

The experimental approach to ecological problems

1. INTRODUCTION

The beginning of all science of course lies in the description and classification of facts and phenomena. Much observation and description remain to be done in ecology, but we also want to understand more about the interrelationships between plants and their surroundings. There are several ways in which we can approach such relationships. To arrive at a predictive ecology, the ecologist has traditionally used the correlational method. Unfortunately, both the plant and its environment are of almost infinite complexity and consequently their interrelationships are equally complex and difficult to unravel. This is where the physiologist steps in. His experimental method enables him to establish causal relationships, despite the complexity of a situation in which a multi-dimensional unit, the plant, interacts with an ever-changing complex of environmental factors.

In the first half of this century there was very little contact between ecologists and plantphysiologists. Their domains were very different: the field and the laboratory, the whole vegetation in contrast with the individual plant or even an individual process, the cosmic problems of forest or tundra as against the esoteric problems of tropisms and metabolism, on the one hand the macro-world and on the other the molecular world. The ecologist was equipped with boots, raincoat, and vasculum; the physiologist was strictly an indoor man wedded to his bunsen burner, coleoptile, and microscope. But some ecologists took a pH meter into the field and the physiologist brought sun and shade leaves into the laboratory, and today fully-equipped field laboratories move where formerly ecologists only set a hesitant foot. Now a new breed of scientists has emerged, the ecophysiologicalist, equally at home in the field and in the laboratory. But his laboratory is no longer in a multistoried building but in a chamber on wheels, and the plant is no longer transported to the laboratory, the laboratory is brought to the plant. This makes it possible not only to study well-rooted plants or even trees with respect, for example, to their water and gas exchange, but also to bring the microscope to the plant. All this has opened completely new horizons for me personally, for instance the world of the root and the surrounding soil.

Since I have only become aware of this soil-root environment so recently, I do not want to go into this subject in any depth, because I feel myself still too much a "babe in the roots". Yet, I have become aware of completely new relationships in a world largely dominated by fungi, not just as decomposers or parasites but also as builders and symbionts. Under the harsh conditions of the desert and the dunes, where the fragile root hairs usually do not survive, hyphae and rhizomorphs seem to have taken over the function of root hairs, and supply the desert plants with water and nutrients, in the same way as the foresters have found in the case of trees. I found a completely unexpected function of the soil fungi in the desert, where they play a dominant role in soil binding and dune fixation. It is not the rather poor or deep root systems of the desert plants which hold the sand together; this is done by the mycelial mats in the surface layers of the desert soil in which each particle is woven into a mycelial network strong enough to resist wind erosion (WENT & STARK 1968).

There is another aspect of ecophysiology which is very important. It is the *trait d'union* between the field problem and its understanding in terms of causal relationships. It is in the field, in nature, that I find the problem I want to understand. For this understanding I need analysis in the laboratory. But then I have to go back to nature, to see whether I have come up with the real explanation, and whether I have gained real understanding. Without the intermediate laboratory phase of the analysis I would feel insecure, floundering in a sea of uncertainties and a multitude of possibilities.

The place where ecologists and physiologists meet at present is in the phytotron, a series of controlled-environment rooms where plants in a reproducible condition can be exposed to controlled environments. In a phytotron not only air temperature but also radiation, humidity, wind, and several other factors governing or influencing organismal behavior can be maintained at the desired levels. The greater the number and the wider the range of the environmental factors, the more useful a phytotron is.

I do not, of course, want to discuss the phytotron here, but I do want to say a few things about its significance for the understanding of the role of environment in the life of a plant. The phytotron does not attempt to reproduce the natural environment in all its details: for those conditions we use the natural environment itself. But if we want to know the effect of a particular temperature or temperature sequence or humidity or light condition, we are able to maintain this condition for any desired length of time in a phytotron.

2. GROWTH CONTROLLED BY PHOTOPERIOD

Before air conditioning for plants was available, only one factor in the environment of plants was controllable, and this was the photoperiod. Therefore, a fairly large body of information on long- and short-day responses of plants

is available. But as yet little is known about interrelationships between temperature and photoperiod, except for the effects of chilling on subsequent photoperiodic responses. For many plants it is known that the preliminary treatment with temperatures below 10°C will make them responsive to long days.

