and summer of 1986. For sampling purposes the field was divided into areas 1.5 meters square containing ten potato plants which were damaged uniformly. The percentage of foliage diseased or destroyed within each square was recorded periodically and the tubers produced within each square were harvested and weighed at the end of the season.

Late blight, caused by the fungus *Phytophthora infestans L.*, was the disease responsible for the 19th Century Irish Potato Famine. The disease thrives in cool, wet weather and can be important early or late in the season. Late blight is characterized by dark gray lesions on leaves which, under the proper conditions, expand rapidly causing the infected leaves to wither and fall. Yield loss can be particularly severe when an infection occurs early in the season because the young plants have less leaf area to capture sunlight and grow replacement leaves. During June and July, the cool, wet conditions favored development of late blight and the disease spread rapidly. By mid-August half of the plants had more than 90% of their leaves destroyed.

The average yield from healthy portions of the field was 4.4 kg per square meter (about a pound per square foot), which is twice the national average. Yield from the infected portions of the field were expressed as a percentage of this average. Figure 1 shows percent yield versus the percentage of foliage destroyed by late blight. I found that there was no significant effect on the final yield until more than 40% of the potato leaves were destroyed by the disease. Beyond this level of defoliation, however, yield declined rapidly. These results can be explained in terms of the penetration of light into a plant canopy, which is determined by the arrangement

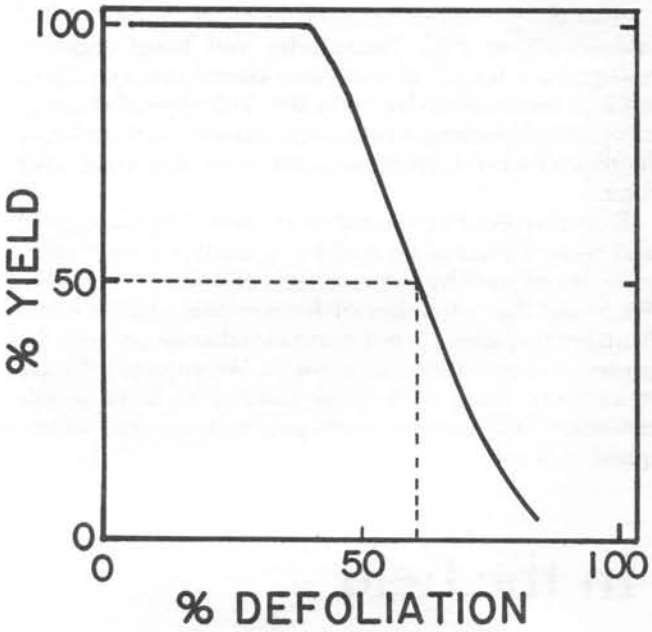

Figure 1. Plot of % tuber yield versus % defoliation. For example, the removal of 60% of the foliage reduces the amount of harvested tubers by 50% (dotted line).

and density of leaves. To determine light penetration into the canopy I made direct measurements of the light absorbed by potato plants during the spring and summer of 1987 and found that a layer of leaves with sufficient leaf area to cover the ground absorbs approximately 60% of the sunlight. A mature potato field has at least five such layers. The top layer of the canopy will absorb approximately 60% of the total light and each successive layer of leaves will intercept less and less light, making ever-decreasing contributions to the potential yield.

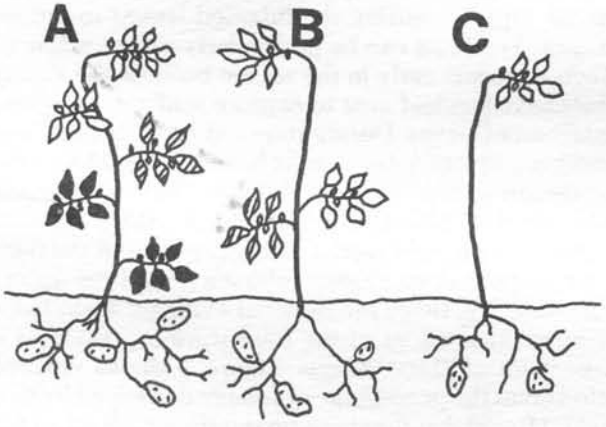

Figure 2. Schematic representation of the light intercepted by a healthy potato plant (A), a plant with 40% of its leaves removed (B), and a plant with 80% of its leaves removed (C). The amount of light reaching a leaf is indicated by shading (white leaves are fully illuminated and dark leaves are immersed in shade).

