CURRENT PROBLEMS IN RESEARCH

Chemical Basis for Adaptation in Plants

Understanding of heat tolerance in plants may permit improved yields in arid and semiarid regions.

Edwin B. Kurtz, Jr.

Everyone talks about the weather, but no one does anything about it. This familiar cry for better control by man of his surroundings is being partly answered by atmospheric physicists, but a more subtle and indirect approach to the problem would be to change or supplement the biochemistry of plants and animals so that they would be better adapted to the existing environment. This is not as fantastic as it seems, for there are a few isolated bits of information in regard to temperature that show that man can adapt a plant to an environment.

The arid southwestern United States is generally characterized by inadequate water and high temperatures. In considering the adaptation and agricultural relation of plants to the high temperatures of this region, we too often think of this factor as affecting only the use and loss of water. Our attention has therefore been centered on the problem of water use by plants, and direct effects of temperature on plant metabolism have been largely overlooked. Many gross effects of temperature on photosynthesis, respiration, and translocation are well known, but the direct question, "How does a high temperature kill or damage a plant?" is seldom asked.

In 1920 the American botanist D. T. MacDougal stated that because the growth of an organism is the result of a great number of activities, temperature may control growth if a single process that is particularly sensitive to temperature changes forms either the retarding or leading process. Now, if an essential metabolic compound that is involved in the process or reaction controlled by temperature is known, then it should be possible to control the growth of the organism by supplying it with the known metabolite, even if the organism is growing under an otherwise deleterious temperature. That is, if the metabolic reaction $A \rightarrow B$ is completely or markedly inhibited at a high temperature, and B is essential for normal growth of the organism, then growth at a high temperature may be restored by supplying metabolite B to the organism. Conversely, if A is an essential metabolite and the rate of reaction $A \rightarrow B$ is greatly accelerated at high temperatures so as to deplete the supply of A, then normal growth of the organism may be restored by supplying A. This hypothesis, suggested and termed by James Bonner the chemical control of climatic diseases of plants, offers an extremely fruitful field of research in plant science and agriculture. Although the present discussion will be limited to the application of this concept to plants, the concept should be of use in the study of the ecology of certain animals, particularly the invertebrates.

Chemical Basis of Climatic Disease

The relationship between temperature and metabolites has been beautifully shown by the work of H. K. Mitchell and his coworkers on temperature-sensitive mutants of the red bread mold, *Neurospora crassa.* The so-called "wild type" of *Neurospora* has the full complement of genetic characters and grows quite well at temperatures of from 35° to 40°C. However, a mutant was found that grows normally up to 25°C, but, above this temperature shows a rapid decrease in growth until, at 28°C, no growth occurs (Fig. 1). Apparently the high temperature limits growth by controlling some essential reaction. It was soon found that the addition of only 2.5×10^{-4} grams of the B-vitamin riboflavin to each liter of culture solution restores growth of the mutant at high temperatures. Because riboflavin is a part of a coenzyme involved in the transfer of hydrogens and the conservation of energy in organisms, it is not surprising that the organism struggles for existence when the production of riboflavin is inhibited in the mutant by high temperatures.

Climatic ills of other temperature-sensitive mutants of *Neurospora* have been cured by the addition of adenine (Fig. 2) and pyrimidines. Adenine is essential for the utilization and transfer of energy in cells, and it also occurs in such critical sites as chromosomes, so that the control of its formation by high temperatures has drastic effects on growth.

Probably the earliest demonstration of the chemical control of a temperature disease in a higher plant was by J. Bonner in 1943. The vegetative growth of *Cosmos* plants is restricted by a low temperature of 20°C to one-half the optimum rate obtained at higher temperatures, but this inhibition by the low temperature can be reduced by 50 percent by the addition of the B-vitamin thiamine to the nutrient medium in which the *Cosmos* are growing. Thiamine, of course, is an essential metabolite of the *Cosmos* plant because it **is** part of a coenzyme in the aerobic respiration cycle.