Much more subtle temperature relationships with flowering and vegetative response are found in biennial and perennial plants. For instance, the older commercial varieties of strawberries were strictly short-day plants at high summer temperatures. Yet in for example northern Sweden, where they are never exposed to short days during their growing season, they flower abundantly, because at low temperatures they initiate flowers even under long days. A similar temperature-photoperiod interrelationship is found in the tuber formation of potatoes. In greenhouse experiments (all carried out at high temperatures) potatoes were found to be strictly short-day plants. Yet in most of the main potato-growing areas (The Netherlands, Ireland) potatoes are harvested toward the end of the summer, after experiencing only long days during their growing period. Thus, as short-day plants one would not have expected them to produce tubers until late in the autumn. This enigma was solved in a phytotron, where it was established that at low night temperatures tuber formation occurs optimally during long days (WENT 1957).

I will not give other examples of temperature control of photoperiodic responses. We know much less about relationship between the photoperiodic response and light intensity. What is the critical light intensity at which the plant switches from its light-metabolism to its dark-response? This could be expected to occur sooner in cloudy than on sunny days, and to be different for plants growing in full sunlight than for those growing in deep shade. I demonstrated this in the case of the coffee tree.

Coffee (*Coffea arabica*) is a strictly short-day plant in its flower initiation. After 75 days under an 8-hour photoperiod, coffee plants had all developed flowerbuds on the nodes of their plagiotropic lateral branches. Three other groups of coffee plants were also exposed to 8 hours of full daylight, but received daily in addition 4 hours of dawn and 4 hours of dusk illumination at 10, 100 or 1,000 lux. The plants with 1,000 lux dawn-and-dusk did not initiate any flower buds and behaved as if they were kept under long days. At 10 lux they differentiated flowerbuds as if they had been under short days, and at 100 lux they just barely started flower initiation. This means that coffee plants grown under shade trees receive effectively a shorter daylight treatment than when grown in full sun. This makes it possible to grow coffee near the equator where it is never exposed to short days except under shade trees. But in Sao Paulo, Guatemala, or Hawaii, where near the tropics of Cancer and Capricorn they are exposed to natural short days in winter, coffee plants produce well without shade trees (WENT 1957).

This shade effect also explains another flowering anomaly. *Cestrum nocturnum* is a flowering shrub belonging to the long-day/short-day type, that is to say,

it only initiates flowers under short days if it has previously been exposed to long days. Therefore, it flowers abundantly in the autumn, but occasionally a few flowers are produced in the spring, presumably when a period of bright days in April is followed by a cloudy period producing effective short days after the long days in April.

It is not just growth or flowering which can be studied in a phytotron. As an example of the other possibilities, let me discuss taste. In the past, most investigations were limited to the effects of soil composition and fertilizer treatment on taste development, and the results were disappointing. But when strawberries were grown under different temperature conditions in the Pasadena phytotron, the typical strawberry aroma developed only in the coolest growth chambers, and no trace of strawberry smell was observed in any of the warmer greenhouses. It turned out that the aromatic taste of strawberries was completely linked with aromatic smell and did not develop at all in berries grown at temperatures of 17°C or higher. When strawberries were scored for taste, solely on the basis of the aroma and disregarding the sugar or acid content, only fruits that had ripened for some time at 10°C in the presence of light were rated tasty. Full flavor developed in any berries exposed to 10,000 lux at 10°C for one or more hours, no matter how high the photo- or nyctotemperatures had been during the remainder of the 24-hour day. At 5,000 lux an exposure of at least 2 hours was required at the low temperature, but the berries never developed full flavor. This explains why the first strawberries ripening in spring are the best-tasting, that is, when the temperatures during the first 1-2 daylight hours are only 10°C , whereas during the summer, with much warmer morning hours, strawberries have an insipid taste except in northern Sweden or Alaska. If the same rule of cool mornings for taste development holds for other fruits, superiority of northern-grown apples would be expected(WENT 1957).