Figure 2 shows a series of plants in a field with varying degrees of defoliation. Each leaf represents a layer of leaves sufficient to cover the ground below. The amount of light reaching this layer is represented by the shading (white leaves are in full sun, black leaves receive little or no sunlight). Panel A represents a full grown and healthy field for which the lower two layers receive much less light and, therefore, contribute little to total photosynthesis. Panel B represents a field with 40% defoliation (two layers out of five damaged). Despite the 40% defoliation, the plants in Panel B and Panel A intercept approximately the same fraction of the total light, since only redundant foliage has been lost. Panel C represents a field with 80% defoliation. The ability of the canopy to intercept light and, therefore, the rate of photosynthesis is now significantly reduced. The fact that yield was unaffected by defoliation of less than 40% but declined rapidly above this threshold (Figure 1) is consistent with my description of the effects of light absorption on yield.

To use the results to predict the yield from a large field, it is necessary to account for the spatial variation in damage which normally occurs in a field. Unfortunately, average values of disease or insect damage for large fields with large variations in leaf damage do not relate directly to the loss in total yield. For example, if plants in 40% of a field were destroyed and produced no tubers, the yield loss would be fully 40% and not the 0% that would result from the assumption that all plants suffered an evenly distributed 40% defoliation. This example is closer to the rule than the exception because both late blight and Colorado potato beetle damage tend to be concentrated in many relatively small areas.

Since any plant which sustains less than 40% damage still produces a full yield of tubers, it is logical to estimate the yield separately from the sections of the field having either more or less than this threshold defoliation. To estimate yield loss in large fields, I first estimate the fraction of plants with less than 40% damage. This fraction of the plants is assumed to give a full yield of tubers. Yield from the rest of the field is then read from Figure 1 using the mean defoliation for these heavily damaged plants. The predicted yields for these two regions are combined to give an overall average. For example, consider a potato field in which half of the plants have less than 40% leaf damage and the remaining half have a mean foliage damage of 66%. I assume that the healthy half would contribute half of a full field's yield. The remaining half of the field would produce only 50% of its potential (Figure 1, dashed lines) which corresponds to one quarter of a full field's yield. The final predicted yield would be 75% of the yield of a healthy field. In this way the effect of defoliation on final yield can be accounted for in large fields.

Predictions of the effect of leaf damage on yield such as I have described will give growers a better basis for deciding how much and how often pesticides must be used in order to ensure full yields.

Chlorophyll fluorescence measurements may help recognize increased plant productivity

By Richard B. Peterson

The overall process of photosynthesis is frequently described by the reaction: $6CO_2 + 6H_2O \rightarrow C_6H_{12}O_6 + 6O_2$. The seeming simplicity of conversion of carbon dioxide and water to carbohydrate and oxygen masks the underlying complexity of numerous molecular processes working in concert.

A more detailed examination reveals that photosynthesis involves net transfer of *electrons* from H_2O to CO_2, with chemical energy stored in the resulting carbohydrates. The sequence of electron transfer beginning with the light-dependent extraction of electrons from H_2O with consequent evolution of O_2 is shown in Figure 1. The zig-zag depiction of this series of reactions is relevant to the pathway followed by these electrons and to the mechanism of energy conservation employed by the subcellular structure where photosynthesis occurs, i.e., the chloroplast. These reactions are referred to as the "Z-scheme".

Light energy is transformed into chemical energy along the Z-scheme at two regions called photosystems. The initial photochemical reaction, resulting in production of O_2, occurs in a chlorophyll-protein complex termed photosystem II (PS II). Electrons are passed from PS II to a second photochemical reaction system called photosystem I (PS I).

The chloroplast uses light energy to raise the energy content of the electrons as they pass to the primary electron acceptors in the respective photosystems. This is depicted by vertical displacement upward in the Z-scheme. Most of the electron carriers and all of the photosynthetic pigments are embedded in a membrane structure called the thylakoid. Ultimately, the electrons are passed to a compound referred to in chemical shorthand as $NADP^+$.

