The Response of Plants to Climate

F. W. Went

Kerckhoff Laboratories of Biology, California Institute of Technology, Pasadena

SOME of the most important problems in biological research are the variability of the experimental material and the control of growing conditions. These two problems are really closely related, because greater reproducibility of the environment usually results in greater uniformity.

We are so used to differences in size and form among plants which presumably should be similar because of genetic similarity, that we take these differences for granted. That probably explains why, in general, more efforts are made to cope with the variability than to reduce it. Mathematicians have devised methods to measure variability by means of statistics, and they have made rules about experimental design that randomize errors, which thus get more evenly distributed over the experiment.

A closer consideration shows that this statistical approach is illogical. Actually, the basic purity of biological material is greater than that of pure chemicals. A chemical that has less than 0.1 per cent impurity in it would, by most of us, be considered much purer and more uniform than a planting of tomatoes or peas. In reality that is not the case. The 0.1 per cent impurity in sucrose may, for instance, be NaCl, which would compare with one corn seed per 1,000 tomato seeds. It is obvious that this type of impurity does not normally lead to errors and can easily be avoided. The impurity in the tomato seed will, for the most part, be connected with deviations in the genetic make-up of some individual plant. It may be that, in genetically uniform material, one seed in 1,000 carries a different gene for leaf shape or fruit color. Yet in all other characters such an abnormal seed would be the same as the others. If we assume that there are 1,000 genes in which one tomato may differ from another, this just means that the purity is 999,999 : 1,000,000. This is a purity not existing in chemicals. An impurity of this type may be compared with one per thousand sucrose molecules containing a deuterium atom instead of a hydrogen atom in a particular location, or with one molecule of maltose instead of sucrose.

All this simply means that the variability of genetically well-selected biological material does not lie in the basic purity of the material, which is superior to almost anything we are acquainted with in physics or chemistry. There are, then, two possible explanations of biological variability. One is that the environmental conditions are so variable that the basic uniformity of the seeds cannot express itself. The other is that it is impossible to transform the potential uniformity of the seed or fertilized egg cell into uniformity in the mature organism. The latter possibility is based on the assumption that the master reactions for development depend on so few molecules that the uncertainty principle holds. Actually this means that, when a certain gene, consisting of two or very few molecules, influences growth directly, the effect will be strongly modified by chance because of the small number of reacting molecules. Thus individual variability would be a corollary of gene-controlled development, and beyond experimental control.

On the other hand, growing conditions for plants have been far from uniform and controlled, so that at least part of the bothersome individual variability of plants within a single strain could be attributed to differences from pot to pot in the degree of packing of the soil, water content, or in position of the pot in relation to light, heat source, air currents, etc. The growing of plants in sand or gravel, regularly watered with a nutrient solution containing all necessary minerals, reduces the variability of the root environment, and plants grown in this manner are considerably more uniform in size and shape.

Whereas the root environment of the plant can be controlled to a considerable extent, control is much more difficult for the parts aboveground. To maintain a constant temperature in stems and leaves, the air temperature has to be controlled, which is simple when the air is damp and light is absent. As soon as heat or light radiation hits the leaf, its temperature tends to increase. Since strong radiation is essential for plant growth, heat must be removed from the leaf during the daily light period, either by radiation or by diffusion of heat toward the surrounding air. Only the latter method is practicable, but it is fraught with many difficulties. Since the specific heat of air is low, large quantities of air have to be moved past the plant

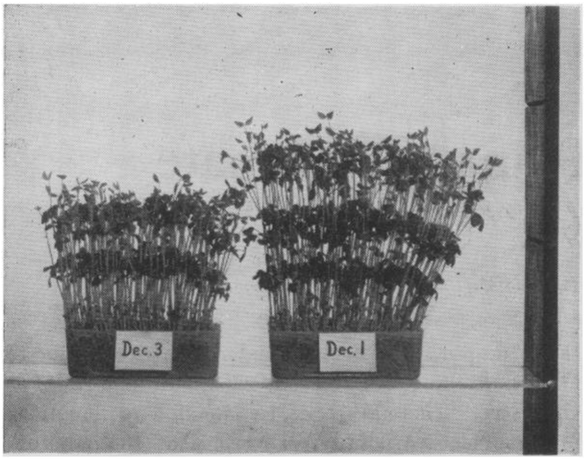

Fig. 1. Peas develop at a uniform rate when grown in air-conditioned and artificially lighted rooms.

parts to be cooled when they are exposed to sunlight.