3. GROWTH CONTROLLED BY TEMPERATURE

To come to a real understanding of the behavior of plants, both the ecologist and the physiologist have to make concessions. If, for instance, we want to determine the role of temperature in the fruit production of the tomato, the physiologist has to simplify the laboratory analysis of the temperature response, by breaking it up into discrete ranges, as A.H. Blaauw did in his analysis of the response of bulb crops to temperature. In tomato analysis the first simplification came from the realization that during the day and the night, different processes with different temperature requirements were in control. Thus, the optimal phototemperature had to be determined independent of the night temperature. Since it also was found that the response to the nyctotemperature was about the same for a constant temperature as for two different temperatures averaging the constant temperatures, provided their

difference did not exceed about 5°C , experimentation became rather simple. It was possible to grow a tomato plant that produced like a field-grown plant by subjecting it to a day temperature similar to the average outside day temperature and during night to a temperature equal to the average temperature in the field during night. How could the ecologist cope with the problem of averaging the continuously changing temperature occurring in the field? This proved to be relatively simple. Instead of integrating thermograph records, which is laborious, we can calculate the effective day temperature by subtracting one-fourth of the difference between the maximum and minimum temperatures from the maximum temperature. In a similar way the effective night temperature can be calculated by adding one-fourth of the difference between the maximum and minimum temperatures to the minimum temperature. Since most meteorological stations record both minimum and maximum temperatures, the effective day and night temperatures can be calculated for almost any location near a meteorological station.

To return to the tomato, it was found that, in the laboratory the highest tomato production occurred at a nyctotemperature of 17°C , and that field production was highest when the effective night temperature was 17°C . Some tomato varieties would set in both the laboratory and in the field at a higher temperature, and in a breeding program in the laboratory it proved possible to introduce this higher optimal temperature response into a commercial variety which now is used in tomato production in warmer climates.

4. GROWTH CONTROLLED BY CIRCADIAN RHYTHM

For the solution of these and many other ecophysiological problems a phytotron is essential, especially when the interaction of factors becomes more complex. I would like to discuss one problem in particular, the existence of which was not even suspected before the advent of the phytotron. This problem concerns the role played by circadian rhythms in the temperature response of plants. Only when plants can be grown entirely in artificial light can we escape the normally unbreakable straight-jacket of the 24-hour day-night cycle imposed upon us by the rotation of the earth. Quite unexpectedly, it was found that without a circadian rhythm of light-darkness tomato plants in continuous light soon showed declining growth, became chlorotic, and ultimately died. These abnormalities could be prevented by interrupting the continuous light with periods of darkness, but only if the interruptions came at intervals of 24 hours. Plants could not be "trained" to a regime of say 6 hours light and 6 hours of darkness or 18 hours light and 18 hours dark. At first it was suspected that these dark interruptions were needed to improve whatever light reaction was critical, but this was disproven by another observation. Tomato plants grew normally in continuous light when they were subjected to a temperature cycle of 24 hours, being kept at an optimal temperature of 26°C

which was interrupted daily by periods of 4-8 hours at 10°C. A 6-hour dark interruption turned out to be just as effective as a 6-hour low temperature interruption. It was concluded that a tomato plant needs a rhythmicity of either temperature or light on a 24-hour basis to develop normally. This means that the tomato has an internal circadian rhythm which is so deeply ingrained that the plant cannot develop normally unless this internal rhythm is synchronized with an external 24-hour rhythm. Seemingly to complicate the picture, it was then found that this internal circadian rhythm had a temperature coefficient of 1.2, so that at higher temperatures the cycle of internal rhythm was less than 24 hours and at lower temperatures more than 24 hours. This suddenly explained a number of very puzzling observations (WENT 1962).

It had been known for a long time that many tropical plants could not be grown in cool climates, but gradually died even though they were never exposed to freezing temperatures. They just could not tolerate prolonged exposure to temperatures of 5° or 10°C. Similarly, it was known that many plants of cool climates would die in the tropics even though they could stand occasional temperatures of 30°C. A biochemical explanation of this behavior could not be given, because no enzyme systems that failed or became toxic at these otherwise physiological temperatures were found in these plants.