Turning now to effects of elevated temperatures on higher plants, we may note that A. W. Galston and M. Hand were the first to show that the temperature disease of a pea plant has a chemical basis. The common pea will grow at temperatures of up to 30°C, the optimum being near 20°. However, if the plant is exposed to a temperature of 35°C for a few days, it turns yellow and dies, even though water and mineral nutrients are amply supplied. The thermal inactivation of growth at 35°C can be largely prevented by the addition of adenine to the nutrient medium. Very recently H. R. Highkin investigated heat tolerance in two genetic strains of peas —one that is heat-susceptible and one that is heat-resistant. In the heat-susceptible variety, the tissues contain equal amounts of adenine at both low (14°C)

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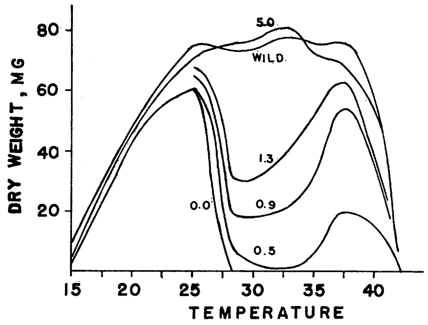

Fig. 1. Growth (in milligrams, dry weight) of the wild type and temperature-sensitive riboflavin mutant of *Neurospora* at different temperatures and riboflavin concentrations (in micrograms per 20 milliliters of culture). [Redrawn from H. K. Mitchell and M. B. Houlahan]

and high (26°C) temperatures, whereas in the resistant variety the amount of adenine doubles at 26°C as compared with that of plants grown at 14°. Thus, heat tolerance in peas is quite similar to that in the temperature-sensitive mutant of the red bread mold that requires adenine to cure its climatic disease. These findings go a long way to explain why the pea plant is a cool-weather crop and also suggest how it may be possible to "adapt" peas or other similar crops to cultivation in warmer environments. Although only one other plant, the common duckweed (*Lemna minor*), has been found to be protected against high-temperature damage by the addition of adenine (in the form of the sugar derivative adenosine) to its diet, the limitation of plant growth at high temperatures by the destruction of adenine may be a rather general phenomenon.

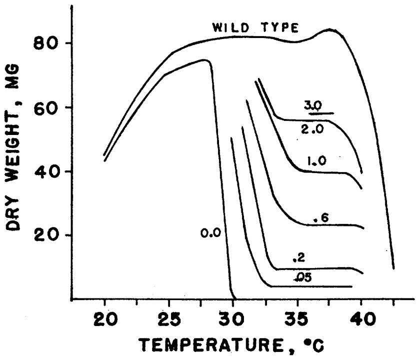

Fig. 2. The thermal inactivation of a temperature-sensitive mutant of *Neurospora* at different temperatures, and its cure by adenine (concentrations in milligrams per 20 milliliters of culture). [Redrawn from W. D. McElroy and H. K. Mitchell]

It is well known that biennial plants must receive a cold treatment at the end of the first year's growth in order that the formation of flower buds and subsequent flowering during the second year may be induced. Apparently some substance which is destroyed at high temperatures and accumulates during the cold period is required to trigger the reproductive cycle. However, no substances tested—until recently—were able to substitute for the cold treatment. Anton Lang has now shown that the new wonder compound, gibberellic acid, will stimulate a biennial plant to flower even though it has not been cold-treated. It is not known definitely whether gibberellic acid is a plant hormone and is iself formed in biennial plants at low temperatures, but in any event this intriguing compound can permit a biennial plant to reproduce in an environment that is warmer than nature intended.

These few examples of the chemical basis of climatic diseases constitute nearly all that are known, but they nevertheless suggest some interesting thoughts about the adaptations of plants in nature and the possibilities for greater control by man of his surroundings. The following comments on the high-temperature tolerances of desert plants may indicate some of these possibilities.