A molecule of NADPH is an $NADP^+$ molecule which has taken up two electrons and one H^+ ion. The pool of NADPH is not bound to the thylakoid membrane but is capable of diffusing to a compartment of the chloroplast called the stroma where all of the enzymes of CO_2 fixation are located. The energized electrons carried by NADPH are donated to a sequence of organic reactions resulting in conversion of CO_2 to starch and sucrose.

A second important product of photosynthetic electron transport is adenosine triphosphate (ATP). This compound is ubiquitous among living organisms and serves as an energy "currency", shuttling energy from cellular processes which provide available energy (i.e., photosynthesis or respiration) to diverse processes which consume energy such as growth. The ATP is as important as NADPH as an energy source for fixation of CO_2. Referring again to the Z-scheme, electrons flow "downhill", energetically speaking, on the route from PS II to PS I. If no means were present to conserve the energy released it would appear as useless heat. However, the chloroplast couples most of this available energy to the transport of hydrogen ions (H^+) from the exterior milieu (stroma) to the interior of the thylakoid membrane. Thus, the concentration of H^+ inside the membrane may exceed the external concentration by as much as 1000-fold. The energy stored in this H^+-gradient is coupled to synthesis of ATP at specific sites on the membrane as the H^+ ions flow back in a controlled manner to the stroma.

We now may consider how the biochemical steps represented in the Z-scheme interact with sunlight. Light is composed of discrete packets of energy called quanta. In photosynthesis one quantum of visible light per electron is required in each photochemical reaction in the Z-scheme. Since four electrons are needed to convert one CO_2 to carbohydrate, a minimum of eight quanta are required per molecule of CO_2 taken up by the leaf. Under ideal conditions in the laboratory, quantum efficiencies of as low as nine quanta per CO_2 have been measured in intact leaves. Values of 10 are more common. Both values are satisfactorily close to the expected value of eight.

Some highly efficient crops such as maize can show an overall solar conversion efficiency of 5%. Most others, however, exhibit efficiencies of only 1% to 2%.

A major problem is finding a means by which increased efficiency would be recognized if induced through genetic engineering. The solution may lie in fluorescence measurements. Extracted chlorophyll in solution fluoresces intensely when illuminated. In fact, if viewed from right angles to the exciting light beam the solution appears red due to emission of red light as fluorescence. Chlorophyll associated with PS II in leaves also fluoresces, but with less intensity because of the presence of other processes which consume much of the available energy.

The primary electron acceptor for PS II, Q_A (Figure 1) is capable of holding only one electron at a time (i.e.,

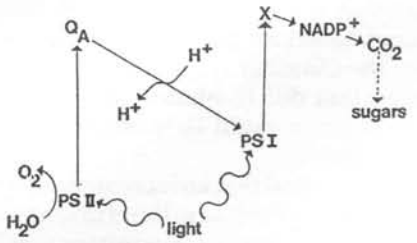

Figure 1. The "Z-scheme" of photosynthetic electron transport.

Q_A^-). When the electron acceptor site is occupied, another quantum arriving at the associated PS II reaction center cannot be used since the resulting second electron has nowhere to go. Thus, the absorbed energy is more likely to be dissipated as fluorescence or heat. Such regulation of fluorescence by the state of the PS II electron acceptor is termed "Q-quenching" since Q_A suppresses (quenches) fluorescence emission. A significant advance in interpreting fluorescence changes in leaf tissue comes from the demonstration that the H^+-gradient formed across the thylakoid membrane during electron transport (Figure 1) is also capable of quenching fluorescence (E-quenching). The two quenching mechanisms operate independently yet frequently influence fluorescence in opposite ways.

