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This colophon has been designed by Charles Mozley. The bull, from time immemorial, has been an inspiration to man, and a model of courage and strength. He formed the watermark of the earliest printing papers used by Caxton and in the printing of Coverdale's Bible.

LIGHT, VEGETATION
AND CHLOROPHYLL

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LIGHT, VEGETATION AND CHLOROPHYLL

J. Terrien, G. Truffaut
and J. Carles

Translated by Madge E. Thompson

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Publisher's Note

The publication in a single volume of the English translations of *Lumière et Végétation*, by Jean Terrien and Georges Truffaut, and *L'Énergie Chlorophyllienne*, by Jules Carles, was not undertaken without consultation with the authors and the French publishers. The advantages of combining these two small books into a comprehensive whole were fully recognized, and it was agreed that excessive overlapping should be avoided by omitting the less explicit of any two passages covering the same ground. No information has, however, been omitted and a few small repetitions have been allowed to remain where their removal would have necessitated rewriting the text. A single index has been provided to cover both works.

PART I

LIGHT AND VEGETATION

To the memory of *M. Georges Truffaut*, whose practical spirit was allied to a taste for pure research and whose penetrating intuition astonished the scientists with whom he loved to surround himself.

I shall always remember with emotion the pleasure of our conversations together when we sketched out the plan of this book.

Jean Terrien

INTRODUCTION

WITHOUT light, there is no vegetation. Light is one of the physical factors which condition the life of the plant, but other physical, as well as chemical, factors are also necessary. The plant is a living organism in which chemical synthesis and decomposition take place and these processes are possible only in suitable chemical and physical conditions.

Every variation in these conditions has its effect on the behaviour of the plant to a greater or less degree; the various factors react on one another and it is often difficult to isolate the influence of one of them. A chemical action, for instance, may be very different in different physical conditions and even the distinction between physical and chemical is to some extent arbitrary. To explain the known facts, however, a distinction has to be made.

The following chapters are concerned with the study of one of the physical factors of plant life, light, whose role is fundamental.

The vegetable organism could be compared to a chemical factory, the gases in the atmosphere and the liquids and solids in the soil being its raw materials. But every factory needs energy—in electrical, thermal, hydraulic or some other form. The plant has the same need; the fundamental synthetic processes by which it creates its own substance and the movements of water and sap demand a continual supply. Whence does it come? Light, luminous energy—nearly always from the sun—provides the “motive power” of the vegetative factory.

The power, in the form of light, furnished by the sun when it is at the zenith, can reach the astonishing figure of 3,200 kW for an area of 1 acre. In the Paris region, the solar energy received per acre in a year is equivalent to an uninter-

rupted average power of 560 kW. Thus, if the area of cultivated land, forests and pastures in France is estimated at 50,000,000 acres, it can be calculated that the average power received by the vegetation in that area is 35,000,000,000 kW. This power supplies an annual quantity of energy which is some thousands of times greater than the consumption of electricity in France in 1954.¹

Such an enormous quantity of luminous energy would be sufficient to prove the fundamental importance of this physical factor. Certainly, the plant absorbs for itself only a small part of what is thus offered to it. Later we shall study in detail what fraction is really utilized and the different functions that it performs. We shall see that their multiplicity also forces us to consider the physical factor of light as being of supreme importance to vegetative growth.

The truly scientific and precise study of the influence of light began only a comparatively short time ago, but very important results have already been obtained. Certain particularly striking observations deserve to be singled out in this introduction.

One of the first of these observations was the surprising rapidity of the growth of vegetation in the far north near the Arctic Circle where, during the summer, there is scarcely any night.

According to Linneus (in 1732) wheat sown on 31st May was ripe and ready for cutting on 28th July, fifty-eight days later, while the rye crop was gathered sixty-six days after sowing. Only the long hours of daylight can explain this phenomenal growth. At Lulea, on the Gulf of Bothnia (lat. 65° 32'N), where these observations were made, the sun scarcely disappears below the horizon at this time of the year so that the insolation is almost continuous.

Among the manifold effects of light—effects of which the importance and variety are becoming increasingly clear to us—

¹The consumption of electricity in France in 1954 was 45,000,000,000 kWh, which is equivalent to an uninterrupted average power of 5,100,000 kW.

there is one which has been known for a long time and is certainly also the most important; we call it photosynthesis.

Plants grow and increase in weight and size; they are composed almost exclusively of carbohydrates. The synthesis of these substances from water and carbon dioxide in the air is endothermic; this means that the plant must be supplied with energy for the chemical reaction to take place. Light is essential for the purpose. Luminous energy in the form of rays of visible light, especially orange and red, is the only form of energy which green plants can assimilate and use to accomplish this extremely important process.

Growth is promoted when conditions are favourable to photosynthesis. In fact, the study of the effect of light brings us to the core of the still mysterious phenomena which govern the life of the plant and its nutrition.