However, phytotron experiments showed that there was nothing wrong with an African Violet (*Saintpaulia ionantha*) which died when kept for many months at 10°C, except the circadian rhythm. These plants develop normally at 10°C if they receive 16 hours of light followed by 16 hours of darkness. Conversely, a cool-climate plant like *Baeria chrysostoma* dies on a 24-hour light-dark rhythm at 26°C but survives at that temperature on an 18-hour rhythm. This means that the general response of plants to temperature is much more complex than was originally supposed. In the case of a tomato plant, for instance, half of its growth response to temperature can be accounted for by the temperature coefficient of physiological and biochemical processes, and half by the effect of temperature on its circadian rhythm. Therefore, it is not a low or high temperature which these plants cannot tolerate, but the wrong circadian rhythm (WENT 1962). During the long geological eras in which these plants grew in tropical or temperate climates, this circadian rhythm was so strongly imprinted on them at the prevailing temperatures that they cannot easily adapt to a different rhythm.

5. GROWTH CONTROLLED BY PHOTOSYNTHESIS

In the preceding sections I have tried to analyze the physiological basis of certain temperature adaptations of plants on the basis of phytotron studies. Let me now use the same approach to analyze other basic processes in plant development. I shall begin with photosynthesis. The information on the extent

to which the photosynthetic process limits plant development is very conflicting. Ever since Wiesner, three-quarters of a century ago, we have been talking about shade plants which are presumably saturated at low light intensities, and sun plants able to utilize full sunlight intensity. However, in studies such as those in which BLACKMAN & WILSON (1951) shaded plants in field experiments, any amount of shading reduced productivity. It seemed as though both sun and shade plants were saturated only at full sunlight intensity. My phytotron experiments were in apparent contradiction with their findings, in that under long-term exposure all leaves, whether of strawberries, tomatoes, or beets, were saturated with light at or slightly above 10,000 lux (about one-tenth of full sunlight intensity). Still different results have been obtained in the most recent work on photosynthesis, based on measurement of the rate of gas exchange of individual leaves, which indicated that in many plants light saturation did not even occur in full sunlight. This disagreement is probably to be ascribed to the entirely different techniques applied in these studies.

Forty-five years ago, EMERSON (1932) had already demonstrated in his flashing light experiments that the photosynthetic process consists of at least two steps: a light reaction followed by a dark reaction, the former being completed in a millisecond but only at exceedingly high intensities. Since Emerson's basic work, other successive light-dark reactions have been found, such as Bunning's photophil and skotophil phases of growth, the occurrence of a dark reaction usually delaying the light reaction. One of these delaying dark reactions in photosynthesis was already recognized fifty years ago by KURSSANOV (1933), when he observed that photosynthesis was slowed down by the accumulation of photosynthetic products, which means that the rate of CO₂ reduction can be higher in the morning than in the afternoon, when leaves are almost saturated with carbohydrates. These carbohydrates have to be translocated out of the leaves (usually during night) before high rates of photosynthesis can be reached again the next day. In addition, two processes are known to counteract high photosynthetic rates very early in the day. The first of these is the circadian rhythm, which slows down light reactions in the skotophil phase. The second process can be observed in the rate of sucrose production in tomato leaves in the early morning light. After a two-hour lag period, sucrose is produced at a maximal rate for 2-4 hours (WENT & ENGELSBERG 1946), after which this production decreases again in the later hours. This suggested that dry-matter production in the tomato proceeds at different rates at different times of the day. This was tested by WENT (1946) in a field experiment as follows.

Growth and total dry matter were measured in five groups of tomato plants, four of which were exposed to light for 5, 6, 7, 8 or 14 hours daily and covered with black cloth the rest of the day and during the night; the sixth group was not covered at all. As usual in such practical experiments the problem was complex, because although the outside temperature and that in the

enclosures were the same during the night, during the afternoon the cloth-covered plants received a higher nyctotemperature than the uncovered ones. Since the experiment was performed in Pasadena during the spring, when the night temperatures are too low for optimal tomato growth and fruit set, the controls did not grow at an optimal rate and barely set fruit. Nevertheless, the results clearly showed that adequate photosynthesis had occurred during the first 7 hours of daylight. The plants given 5, 6, 7, 8, and 14 hours of daylight had mean weights of 65, 325, 680, 500, and 310 grams and mean fruit weights of 0, 3, 260, 140, and 25 grams, dry weight and fruit production being optimal for the plants given 7 hours of light each day (WENT 1946).