By the application of these basic principles the plant environment can be controlled. Control has been accomplished in several commercial greenhouses and in a few research greenhouses. It actually has been found that, under such controlled conditions, individual variability among plants is enormously reduced, because the essential purity of the genetically homogeneous seed material is translated into uniformity of the plants grown from the seeds.

Fig. 1 demonstrates the uniformity of peas grown in air-conditioned and artificially lighted rooms. All plants of the same age have grown to the same size; all stems up to the first leaves have approximately the same length; the length of the stem between first and second leaves is the same, etc. Thus the leaves seem placed in tiers. No plants were removed from the containers to take this picture, which proves that the phenotypic variability usually encountered in growing plants, even when they are genetically uniform, has no deep theoretical meaning but is due to uncontrolled growing conditions. Therefore, the significance of the uncertainty principle in biology is not as great as sometimes supposed.

The most complete air-conditioned laboratory that uses these principles is the Earhart Plant Research Laboratory at the California Institute of Technology (Fig. 2), which has been in operation since July 1, 1949. Built and equipped with a gift of $407,000 from the Earhart Foundation, of Ann Arbor, Michigan, it was the outgrowth of two small experimental greenhouses, built in 1939 at the California Institute of Technology through the initiative of Dr. H. O. Eversole. It comprises these first two greenhouses and, in addition, four larger air-conditioned greenhouses, in which temperature and humidity can be controlled within relatively narrow limits. For complete control of light, as well as temperature, there are thirteen rooms with artificial light panels producing as high as 2,000 ft-c light intensity. The panels can

Fig. 2. Earhart Plant Research Laboratory.

be switched on and off with time clocks and can be separated by curtains, so as to produce any photoperiods required. Each of the thirteen rooms has its own air-conditioning system, which keeps the temperature of each room within one-half degree of the set temperature. To insure good distribution of air throughout the greenhouses and laboratories without causing excessive drafts, a new method of air introduction was used. The air, after leaving the air conditioner, is blown into a space under the greenhouse floor, which consists of 4-inch wide steel channel beams, placed side by side with three-eighth-inch spaces between them. The air is forced up between the steel beams, mixing immediately with the greenhouse air as it moves upward past all objects in the greenhouse, absorbing the heat produced by light rays that strike all solid surfaces. The air, which is thus heated about 4° C in the middle of the day, is drawn out of the greenhouse through ducts in the side walls, and is either ejected or reconditioned. Plants are grown on movable tables, which can be wheeled from greenhouse to laboratory or darkroom. In this way all combinations among the different conditions can be made. For instance, groups of plants are kept from 8:00 A.M. till 4:00 P.M. in four different temperatures in full daylight and at nine different temperatures in artificial light. During the remainder of the twenty-four hours they are kept at any of nine different night temperatures; or they receive extra light during part or all of the night. Thus, a considerable number of independent variables can be studied simultaneously, and the interaction of their effects can be established.

Simultaneous study of a number of variables is more important than appears superficially. In the first place, there is a theoretical reason. The response of a plant to a particular environmental factor, like temperature, is very complex. Practically all its processes are influenced, and to different degrees. For example, the effect of light will differ according to how the leaf surface or chlorophyll content is affected by temperature. At present the degree of interaction of these factors cannot be predicted, and this is one of the problems that will have to be solved in this new laboratory.

In the second place, the study of the interaction of different climatic factors is important from the standpoint of practical application. In the field a plant is never subjected to a single variable. Usually, high light intensities are correlated with high temperatures and low humidities. Therefore, the practical grower must know not merely how temperature affects his crop, but how it does so at different light intensities, at different ages of the plants, and at different photoperiods. The reason plant physiology is not as basic a discipline for the practical plant sciences as one would expect on purely logical grounds probably lies in the methods heretofore used. The experimental setup did not permit the study of the interactions of various factors, because usually only one factor at a time could be varied. Where more factors could be controlled simultaneously, more progress was made. A good example of this is in the field of mineral nutrition, where different mineral elements could be varied independently, giving agriculture a satisfactory insight into the interactions between nitrate and phosphate nutrition, for example.