It is a commonplace to say that all the energy available to man comes from the sun: the waterfalls of hydro-electric power stations are fed by the rain and snow proceeding from evaporation under the heat of the sun; the wind which drives windmills is due to the differences of temperature of the air heated by the sun; even wood, coal and petroleum, vegetable foodstuffs and the animals which feed on them—all the things that man rightly regards as valuable resources have been created, with the help of solar energy, by photosynthesis.

If plants did not perform this function, the radiant power of the sun would be converted directly into heat; we owe to photosynthesis the fact that a small part is turned into chemical energy—a form infinitely more valuable to us. The aim of cultivation is to promote this transformation as much as possible; the process is unique, because no practical means has yet been found of artificially converting solar energy into chemical energy, but it has certainly not reached its maximum efficiency. It is not impossible that a systematic study of the action of light would lead to great advances in agriculture, comparable, for example, with those which have resulted from the use of chemical fertilizers.

Under present conditions, what is the proportion of solar

radiation used effectively for photosynthesis? To take the best examples, the chemical energy accumulated in the products of the earth (we should say of the sun) represents about 1 per cent of the solar energy which has reached the cultivated area in the form of visible light, ultra-violet or infra-red. This is already a strikingly good result if we compare it with the results obtained at the few experimental stations which have been set up to study the utilization of solar energy and where the efficiencies scarcely attain this figure.

Are we right, however, to think that it is theoretically possible to obtain an enormous increase in vegetative growth by a better utilization of light? Some progress is certainly conceivable, but a few simple considerations show that it is limited.

Chlorophyll seems to be the necessary intermediary between light and photosynthesis, but chlorophyll absorbs only the visible light, while about 50 per cent of the solar energy consists of invisible infra-red radiations. The width of the absorption band of chlorophyll means that it can absorb only a third of the solar energy. Then again chlorophyll can do nothing by itself, it plays its part only inside a living vegetable organism, which, like all matter, absorbs, this time without any benefit for photosynthesis, a part of the light which could have been absorbed by chlorophyll. Hence there is not quite a third, but perhaps only a quarter, of the solar energy available to chlorophyll.

Finally, the plant, like every living thing, must breathe, which means that it burns a part of its substance by combination with the oxygen in the air. This process, which continues day and night throughout its life, consumes a part of the products accumulated during the day by photosynthesis and the crop is consequently deprived of them.

Therefore the agricultural efficiency of photosynthesis could never exceed 20 per cent in the use of sunlight. We are still very far short of this, since the best efficiencies obtained are twenty-five times lower; there is still room for enormous improvement.

The greater part of our planet is covered by the oceans; there, also, solar illumination produces crops with the help of the microscopic algae which float between the depths of 100 and 150 metres; in the Channel, the yield is 5·6 tons per acre of vegetable plankton. The algae of this plankton are chlorophyll plants, and the catch of certain fish which feed on them can be estimated according to the number of hours of sunshine at the beginning of spring. In Scotland, fertilizers poured into some almost enclosed lochs have produced a notable increase in plankton and a more rapid development of the fish living in these cultivated marine fields.

Photosynthesis is only one aspect of the action of light on vegetation. In the following chapters we shall give some details of other influences and a glimpse of the immense discoveries which are still possible. But first it is necessary to define what light is and to state the facts which, in the knowledge acquired by physics of the nature of radiation, will enable us to understand a small part of the still mysterious effects of light on the life of the plant.

CHAPTER I

LIGHT AND THERMAL RADIATIONS

How can light be defined physically, and without ambiguity, in quality and in quantity? Why is it not sufficient to say, for example that a certain plant was cultivated in the laboratory under an illumination of 1,000 lux of yellow light? What are the imprecisions, for there are several, in that statement? We cannot answer the question without explaining some physical characteristics of light.

One of the fundamental quantities of physics is energy. The principle of the conservation of energy has always been confirmed. It has survived all the evolutions of physical thought, from relativity to wave mechanics. It has even acquired in those theories a still deeper significance. Now, light is a form of energy and sunlight brings us an enormous quantity of it—nearly the whole of that which is available to us.

Light-waves

Light consists of waves, of an electromagnetic nature, which are propagated as well, and even better, in a vacuum than in the air or transparent media. Of the same nature are the ultra-violet and infra-red rays, the X-rays used in medicine, the γ -rays of radioactive substances, and the long or short Hertzian waves used in radio transmission.

We know that the Hertzian waves of telegraphy and of wireless telephony are characterized by their wave-length. The nature of light is specified in exactly the same way. The apparatus which separates its various wave-lengths is called a monochromator. It generally contains one or more prisms and isolates pure, or monochromatic, waves. The energy of

each of these waves is measured with delicate instruments, thermocouples or bolometers, whose temperature rises as they absorb the energy and transform it into heat; it is this rise in temperature which is measured.