This and many other experiments have shown that measurement of the rate of CO_2 reduction in one particular period during the daily photosynthetic cycle cannot possibly establish whether a plant can utilize more or less light; this utilization depends on the physiological condition of the leaf, which varies throughout the day. Since most of the experiments done on rates of photosynthesis with gas-analytical methods have been carried out in the morning, when rates of CO_2 reduction are highest, the rates obtained by such instantaneous determinations of photosynthesis are undoubtedly too high.

6. PHOTOSYNTHESIS CONTROLLED BY GROWTH

To avoid this possible source of error, I suggest that photosynthesis should be measured over a long experimental period, for instance 1-2 weeks. To avoid tying up CO_2 analysers for weeks at a time, some other method should be used. Theoretically, the very best method is unquestionably the measurement of fixed chemical energy, which in most plants is equivalent to dry matter production. Unfortunately, this method is hardly possible with unstandardized plants in the field (except certain agricultural crops); it requires laboratory tests with properly matched groups of uniform plants.

In the Earhart phytotron in Pasadena a standard method for growing tomato plants for dry weight increase determinations was worked out. The plants were grown under optimal temperature and nutritional conditions in such numbers and groupings that statistical uniformity was attained. Under the most favorable light conditions the plants reached a photosynthetic efficiency of 9.2 per cent, that is to say, 9.2 per cent of the light energy falling on these plants over a period of 1-2 weeks could be harvested as chemical energy. This is not the highest efficiency for the photosynthetic process but it is for plant dry matter production, and indicates that the plants were grown under the most favorable conditions. The question was then raised as to whether, if it was not due to photosynthetic CO_2 reduction, this limitation of dry matter production could be attributed to some other process or processes occurring in the growth of tomato plants.

Fig. 1 probably gives the clearest indication of where the control of dry

matter production lies. Groups of 24 containers with standardized tomato plants were grown in different colors of light. To achieve light saturation, use was made of fluorescent tubes with different "fosfors" which produced light over a wide range of wavelengths, in general 100 m μ but hardly overlapping. For all colors except green, light saturation was achieved. Before light saturation was reached, the efficiency of light utilization (the slope of the curve) for blue, red, and a mixture of blue and red light was the same, as had been found in

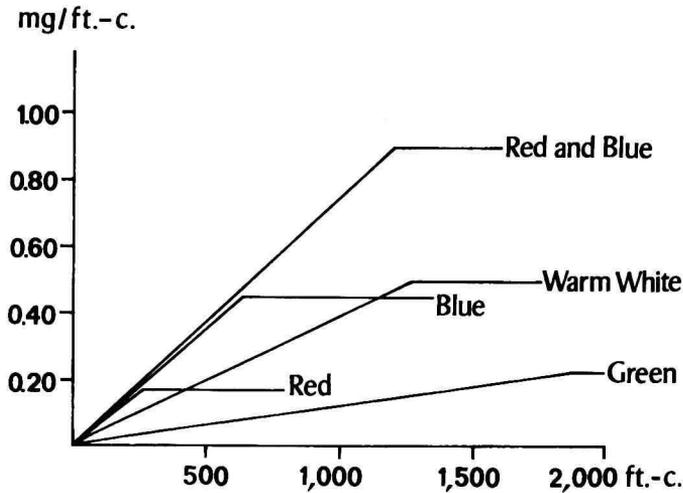


FIG. 1. Dry matter production (produced in 6 days per square of tomato plants) as a function of the incident light intensity. Colors indicate the type of fluorescent lamp used; for "Red and Blue" two of each color were used. Data of S. Dunn (WENT 1957).

many other experiments done with different techniques. The efficiency of the green light was much lower, because of its lower absorption. The white fluorescent light was slightly less efficient, because of the mixture in the white tubes of red and blue light with green. The main difference between blue and red lies in the saturation intensity, which is much higher for the blue than for the red, but is far outstripped by the combination of red and blue light. This is due not to the efficiency of the light in energy transformations but to the fact that the plants growing in red light become very spindly, in blue sturdy but short, and largest in the combination of red and blue light. Thus, the efficiency of the light is due to the utilization of the photosynthates in growth. This was confirmed in other experiments in which growth was not controlled by light color but by restricting it in other ways, e.g. by cutting off roots, which reduces both growth and dry matter production. It is not a question how much photosynthate is produced, but how it is used.