Fortunately, not all possible climatic variables are equally important in the development of a plant. Therefore, in a study of a plant's climatic responses, the interaction of only a limited number of variables needs to be taken into account. Let us consider the tomato plant as an example. This plant is particularly sensitive to differences in night temperature, whereas the day temperature may vary within wider ranges without affecting its response. But the night temperature response is dependent upon (1) the age or, rather, the size of the plant, (2) the previous night temperatures, (3) the light intensity on the previous two days, and (4) the variety. Such complex temperature responses are not restricted to the tomato in particular or to plants in general. In human beings we find something similar. There is not just one temperature at which a person feels most comfortable. The optimal room temperature is lower as the relative humidity rises, or as the rate of air movement decreases. It also is lower as the outdoor temperature is lower, and it depends on the degree of activity of the person and on radiation.

With respect to the tomato plant, it was found that the night temperature controls the rate of stem growth. In the young seedlings most rapid growth occurs at 26°–30° C. As the plant grows older the optimal night temperature gradually drops to lower temperatures, passing through 23° and 20°, and finally reaching optimal temperatures of 13°–18° C, depending upon the variety. Varieties developed in the Central Valley of California exhibit the highest optimal temperature; the lowest optima are found in English and greenhouse varieties. For fruit set the same rules hold. That is, the night temperature completely regulates fruit set, the first fruits being formed at higher temperatures, with the optimum gradually shifting toward lower temperatures as the plant grows older and taller, but generally being near 17° C, regardless of light intensity (Fig. 3). However, when the latter has dropped below 1,000 ft-c, no fruit set is possible at any temperature. With low day temperatures the optimal night temperature for fruit growth is higher but remains essentially unchanged

FIG. 3. Tomato plants in air-conditioned greenhouse. Plants at left show good fruit set, because they are exposed to optimal night temperature (17° C); those at right were kept at 30° C during night (no fruiting). Notice slots in floor through which air enters greenhouse, and registers in rear wall through which air returns to air conditioner.

for vegetative growth. With light intensities below 1,000 ft-c, the optimal night temperature for stem elongation gradually decreases with light intensity.

We do not have enough data as yet to express these relationships in mathematical form, but, to give an idea how the formula for the optimal night temperature for stem elongation of a tomato plant might look, the following notation is given:

$$\text{Optimal night temperature} = a + b\ (c - \log l).$$

Here l means the length of the stem in cm, a, b, and c being constants. For several varieties these constants would be about:

	Tomatoes		Chili Pepper
	San José Canner	Essex Wonder	Californian
a	20	16	8
b	10	10	20
c	2	2	1.9

There are other terms to be introduced for light intensity (below 1,000 ft-c) and perhaps for day temperature.

The temperature relationships of the tomato plant can also be expressed by plotting its optimal growing conditions at maturity, when the second term in the formula above for optimal night temperature has become constant at lengths of more than 1 m. We can then indicate the climatic response of the tomato in terms of the three most important climatic variables that cannot easily be changed by cultural treatments, namely, day temperature, night temperature, and length of day. In Fig. 4 this is attempted. In plane *ABCD,* the optimal fruiting conditions of the San José Canner Tomato are shown as a function of night temperature (*A-B* axis) and day temperature (*B-C* axis). This shows a narrow range of night temperatures, slightly modified by the much larger range of day temperatures, within which most fruit is set. In plane *ABEF* the photoperiod (*B-E* axis) is considered in relation to night temperature, and it appears that fruit set is good over a wide range of photoperiods but, again, is restricted by night temperature. Similarly, in plane *BCGE* the interrelationship of day temperature and photoperiod is shown, which is not critical at all. The optimal fruit setting conditions can now be presented in a three-dimensional grid *ABCDEFG.* The solid figure thus produced has been projected on planes *ABCD, ABEF,* and *BCGE.*

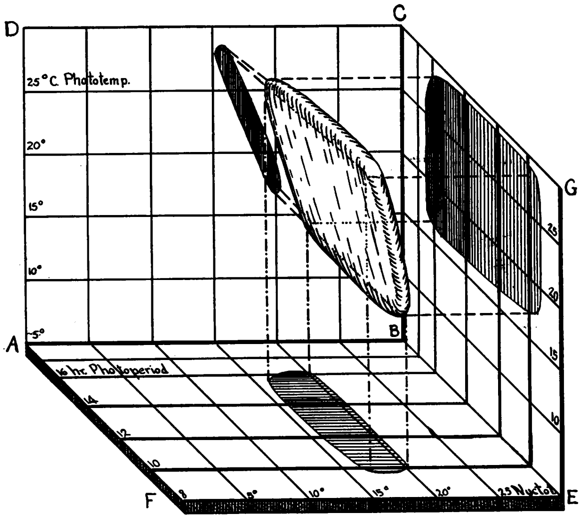

FIG. 4. Three-dimensional diagram showing optimal fruit-setting conditions of San José Canner Tomato plant, in terms of interactions of day temperature, photoperiod, and night temperature. Shaded areas on planes represent favorable combinations of any two of these factors. By projecting lines from these areas, three-dimensional figure in center is obtained, which represents favorable combinations of all three factors.