The monochromator can isolate, in the exposed spectrum of light, not only visible waves but other waves, on both sides of the visible, which also transport a measurable quantity of energy. These waves, called infra-red if they are less refracted by the prism than the visible, and ultra-violet if they are more refracted, exist in solar radiation, the normal source of light for vegetation, and are nearly always present in the light given by ordinary lamps.

The fact that they have no effect on our retina and are invisible to us does not at all imply that plants are indifferent to them. A description of the light received by a plant must therefore necessarily include not only the radiations which excite the human retina but also the electromagnetic waves of the same nature, ultra-violet and infra-red.

The quality of a monochromatic radiation is wholly determined by its wave-length, which is expressed in microns ($1 \mu = 0.000001 \text{ m.}$) or in Ångströms ($1 \text{ Å} = 0.0001 \text{ micron.}$) For example, the wave-length of yellow sodium light, which is nearly monochromatic, is $5,893 \text{ Å}$, or 0.5893μ .

Maxwell's experiments showed that light, visible or invisible, is an electromagnetic radiation. It is a double electric and magnetic field. The small electrified particles in matter, such as electrons, come under the influence of these waves and in turn react on them, converting all or part of their energy into another form and retarding their propagation, thus giving rise to the two classic phenomena of absorption and refraction.

Photons or Quanta

The properties of electromagnetic radiation are often perfectly represented by means of the waves of which we have just spoken. Other properties indicate that this radiation consists of a shower of particles, or grains of energy, called

photons or quanta. The energy of each photon is proportional to the frequency of the wave, the coefficient of proportionality being the well-known universal Planck's constant, h . Between the wave-length λ (or the frequency $\nu = \frac{c}{\lambda}$) and the energy E of a photon there exists the very simple relationship

$$E = h\nu = h\frac{c}{\lambda}$$

where c is the velocity of light in a vacuum.

We shall then ask, "Does light consist of waves or particles? Must we imagine continuous spherical waves expanding round the source of light, or a shower of discrete particles, projected in straight lines in all directions?"

Fig. I, 1. Scale of electromagnetic radiations. λ : wave-length in microns. ν : frequency in cycles per second

The physicist will reply that the two aspects are equally indispensable; they are prescribed by experimental observation for light as well as for all electromagnetic radiations. Sometimes we shall employ terms applicable to waves, sometimes those applicable to photons, passing freely from one mode of expression to the other, since they represent two aspects of the same phenomenon, which is beyond our range of imagination and to which our words and familiar concepts are ill adapted.

These are the properties, not only of light, but of a continuous series of radiations which extend over an extraordinarily large range of wave-lengths and which are also electromagnetic. Fig. I, 1 shows them in diagrammatic form.

The visible radiations occupy an extremely small portion

of the electromagnetic spectrum, but it is of the highest importance to us since it is the only part to which our eye is sensitive; in addition it contains the active rays for photosynthesis and rather more than half of the solar emission is situated in this band of wave-lengths.

It is, however, the larger band, lying approximately between 1,850 and 40,000 Å, that we shall call "light", thus extending the meaning of this word which was formerly limited to the visible rays. It has become customary to speak of ultra-violet or infra-red light although these rays are

Fig. I, 2. Scale of visible and invisible rays the effects of which are discussed in this book

λ : wave-length in microns

ν : frequency in 10^{12} cycles per second

invisible. Fig. I, 2 gives the boundaries of the spectrum of light with which we are now concerned.

Absorption of Light Rays

The essential property of light, to which we shall often return, is its transport of energy. This energy can be measured in joules or in kilogram-metres, in kilowatt-hours or in calories.

Light from the sun has traversed interplanetary space, the earth's atmosphere and, sometimes, sheets of glass, before it reaches us; it has thus been filtered and deprived of certain parts which have been absorbed. One of the properties to be studied is therefore the transparency of various media to different radiations.

Although light is propagated in a vacuum without loss of energy it is not so propagated in matter—nearly all bodies are opaque to the radiations that we have agreed to call

light. The energy which is not transmitted is partly reflected, often in a diffused way; the rest is absorbed and transformed, especially into heat, after a more or less deep penetration.

Pure, dry air, up to a thickness of some metres, possesses an almost perfect transparency for all the wave-lengths that we are considering. It begins to absorb again, strongly, only the photons of a wave-length of less than $1,850 \text{ \AA}$, but these are situated in the extreme ultra-violet which does not appear in the solar radiation that reaches us. (This extreme ultra-violet is produced, however, by sources of artificial light such as the spark, or the mercury arc in a quartz envelope.) The absorption is due to molecules of oxygen. In the infra-red, a partial absorption takes place, due to molecules of carbon dioxide and especially of water vapour. The whole of the atmosphere that the solar radiation has to traverse presents the same absorption bands in the infra-red, particularly in the neighbourhood of the wave-lengths $14,000 \text{ \AA}$ and $19,000 \text{ \AA}$.