This suggests that we should seek ways to improve growth processes rather than to increase photosynthetic CO₂ reduction if we want to increase plant production (WENT 1957).

I had reached a somewhat similar conclusion after my first comprehensive investigation in airconditioned greenhouses. The first phytotron-like structure I built forty years ago -the Clark greenhouse in Pasadena- was used to obtain maximum growth and production, in this case in tomato. After years of work, higher productivity could not be achieved by further changes in temperature, light, water, nutrition, chemicals, root medium, breeding, etc. I then tried to identify the processes which limited growth under these optimal growing conditions. At that point I was no longer led by my own preconceived ideas, but entirely by the plant (WENT 1945).

Up till that time I had always worked with plants under conditions in which auxin was limiting for growth, conditions which I had deliberately chosen. Therefore I had become too convinced of the importance of auxin for growth, it is hardly surprising that I received one of the greatest shocks in my scientific life when it turned out that auxin was not an important factor limiting growth of the tomato plant. The decisive factor proved to be the rate at which photosynthates were translocated from the leaves to the growing areas: roots, stems, and fruits. This means that growth limitation is basically controlled by the utilization of photosynthates and not by photosynthesis itself. The lesson to be drawn from this experience is that we should not have preconceived ideas about the factor or factors involved in controlling a plant or a process: we should be led by the plant and not by our own (clever) ideas.

7. SATURATING LIGHT INTENSITY FOR PHOTOSYNTHESIS

I have already referred to the perhaps unexpected fact that for most plants investigated in the Pasadena phytotron the saturating light intensity was around 10,000 lux, which is only one-tenth of full sunlight. This was determined for tomatoes, sugar beets, strawberries, *Bryophyllum*, and a few other plants; all on the basis of the dry matter production over a 1-2 week period. The leaves were exposed as much as possible in a single layer perpendicular to the incident fluorescent light. If in nature all leaves were exposed in this position to sunlight at 100,000 lux, there would be an enormous waste of solar energy, since only 10,000 of the 90,000 lux absorbed light would be used in photosynthesis. If, however, the leaf was exposed at a 30° angle, the average light intensity in full sunlight would be only 50,000 lux with a wastage of 40,000 lux, and at an angle of 8° theoretically no light would be wasted.

In nature only shade plants place their leaves perpendicular to the incident light, which intensity is so much lower that most of it can be used. Also, they

usually have all their leaves in a single layer, because there would not be enough light for effective photosynthesis in a second layer underneath their leaf mosaic. The compensation point for light utilization is generally 1,000-2,000 lux. In any plants which normally grow in full sunlight, such as trees and most crop plants, the leaves are never placed perpendicular to the incident sun rays. Many plants, specifically *Leguminosae*, even have a mechanism by which at high incident light intensity the leaves assume a position parallel with the light. In sugar cane and corn, the leaves or at least their upper parts usually hang down making an acute angle with the noon sunlight. In sugar beets the young leaves also stand up vertically, and the older leaves, which are spread out almost horizontally, are shaded by the younger leaves. Needles of conifers and the hanging *Eucalyptus* leaves are never placed perpendicular to sunlight. The leaves of quaking aspen not only hang down, but are exposed to flashing light, which would increase their photosynthetic activity (WENT 1958).

At low light intensities, below the compensation point, there is an excessive weight loss in tomato plants, even exceeding the loss suffered in complete darkness. This may be due to photorespiration that is not balanced by photosynthesis, and is probably the herald of premature death. This would mean premature death of the lower leaves, which do not receive enough light to continue to be productive. It would also mean that the plants prune off their photosynthetically ineffective leaves and merely keep the optimal number of leaves to utilize all the light to which they are normally exposed. This is illustrated by the contrast between a plant growing in a greenhouse in full daylight and a plant growing in artificial light of 15,000 lux: the former has many more leaves, even though the upper leaves of both plants are light-saturated and look comparable. The same mechanism probably causes self-pruning of trees where the lower leaves and those nearest the trunk are shed instead of living a parasitic existence at the cost of the rest of the tree.