Within the same grid the climate of any particular region can be plotted by connecting the monthly averages, giving an oval-shaped figure. When a sufficiently long part of the climatic oval falls within the solid representing optimal fruit-setting conditions for the San José Canner Tomato, it means that during those months it can be grown successfully in that particular climate. We can now fit any tomato variety to the climates that follow most closely its optimal growth requirements, or we can take a given climate and see which tomato varieties are most nearly optimal in it.

This shows that the effect of temperature is rather complex and cannot be expressed simply as a heat-sum. The heat-sum concept was introduced about 200 years ago and was worked out in some detail 100 years ago by Boussingault and DeCandolle. It holds that the development of a plant is dependent upon the total amount of heat to which it was subjected during its lifetime, expressed as degree-days. For wheat it was calculated that it ripened after having been exposed to 2,200 degree-days. This accounted for the fact that in colder climates it took wheat longer to mature than in warmer climates. A refinement of this method was introduced by Nuttonson, who incorporated the effect of day length in the heat-sum to account for the behavior of garden peas. Yet all heat-sum calculations are based on the false assumption that there is a direct proportionality between growth and temperature. Actually, above a certain optimal temperature the rate of development decreases with rising temperatures. Besides, it does not take into account that mainly night (or day) temperature controls development in certain plants. No heat-sum can account for the date of first ripening of tomato fruits, but forty days after flowering plants have been exposed for the first time to a series of five or more successive nights when the temperature did not drop below 15° C, the first ripe fruit will be harvested.

Other experiments lead to the same conclusion, that the development of a tomato plant does not depend on the total amount of heat to which it is subjected but on the proper diurnal distribution of heat. A set of tomato plants was subjected to eighteen different temperature treatments. All of them received exactly the same amount of artificial light. When the growth rates or the final weights of these plants were plotted as a function of either day or night temperatures, combining only the plants which received equal heat-sums (e.g., eight hours at 30° in light and sixteen hours at 4° in dark, or eight hours at 4° in light and sixteen hours of darkness at 17°, or eight hours at 17° in light and sixteen hours at 10° in darkness), a very pronounced optimum was found at 17° in light and 10° in darkness (and 20° in light and 17° in darkness), with growth dropping to one-third or less at the extreme lows in day or night temperatures. Therefore, not a heat-sum, but a proper day-night temperature balance determines their growth.

Instead of adding other details about the climatic response of the tomato plant, a few details about other plants will be given. Whereas the tomato needs a fairly warm night (15°–18° C) for reproduction through fruit set, other plants require much lower temperatures. The English daisy, for instance, only grows and flowers when the days are cool and the nights are 8°–13° C, with much the best flowering at the lower night temperature. The Iceland poppy has similar temperature requirements but, in addition, it needs long light treatments for flowering. At the other extreme we find the African violet, which flowers and grows best at temperatures higher than tomatoes. Under the conditions ideal for the African violet, the English daisy dies, and the tomato does not set fruit. On the other hand, the African violet dies when brought under the optimal conditions for the English daisy, which are also too cool for fruit set in the tomato.

Therefore, when the climatic responses of a number of plants are worked out in detail, we find marked differences that have a significant bearing on the distribution of these plants over the earth. It is necessary to revise our ideas about the temperature limits within which a plant can exist. It has been thought that freezing is the lower limit that most plants could stand, and this could be explained rather simply by the damage done inside the tissues by the formation of ice crystals. But an African violet dies if it is subjected for long periods to night temperatures of 10° C, far above any possible frost injury. Similarly, the English daisy dies when it is kept for a long enough period at temperatures of 20° or over. Such relatively low temperatures are far removed from any where actual heat damage to protoplasm can occur.

