Alanon, an AA offshoot set up for that purpose.

Further uptown is the New York headquarters of General Motors (GM), which last year became the first auto company to announce the establishment of a corporation-wide program. GM is also acutely sensitive to the possibility that people will think an alcoholism program means that "GM must have more drunks." "The problem has been kept in the closet," says Nicholas Pace, an internist who is director of the program. "It takes guts to come forward." Most major automobile companies have now set up employee programs in cooperation with the United Auto Workers union. Combined labor-management committees are in the process of being set up at every GM plant.

Not all programs are of recent vintage —two old-timers that deserve mention are DuPont and Eastman Kodak. Another is at the New York Transit Authority (TA), which *Science* visited. The TA, according to program director Joseph Warren, is the first civil service agency to take such a step. Despite the fact that the workers are unionized, it is basically a management-run operation and, in its early years, it was plagued by union complaints of "witch hunts." It was pretty much by chance, however, that the program came into existence at all. It was started on a part-time basis in 1951 by a TA employee who recovered from alcoholism on his own, with the help of AA. He asked for a regular program, but the TA had the conventional reaction: "We don't have a problem—and when we do, we fire them." But in 1956 (after they had hired Warren, who himself was a practicing alcoholic at the time), they agreed to have a full-time counselor on a trial basis. Warren now has under him seven counselors at the Brooklyn headquarters and two in Manhattan, all of them arrested alcoholics. Of TA's 42,000 employees, close to 300 enter the program each year.

The TA takes a tough approach. Company regulations say anyone who displays signs of inebriation on the job is in for trouble, and anyone who acts funny, like a motorman who misses two stops in a row or a stationman who gets into a fight, gets trundled up to Warren's office. "When a guy comes in, he's intimidated by the Establishment coat and tie," says Warren, "so we deliberately let out a nice juicy curse word," which puts him at his ease. Warren, speaking as one who has been there, cannot overemphasize the danger of "killing them with kindness." He is also wise to the ways of a drinker who manipulates his supervisors by putting on an extra good performance after a reprimand or a binge. "The alcoholic is using them by effective production between drunks."

Warren points out that supervisors have to be trained in objectivity. A nondrinker will have little tolerance for the alcoholic, and there is danger of friction on the job when the employee returns from his drying-out. On the other hand, a supervisor who himself drinks too much is inclined to cover up for an errant underling.

Once Warren and his troops enter the picture, there is little dallying. If an employee is suspected of being boozed up, he is sent to the company clinic for a blood alcohol test. If this verifies suspicions, he comes to Warren's office, where they "attack his denial system." Judging from the yells coming through the wall during the interview with *Science*, this can be a very dramatic affair. (Warren says that, in the early days of the program, a union representative often came along to defend the employee, but he usually ended up seeing that no one benefited by shielding him.)

Following the confrontation, the employee is sent, if necessary, to Mt. Carmel Hospital in New Jersey for a 4-day detoxification program. Blue Cross, the insurance carrier, covers this, but Warren says the company tries to bypass the insurance. Instead, the company pays, and the employee is docked $25 a week out of his paycheck on his return. The reason is twofold. First, this is a way of erasing any mention of alcoholism from the employee's record:

(Continued on page 413)

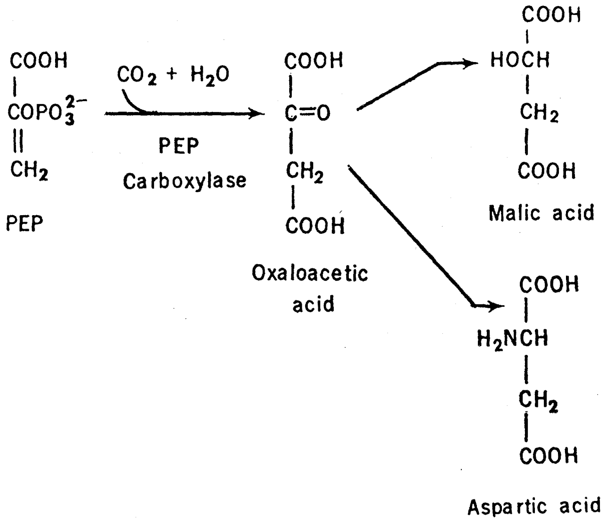
RESEARCH NEWS

Photorespiration: Key to Increasing Plant Productivity?