This behavior is of considerable importance to ecologists. Plants are not adapted to a particular light intensity, they adjust themselves to an existing light intensity; thus, the same plant species, even the same ecotype, can also live just outside a forest or at different distances from its edge, and in general plants can tolerate a wide range of light intensities.

8. GROWTH CONTROLLED BY RAIN

Thus far, I have dealt mainly with an experimental approach to ecology for which a phytotron is essential. Fortunately for those who do not have access to a phytotron, it is possible to approach many ecological problems without such facilities but still using physiological thinking and employing the experimental approach. This has been demonstrated in this monograph by many investigators, among them Woldendorp, Ernst, and Brouwer. I would like to add

just one more example, in which the main instrument is a lawn-sprinkler. Anyone who has made observations in a desert has been struck by the fact that in some years the surface of the sandy desert plains are covered by an extensive vegetation of annuals, all of which burst into bloom simultaneously, whereas in other years there may not be a single annual in evidence. The drier the desert, the more infrequent these blooming years. In Death Valley, on the border between California and Nevada, the intervals between good flowering years perhaps range from 5 to 20 years. The annual rainfall fluctuates widely from year to year in Death Valley, ranging from 0 to over 100 mm/year, with an average of 43 mm. What factor or factors cause the seeds of these desert annuals, which have been lying dormant throughout these 5-20 years, to abandon their inactivity suddenly and all at the same time? One would immediately suspect moisture or rain, but with an average of five or more rains a year, how did all seeds select the same rain? A correlational analysis soon suggested that only a rain amounting to more than 30 mm was responsible, provided it fell in the month of November. When this problem was taken to the laboratory, a few facts immediately became clear (JUHREN et al. 1956). For one thing, none of the annuals growing in a rainy year in Death Valley germinated when watered by soaking alone. But when the seeds were rained upon by a lawn-sprinkler for a sufficient time, they all germinated provided they received the equivalent of 30 mm rain over a sufficiently long period, such as 10 hours. It was then found that these seeds contained water-soluble inhibitors which could be leached out by a prolonged period of artificial rain. The response to a "November" rain was controlled by the temperature to which the seeds were exposed afterward. Summer annuals germinated exclusively at high temperatures, e.g. 26°C (*Pectis papposa*, *Bouteloua* spp.). December germinators, such as *Gilia aurea* and *Eriophyllum wallacei*, needed low greenhouse temperatures. But the most spectacular desert annuals, germinating late in the fall, such as *Garaea canescens*, developed in the greenhouse at intermediate temperatures. Thus, depending upon the temperatures prevailing after the artificial rain, quite different plants developed. This was not a question of survival of the cold- or warm-adapted plants, but rather of differential germination. Therefore, in each year when germination occurs after a sufficiently heavy rain, the composition of the annual vegetation in our deserts is different. There are years when *Plantago insularis* is dominant in a certain location; in other years it is *Oenothera clavaeformis* or *Chaenactis carphoclinia*.

There are many other mechanisms besides germination inhibitors by which desert plants delay their germination until the arrival of a rain of sufficient intensity to insure their survival in a normally dry climate. Many of the shrubs and trees that grow in dry washes are hard-seeded, i.e., their seedcoat has to be abraded before they can germinate. This abrasion can only occur after a heavy rain, when a slurry of water, sand, and stones runs down

an otherwise dry wash and soaks the soil of the wash to a considerable depth.