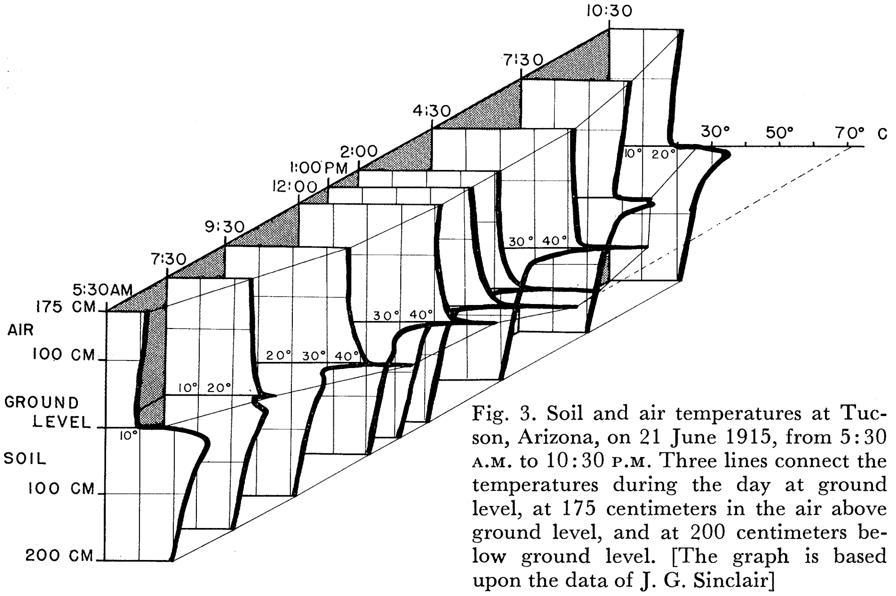

Fig. 3. Soil and air temperatures at Tucson, Arizona, on 21 June 1915, from 5:30 A.M. to 10:30 P.M. Three lines connect the temperatures during the day at ground level, at 175 centimeters in the air above ground level, and at 200 centimeters below ground level. [The graph is based upon the data of J. G. Sinclair]

Desert Plants

It is generally recognized that desert areas of the type found in the southwestern United States experience high temperatures during a large part of the year, but it is not often realized just how high these temperatures may be. On the basis of data that Sinclair obtained in Tucson, Arizona, on 21 June 1915, a three-dimensional graph was constructed to show the soil and air temperatures at various times of the day (Fig. 3). Because the maximum air temperature at 175 centimeters above ground level was only 43°C (109°F), which is not an exceptionally hot day for this area, the values given should not be considered the maxima that plants and animals must tolerate. Even so, of special note are the extremely high temperatures at or near the soil-air interface. On the particular day studied, the soil surface heated up to 71.5°C at 1:00 P.M., and the region between 4 centimeters above and 4 centimeters below ground level remained at a temperature greater that 40°C for about five hours. Such prolonged heat is not a rarity in desert regions of the Southwest but is of almost daily occurrence from May to September or October of each year.

As might be expected, plants that are indigenous to the desert region are remarkably tolerant of high temperatures. D. T. MacDougal and E. B. Working, of the now extinct Carnegie Desert Laboratory, Tucson, observed that stem joints of young *Opuntia* cactus grow at an air temperature of 58°C. Growth ceases when the air temperature reaches 63°C and the internal temperature of the joints is 62°C. However, joints exposed to these high temperatures resume growth immediately upon "cooling" to 50°C. Other workers at the Desert Laboratory found that the roots of the creosote bush, a plant which is known to flower and set fruit during a drought and heat spell lasting several months, have their maximum growth rate at temperatures of from 30° to 35°C, and the rate of growth at this temperature is ten times that at 20° to 25°C. The roots of mesquite, another common desert shrub, have their maximum growth rate at a temperature of 36°C and grow nearly as rapidly at 41.5°C. As shown in Fig. 3, these temperatures do actually occur in the upper regions of the soil, and many desert plants have the majority of their roots in this region.