The photosynthetic conversion of solar energy to chemical energy is essential for the maintenance of life on Earth. Certain plant species are two to three times more efficient than others at the photosynthetic fixation of CO_2 into useful organic compounds (Table 1). Although some important crops, such as sugarcane and maize, are high-efficiency plants, most, including soybeans, peanuts, cereal grains, and cotton, belong to the inefficient category. Recent research advances in the plant sciences have delineated some of the fundamental differences between these two categories of plants. These advances, in a broad spectrum of scientific disciplines, are of potentially great consequence from an economic point of view because they suggest the possibility of increasing the yields of the inefficient food and fiber crops by as much as 50 percent.

A battery of criteria may be used to distinguish the more efficient species from the less efficient; these include differences in pathways for assimilating CO_2, the amount of photorespiratory CO_2 evolution, and the responses of the plants to alterations in O_2 concentration, temperature, and light intensity. Although there is little disagreement concerning the existence of these differences, there is substantial controversy about the mechanism of their relationship to plant productivity.

The high-efficiency plants are frequently called C_4 plants because they contain enzymes for a series of reactions that form four-carbon acids—such as oxaloacetic, malic, and aspartic acids—as the first products of CO_2 assimilation. H. P. Kortschak at the Hawaiian Sugarcane Experiment Station, Honolulu, and M. D. Hatch and C. R. Slack at the David North Plant Research Centre, Queensland, Australia, found that in sugarcane and certain



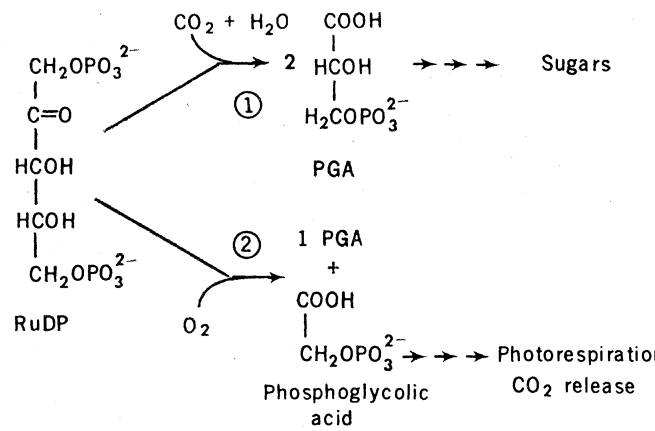


Fig. 1 (left). CO_2 fixation by the Hatch-Slack pathway. Fig. 2 (right). Reactions catalyzed by ribulose-1,5-diphosphate (RuDP) carboxylase. Reaction 1 is favored by high CO_2 and low oxygen concentrations. Reaction 2 has been proposed to occur in the presence of low CO_2 and high oxygen concentrations (normal atmospheric conditions).

other plants, CO_2 is enzymatically attached to phosphoenolpyruvic acid (PEP) to produce oxaloacetic acid, which may then be converted to the other acids (*1*) (Fig. 1).

The C_4 plants also have the enzymes of the Calvin cycle, which was elucidated during the 1950's by Melvin Calvin and his associates at the University of California at Berkeley. The first product of CO_2 assimilation by the Calvin cycle is the three-carbon compound 3-phosphoglyceric acid (PGA). Sugars, usually considered to be the final product of photosynthesis, are then formed from PGA by a complex chain of reactions. The Calvin cycle is the predominant pathway of CO_2 fixation in the low-efficiency plants; for this reason they are called C_3 plants.

Plants not only trap CO_2 to produce organic compounds and the important by-product, oxygen, but they also respire—that is, use oxygen to oxidize sugars and other compounds to CO_2 and water. Consequently, in order to gauge productivity, it is necessary to measure *net* photosynthesis—the difference between the CO_2 assimilated and that lost in respiration. Dark respiration, which occurs in mitochondria and does not require light, is a major source of essential chemical energy for both plant and animal cells. Photorespiration, on the other hand, is light-dependent, and the energy is not released in a form known to be useful to the plant cell. Photorespiration would thus appear to directly decrease plant productivity.

In fact, photorespiratory CO_2 evolution is much higher in the inefficient C_3 plants than in the efficient C_4 plants. Israel Zelitch, at the Connecticut Agricultural Experiment Station, New Haven, has observed that maize, an efficient plant, and tobacco, an inefficient plant, have similar rates of dark respiration, but that the photorespiratory rate of tobacco is much greater than that of maize. He finds that the rate of photorespiration in inefficient plants can be 50 percent of that of net photosynthesis. Zelitch believes that photorespiration is the most important factor affecting photosynthetic efficiency.