For six months during 1987 I spent a sabbatical at the Research Institute for Photosynthesis at the University of Sheffield in England. My intention was to gain new experience and insights to apply to research in Connecticut. Fortunately, I was introduced to a new fluorescence technique which has greatly facilitated study of biochemical processes in the chloroplast. The method, called amplitude modulated fluorescence, uses a low intensity beam of red light to excite fluorescence in the leaf. The beam consists of a series of rapid pulses of light (100,000 pulses per second). Fluorescence thus excited by this beam will be modulated at precisely the same frequency. A system of fiber optics directs the excitation light to the leaf and simultaneously collects fluoresced light. A suitably tuned detection system responds only to fluorescence of the prescribed frequency; all other signals are rejected. This enables use of the system under conditions of continuous white light illumination including sunlight, since nonmodulated stray light of comparable wavelength to that of the fluorescence will not be seen by the detector. Furthermore, application of a brief (less than one second) flash of very intense white light will transiently convert the entire Q_A pool to Q_A^- thus temporarily eliminating Q-quenching. Any residual fluorescence quenching observed during this flash is assumed to reflect E-quenching. From the change in the level of modulated fluorescence during the flash, I could respectively distinguish the extent of fluorescence quenching due to the H^+-gradient and the proportion of PS II units closed to additional photochemical reactions due to accumulation of Q_A^-

My experiments were conducted with spinach leaf tissue which was grown in a greenhouse. The leaf was enclosed in a specially designed chamber and maintained at 20C. The O_2 and CO_2 concentrations in the atmosphere surrounding the leaf were controlled by flowing gas of known composition through the chamber. An instrument called an infrared gas analyzer downstream from the chamber responded to changes in the CO_2 concentration due to photosynthesis. Changes in fluorescence were so rapid they could only be monitored by a computer.

The results indicated that an increase in E-quenching was associated with a decline in the efficiency of utilization of light in photosynthesis. For instance, at high light intensity (i.e., similar to direct sunlight) and low levels of CO_2 (similar to natural atmospheric concentrations) the $NADP^+$ will largely be converted to NADPH.

Since photosynthesis is effectively limited by the availability of CO_2 under these conditions the efficiency of utilization of light is low and the H^+-gradient will be high; E-quenching and the dissipation of light energy as useless heat are increased. Indeed, others have recently reported a decline in the quantum efficiency of photosynthesis, measured by uptake of CO_2, as E-quenching increased with light intensity.

These observations and others are interpreted in terms of the key role of the H^+-gradient (E-quenching) in regulating the activity of the "light reactions" in the thylakoid so as to proceed at a rate to match the capacity of the "dark reactions" to utilize NADPH and ATP during the fixation of CO_2 and associated organic interconversions. This will prevent a backing up of electrons along the Z-scheme which could severely damage the photosynthetic apparatus. An important consequence of this work is the observation that fluorescence reports on the capacity of the dark reactions to assimilate additional CO_2.

One target for manipulation is photorespiration. Station scientists have been studying photorespiration which accompanies photosynthesis in the leaves of many economically important plants (legumes, cereal grains, most common vegetables). This process, which is part of the dark reactions, converts a significant fraction of recently fixed carbon black to CO_2, therefore nullifying some of the photosynthesis that has already occurred.

Photorespiration is notoriously difficult to measure in intact leaves because CO_2 released by photorespiration is refixed rapidly by photosynthesis without escaping the leaf.

Fluorescence measurements may enable an important step forward in the measurement of photorespiration. In my experiments with spinach I observed a strong correlation between the quantum efficiency of photosynthetic electron transport and the ratio of Q-quenching to E-quenching when photorespiration was suppressed by lowering the O_2 level to 2%. This relationship existed over a wide range of light intensities.

When the O_2 level is raised to 21% the observed quantum efficiency of electron transport, based on measurements of the rate of uptake of CO_2 from the atmosphere, drops considerably due to diversion of a portion of the electron flow to internal refixation of photorespired CO_2. Nevertheless, the observed ratio of Q-quenching to E-quenching under 21% O_2 indicates the total rate of electron transport. The difference between total electron transport and the rate of electron transport supporting growth of the plant should yield the proportion of electron transport wasted in photorespiration.

Some preliminary experiments I have performed with spinach under approximately normal air conditions (21% O_2, 0.035% CO_2) suggest that as much as 40% of the total photosynthetic electron flow is diverted to photorespiration. Such information should prove invaluable in assessing the adequacy of biochemical models of photosynthesis and photorespiration as well as aid in the identification of mutants with altered photosynthetic properties.

Further Reading

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