The seeds of desert plants are even more remarkably tolerant to high temperatures. In our work with the giant cactus or saguaro, we were not too surprised to find that the dry seed was still viable after being cooked continuously for seven days at 83°C. Such heat resistance is essential for survival of the cactus, because the seed must be able to tolerate extremely high temperatures for days or weeks as it lies on the soil surface waiting for a rain to set the germination process into action. And this is not an isolated example, for Faith Poole found that the seeds of three desert shrubs—ironwood, mesquite, and blue paloverde—also remain viable after exposure for six hours to temperatures up to 82°C on four consecutive days. Obviously, not just the seeds of these plants are able to survive the high temperatures encountered at the soil-air interface; the tender seedlings and young plants also must be extremely heat-tolerant.

Implications

Unfortunately, no mechanisms are yet known that explain the ability of desert plants to prevent heat damage at the high temperatures in which they must live. Nevertheless, the few examples given here in support of the chemical basis for heat tolerance suggest a new approach to the study and understanding of desert plants. From an agricultural viewpoint, research along these lines may permit increased yields of crops or even the cultivation of economically desirable plants in areas that normally would not support their growth. The arid and semiarid areas of the earth account for more than one-third of the total land surface, and many of these regions not only are arid but also have high temperatures. As a consequence, the agriculture of these areas is restricted to a relatively few plants, often with poor yields. There is, then, the possibility that a knowledge of how desert plants tolerate high temperatures, and the use of this information for the chemical cure of climatic ills of economic plants, will help to solve the critical food problem of the world by permitting agriculture to extend into new lands and by increasing yields of presently cultivated areas. There is much to be understood about the plants and environment around us, but the concept that temperature damage of plants has a chemical basis, as actually demonstrated experimentally in a few cases, offers a new and fascinating avenue of exploration.

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University of Michigan Radiocarbon Dates III

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The list of 94 dates shown in Table 1 is a continuation of our previous lists (*1*). The introductory statements concerning the method of measurement and the meaning of the stated limits of error given in list II (*2*) apply to this list also.

Since this is our final list to be published in *Science* (*3*), and since we have not previously included more than a brief mention of the technical method, it seems appropriate at this time to give a somewhat more complete statement about the technique we use.

We use a CO_2-filled counter, which is operated in the Geiger, rather than the proportional, voltage range. The envelope is a copper tube of 3-inch inside diameter and 22 inches total inside length. The anode wire is of 0.005-inch platinum, and is 14 inches in active length. There is a cylindrical grid 2¼ inches in diameter, composed of 0.01-inch copper wires spaced ¼ inch apart, situated concentrically with the anode and cathode, and extending well beyond the active region at either end. The grid normally has a potential of about 150 volts positive with respect to the cathode, and it is pulsed to about 1000 volts positive with respect to the cathode to quench each discharge. The active counting region extends radially all the way to the cathode surface, inasmuch as the grid is at a positive potential. The counter is filled to a pressure of 74 centimeters of mercury by admission of 3 centimeters of CS_2 vapor, 3 centimeters of hydrogen, and 68 centimeters of CO_2. The counting threshold is at 5000 volts, and the plateau extends to about 5400 volts. The anticoincidence ring consists of eight 2- by 20-inch copper, neon-filled Geiger tubes, in a single layer around the CO_2 counter. The tubes are connected in parallel and are operated with a univibrator type quench circuit. We have found that the use of the external quench is a worthwhile economy. Tubes give perfect performance in externally quenched operation far beyond the time that would mark the end of their useful life as self-quenched counters.

We find that the CO_2-CS_2 Geiger counter has an advantage and a disadvantage, in comparison to the pure CO_2-

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