Role of Glycolic Acid

Because of the many similarities between the properties of glycolic acid metabolism and those of photorespiration, many investigators agree that this two-carbon acid is the primary source of CO_2 evolved during photorespiration; however, they disagree on the mechanism of the overall process with the possible exception of the first step, the oxidation of glycolic acid to glyoxylic acid. N. E. Tolbert, at Michigan State University, East Lansing, has found that many of the reactions of photorespiration, including glycolate oxidation to glyoxylate, occur in subcellular organelles called peroxisomes. Participation of certain mitochondrial enzymes is also required. According to Tolbert, glyoxylic acid is converted, in a series of reactions, to the amino acid glycine; CO_2 is released as a result of the condensation of two glycine molecules to form serine. Photorespiration may thus serve as an alternate route for the synthesis of these amino acids. Zelitch, however, has presented evidence to indicate that the glyoxylate is oxidized to formic acid and CO_2.

Although the mechanism of photorespiration is still uncertain, some investigators believe that it may be possible to manipulate plant metabolism to increase crop yields. Zelitch found that an inhibitor of glycolic acid oxidation produced an accumulation of glycolic acid in the treated leaves and also inhibited CO_2 release. The rate of glycolate accumulation was much more rapid in tobacco leaves than in those of maize. Zelitch concluded that the slow rate of photorespiration in efficient plants could be attributed to the slow production of glycolic acid.

Net photosynthesis by efficient species increase with increasing temperatures until it reaches a maximum between 35° and 47°C. The inefficient plants are less influenced by temperature and have their maximum CO_2 assimilation around 25°C. Zelitch found that treatment of tobacco leaves with the inhibitor of glycolate oxidation tripled net photosynthesis at 35°C but had little effect at 25°C. At the higher temperature and in the presence of the inhibitor, tobacco behaved like an efficient plant. Thus, the use of selective inhibitors of photorespiration is one approach to increasing plant productivity.

Another approach, under study in several laboratories, is to breed strains of plants with lower than normal rates of photorespiration. For example, Zelitch and his colleagues recently found individual plants of a standard tobacco variety, Havana Seed, with unusually slow photorespiration. When these plants were self-pollinated and their progeny examined for photorespiration and net photosynthesis, Zelitch found that the rates of the two processes were inversely related. In plants with slow photorespiration—about one-third of the total progeny—net photosynthesis was as much as 38 percent higher than normal for this species. Thus, plant selection and breeding may enable the cultivation of more efficient C_3 species.

The identification of the source of the glycolic acid oxidized by photorespiration remains somewhat problematical. However, the rediscovery of the Warburg effect—oxygen inhibition of photosynthesis in C_3 plants but not in C_4 plants—and current investigations into the effects of environmental oxygen and CO_2 on photosynthesis have indicated some possible mechanisms for glycolate synthesis. Olle Björkman, George Bowes, and Joseph Berry at the Carnegie Institution of Washington at Stanford, California, have concluded that the normal atmospheric concentration of oxygen, 21 percent, inhibits CO_2 fixation in C_3 plants in two ways. The major effect is a direct inhibition of the ribulose-1, 5-diphosphate (RuDP) carboxylase reaction of photosynthesis; less significant, according to these investigators, is the stimulation of photorespiratory CO_2 evolution. Because the inhibitory action of high oxygen concentrations on RuDP carboxylase is overcome by CO_2 concentrations much higher than the normal 0.03 percent, they propose that oxygen is a competitive inhibitor of CO_2 fixation by the enzyme.

W. L. Ogren, at the U.S. Regional Soybean Laboratory, Urbana, Illinois, and Bowes have postulated that RuDP carboxylase, in addition to catalyzing CO_2 fixation, can catalyze the oxidation of RuDP to phosphoglycolate and PGA (Fig. 2). Glycolic acid is then formed by the enzymatic removal of the phosphate group from phosphoglycolate. Normal atmospheric concentrations of oxygen and CO_2 favor the oxidation reaction—and thus favor photorespiration—in C_3 plants. Increasing the CO_2 concentration facilitates photosynthetic CO_2 assimilation by stimulating the carboxylation of RuDP. Thus, net CO_2 fixation by C_3 plants is limited by the low concentration of CO_2 and the high concentration of oxygen in air. These observations have prompted investigations into a third possibility for increasing plant productivity—the alteration of the composition of the environment, especially by increasing the CO_2 concentration.