It must be concluded that the distribution of plants is not just a question of frost damage or heat coagulation, but is correlated with very specific temperature requirements, which are met only in certain climates. Whereas it was formerly supposed that plants from temperate climates could grow in the tropics but were crowded out by tropical plants better adapted to the climate, we now can say that many such cool-weather plants would die within a relatively short time in the tropics even without competition. Part of the reason for these misconceptions concerning temperature requirements of plants was the limitations of experimental facilities, which allowed only study of the seedling stages. Germination and seedling growth are usually best at temperatures substantially higher than optimal for later growth. Since we had exact information only about these early stages of plant development, we were misguided by extrapolation.

The adaptation of the plant to its physical environment goes much farther than merely a general relationship between type of climate and optimal growing conditions. In nature we almost invariably find a higher temperature during the day than at night, a fact that is understandable on the basis of heat radiation from the sun during the day and radiation toward space at night. The range between day and night temperatures is greater as the climate is drier. Plants follow the daily shift in temperature with a similar shift in optimal growing temperatures. This can most easily be demonstrated in tropical plants where, throughout the year, day and night temperatures fluctuate over the same range. The orchid *Phalaenopsis amabilis* has an optimal night temperature of 21° C and an optimal day temperature in full sunlight of about 28° C. In its native habitat in the lowland Malaysian jungles, the mean night temperature is 20°–22° C, and the day temperature rises to as high as 30° in the full sun, but on the average is 27°–28°. Similarly close correlations between existing and required temperature ranges may be identified in other plants, but most of these still need much experimental work before they are well established.

Since plants in their natural surroundings are so closely adapted in temperature response to the existing temperatures, it follows that, once the temperature requirements of a particular plant are known, it is possible to find the best climate for this plant. But something else can be attempted. By a breeding program a recombination of characters of a given plant species can be accomplished. Once we know on which individual genetic units the climatic response to day temperature, night temperature, and photoperiod depends, we can create the plant variety that most closely harmonizes with the climate in which we want to grow that plant. Such a deliberate synthesis would then replace the standard method of selection for yield or general performance. The latter values depend on a large number of individual physiological processes, among which the responses to temperature and photoperiod are among the most important for the performance of the plant in the field.

An analysis of the genetical basis of climatic response may provide some interesting insight into the problem of evolution and migration of species, because it will indicate how many genes have to participate to allow invasion into new climatic territory, and it will show the limits of migration on the basis of available genetic material in the species. For there is no doubt that the genes controlling climatic response are most important in the survival of a species.

There are many other climatic factors that can be studied in the Earhart Plant Research Laboratory, which has one room equipped to maintain very low humidities (down to 10 per cent relative humidity), and another containing a wind tunnel, in which plants can be subjected to strong, even winds at constant temperature, humidity, and light. Another room has equipment to produce fog or rain at constant temperature and light. Two airtight rooms can be used for the study of effects of gases on plants and are now in use to establish which of the air contaminants cause such typical damage symptoms on plant leaves as are found in many large cities and were recently headlined for the Los Angeles area and connected there with smog.

One of the unique features of the laboratory is that a state of relative sterility is maintained. There have been no insects in the building, with the exception of a small outbreak of aphids, which had its source in some insufficiently fumigated plant material. Within half an hour of their discovery, the few aphid colonies were completely eradicated. Neither are there any virus or soil-borne diseases. Thus reactions to climatic conditions are not obscured by various degrees of insect infestation or spray damage. This relative sterility is maintained by strict adherence to quarantine measures. All materials entering the building are either sterilized with steam, fumigated with methylbromide, or sprayed with DDT. All persons entering change into special laboratory clothing and wash their hands so that they do not carry insects or virus into the building. The very large volume of air entering the building through the air-conditioning system is filtered, mechanically and electrically, to remove all solid particles, such as insects. The building is insectproof and is kept continuously under positive pressure, preventing the passive sucking in of contaminants. Visitors are restricted to professional biologists. Such restrictions are essential and have thus far proved completely successful. As a result, thousands of plants are growing without diseases or pests, with almost complete uniformity, provided they are subjected to the same environmental conditions. The number of fungus spores and bacteria carried by the air into the greenhouses is surprisingly low.

Now that the Earhart Plant Research Laboratory has passed the rigorous tests of actual operation, the greatest problem has become how to make it as effective as possible in furthering our knowledge of plants and plant behavior. At present the solution of this problem is sought along three lines: first, by appointing research workers and graduate students to study specific problems for which the laboratory offers special facilities; second, by making the facilities available to research workers from other institutions, who contribute to its maintenance cost; and, third, by attracting volunteer workers.