To me, the most amazing phenomenon I observed in the desert was the lack of competition between desert annual plants. Sometimes, after a particularly heavy rain, excessive numbers of seedlings develop. Under these conditions, essentially the whole seed pool of the desert develops, and thousands, even up to 50,000, seedlings per square meter may come up, resulting in a green cover of the soil composed solely of cotyledons. Under such conditions one would expect a fierce competition for light, food, water, and space between the crowded seedlings, but this is not the case. On average, 45 per cent of all seedlings not only survive but manage to flower and fruit. Whereas normally each germination results in 10-20 new seeds, under these crowded conditions perhaps only one or two viable seeds per germination are formed, and all plantlets share all resources equally. Therefore, there is no selection during the vegetative and reproductive stages in these desert plants, and since most of their seeds have an extraordinarily long life span, one would expect an ever-increasing seed mass in deserts. That is obviously not the case; we found that after a good seed year the seed population is reduced to normal levels by the activities of seed-eating rodents and harvester ants. If one still wanted to use the term selection pressure, one would have to state that for desert annuals, selection pressure is exerted by seed-eating animals. In general, it can be stated that ideas on Darwinian evolution must be drastically revised, certainly for deserts.

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10. DISCUSSION

QUESTION: You mentioned that growth of the tomato plant depended entirely on the night temperature. This observation does not necessarily apply to all plants or every region involved, since you will have noticed that day temperature often is important as well.

ANSWER: Each plant has different factors to which it responds. The pea responds to day temperature and not to night temperature. Several varieties of tomato respond to a high temperature as well, a factor which was bred into a commercial variety to make it possible to grow tomatoes in hot climates, for instance in Texas. In general, however, the tomato has a very limited range of night temperatures in which it will set fruit.

QUESTION: Do you want to say that these desert plants suffer from stress? They are so well adapted to this environment! Do they live in a stressed environment?

ANSWER: Stress is one of those words I do not like. What do you mean by stress? Actually, the desert provides the optimal conditions for the growth of desert plants. They are typically adapted as regards temperature, water economy, etc. Imitation of desert conditions in a climate-room gives exactly the same plants. Therefore, you have to define what you mean by stress. For man, the desert is a stressful environment. The desert animals who live there are very happy; they are not under stress. Only under extreme conditions may one speak of "stress".

QUESTION: We both attended the lectures of Professor NIERSTRASZ in Utrecht. He emphasized the point that survival is not a question of fitness but of chance. Do you think the same applies to annual plants in the desert?

ANSWER: I do not think the factor "chance" is very much involved when the organism is completely adapted. I will give you an example of the misunderstanding that can arise. A plant is not particularly adapted to a certain light intensity, but adapts to the intensity under which it normally lives. In the tomato, photosynthesis in the leaf is saturated at 10 per cent of full sunlight. It does not waste the extra light, however, since the leaves are almost never perpendicular to the direction of the sunlight. Especially older leaves do not stand upright but hang to some degree (corn, tomato, sugar beet). The plants adapt themselves to the prevailing conditions.

QUESTION: Stress conditions must occur in the field, or how would you otherwise explain the spacial problems observed there?

ANSWER: Spacial problems do not exist for annual plants; we notice them in perennials and in shrubs. Under favourable rain conditions in the desert we can see millions of seedlings of the shrub *Larrea divaricata*, the creosote bush, but these seedlings are not found in the immediate vicinity of the shrubs themselves, because of a germination-inhibiting excretion product that we have been unable to identify. There is no effect of the surrounding seeds on germination, just as is the case with agricultural plants.

QUESTION: Do you think use of the word "stress" may still be meaningful to explain why certain areas have a very low productivity or why so many plants are absent in a certain environment?

ANSWER: In most cases the problem is not that only a few species survive but rather that relatively few germinate. Once a tomato plant has germinated in the wild (this species has a high temperature requirement for germination), it survives and it rarely happens that it is actually killed as a plant. It might be attacked by fungi or later by animals, but I would not call this stress. Stress should only be referred to if you can express the phenomenon in quantitative terms, e.g. growth.

QUESTION: What controls the density of seedlings of annual desert plants?

ANSWER: This is entirely determined by the number of seeds present. Densities of 50,000 seedlings per m² have been reported, but a density of 5,000 is more usual. Of the 50,000 seedlings, at least 20,000 survived and in such cases the production of seeds per plant will be reduced considerably by the crowded conditions. In these plants "competition" is not between species but within the species.

I would like to express my admiration for Professor HARPER's work as regards the quantitative aspects and the numerous measurements on plants included in his research. In my opinion, ecologists should pursue this line much more than is the case at present.