Table 1. Typical rates of net photosynthesis in single leaves of various species at high illuminance in air containing 0.03 percent CO_2 at 25° to 30°C. Net photosynthesis is given as milligrams of CO_2 fixed per square decimeter of leaf surface per hour. [Source: I. Zelitch, Connecticut Agricultural Experiment Station, New Haven]

Species	Net photosynthesis
High-efficiency plants	
Maize	46–63
Sugarcane	42–49
Sorghum	55
Pigweed (*Ameranthus edulis*)	58
Bermuda grass (*Cynodon dactylon*)	35–43
Low-efficiency plants	
Spinach	16
Tobacco	16–21
Wheat	17–31
Rice	12–30
Orchard grass	13–24
Bean	12–17

Photosynthesis by efficient C_4 plants is not inhibited by oxygen, except at concentrations well above normal. Several investigators have postulated that this reduced susceptibility to oxygen is due to the fact that the C_4 cycle in effect increases the CO_2 concentration in the vicinity of the RuDP carboxylase. According to this hypothesis, the anatomy and biochemistry of the plants are intimately related. Although both C_3 and C_4 plants have mesophyll cells that contain chloroplasts, C_4 plants also have bundle-sheath cells that surround the vascular bundles of the leaves and have a somewhat different kind of chloroplast. The details of the proposed mechanisms vary from investigator to investigator, but, in essence, they propose that all or most (85 percent, according to C. C. Black at the University of Georgia, Athens) of the CO_2 is assimilated by the C_4 cycle in the mesophyll cells. Phosphoenolpyruvate carboxylase has a very high affinity for CO_2—higher than that of RuDP carboxylase—and is a more effective trap for CO_2 at low concentrations. The four-carbon acids produced in the mesophyll cells are then transported to the bundle sheath cells, where they are decarboxylated and the CO_2 refixed by RuDP carboxylase. Even in C_4 plants, the primary pathway for sugar formation still involves PGA and the enzymes of the Calvin cycle.

Photorespiratory evolution of CO_2 is very difficult to detect in C_4 plants, but they apparently do possess the capability to perform these reactions. For example, Zelitch found that maize produces limited quantities of glycolic acid; Tolbert used electron microscopy to verify the presence of peroxisomes in high-efficiency plants; and Black demonstrated that chloroplasts, mitochondria, and peroxisomes are densely packed in the bundle-sheath cells of C_4 plants. Many investigators think that the CO_2 released by photorespiration in C_4 plants is also trapped by PEP carboxylase, with the formation of oxaloacetic acid. Thus, the CO_2 never escapes from the plant.

Numerous and substantive points concerning the relationships between the C_4 pathway, photorespiration, and photosynthetic efficiency remain to be clarified. One issue of particular significance is the biological role of photorespiration. In the views of some investigators, this process appears to be both detrimental to the plant and dispensable, in the interest of greater productivity for man's crops. Yet, within the context of evolutionary theory, it is difficult to envision a process that is harmful—that decreases plant efficiency and therefore makes some species less competitive than others—without a counterbalancing benefit.

The advantage, if any, conferred on plants by photorespiration is still obscure. It may serve as a source of the amino acids glycine and serine, as indicated by Tolbert. Alternative (or additional) roles include the possibility that photorespiration may serve as a protective mechanism for the plant cell by draining off excess energy-rich compounds formed in the chloroplast when light intensity is high but when CO_2 is scarce—both conditions that would favor photorespiration.

The interchange of ideas—although spirited on occasion—between plant biochemists, ecologists, morphologists, and physiologists has stimulated new research into the life-giving process of photosynthesis and its relationship to photorespiration. A better understanding of these processes may begin a new era in the "Green Revolution" and pay rich dividends in improved crop yields.

—JEAN L. MARX

References

1. M. D. Hatch, C. B. Osmond, R. O. Slayter, Eds., *Photosynthesis and Photorespiration*, proceedings of a conference, Canberra, Australia, November 1970 (Wiley-Interscience, New York, 1971).
2. I. Zelitch, *Photosynthesis, Photorespiration, and Plant Productivity* (Academic Press, New York, 1971).