In addition, we know that all wave-lengths of less than $2,900 \text{ \AA}$ are absent from the solar spectrum and that these radiations are absorbed in the upper atmosphere by molecules of ozone.

Ozone is a gas the molecules of which consist of three atoms of oxygen, while the molecule of oxygen has only two. It is produced when ultra-violet photons are absorbed by oxygen (we have just seen that those of a wave-length of $1,850 \text{ \AA}$ or below are very strongly absorbed); its odour is perceptible in the neighbourhood of mercury vapour lamps in a quartz envelope.

A small quantity of ozone, created by the ultra-violet of sunlight, thus exists in the atmosphere. Measured at atmospheric pressure, at a temperature of 0°C , this ozone would form a layer of gas 2 to 3 mm. thick, surrounding our globe (the entire atmosphere under these conditions would be 10 km. thick). It is this infinitesimal proportion of ozone which cuts the solar spectrum on the ultra-violet side and suppresses all wave-lengths of less than $2,900 \text{ \AA}$. Later we shall see the extremely harmful effect that ultra-violet rays,

absorbable by ozone, have on vegetation. We know also that they scorch the human skin and that their powerful action is used, with caution, in medicine for the treatment of certain diseases.

These 2 or 3 mm. of ozone, by their presence and the thin screen of their molecules, therefore protect animal and vegetable life from the action of these dangerous ultra-violet rays of short wave-length, but they permit the passage of small quantities of rays, of wave-lengths a little greater than $2,900 \text{ \AA}$, which still have a slight lethal action on bacteria and fungi. They cause "sunburn", but they purify our globe and,

Fig. 1, 3. Transmission curves for pure water and for a solution of cupric chloride in water for the visible and near infra-red radiations

without them, we should perhaps be submerged by decaying matter. This shows the admirable equilibrium of adaptation between life and the conditions of radiation in which it develops.

A shallow depth of water is transparent enough to visible and ultra-violet light, but it is opaque to infra-red of a wave-length greater than $13,000 \text{ \AA}$ (or 1.3μ), i.e., to nearly all the infra-red in which we are interested (Fig. 1, 3).

Particles dissolved or suspended in natural water (lakes, rivers and seas) greatly reduce its transparency, especially to ultra-violet. Thus it has been found that in a lake of clear water there is about 100,000 times less visible light at a depth of 30 m. than at the surface. But an ultra-violet lamp can act on algae which are submerged at only a shallow depth.

The absorption of infra-red by water is a property often used in the laboratory for eliminating these wave-lengths from the light emitted by incandescent sources. The passage through a solution of copper sulphate, or better still through a 2 per cent solution of cupric chloride 2 cm. thick, is a more effective means of almost completely eliminating the invisible rays of long wave-lengths (see Fig. I, 3).

Glass absorbs all wave-lengths less than about 3,500 Å. Thus, in front of a lamp emitting ultra-violet, our eyes are protected by a thin sheet of glass or by ordinary glass lenses. Plants cultivated in a glasshouse never receive the photons of

Fig. I, 4. Transmission curve of three coloured glasses. Note their strong transmission in the near infra-red, particularly that of the blue glass (which is unexpected)

the sun of wave-lengths between 3,600 and 2,900 Å, with which plants in the open air are well provided.

Coloured filters, whether they are made of glass or of gelatine containing certain pigments, or whether they consist of liquids contained in vessels of glass or quartz, permit the passage of large bands of wave-lengths of which the limits are not very clearly defined. The properties of a filter are described entirely by its transmission factor for each wave-length; Fig. I, 4 gives some examples of the transparency curves of common coloured glasses.

Some large firms give, in their catalogues, lists of coloured glasses with their transmission curve; these glasses vary in price and durability.

Before we can know the composition of the radiation transmitted by a coloured filter, obviously we must know that of the initial radiation; this is a fact which should not be overlooked.

Sensibility of the Eye to Light

For a rather small part of the radiations that we are considering—but a part nevertheless which is important because of its properties—the human eye is an extraordinarily sensitive and flexible detector. A given flux of monochromatic light entering the eye under given conditions produces a sensation which depends qualitatively and quantitatively on the wave-length of the radiation.

Fig. I, 5. Scale of colours of the visible spectrum

λ : wave-length in microns

ν : frequency in 10^{12} cycles per second

The colour varies in a continuous fashion with the wave-length, but we have become accustomed to distinguish the following colours: violet, blue, green, yellow, orange and red, with their boundaries marked as shown in Fig. I, 5.

Wave-lengths shorter than 3,900 Å are almost invisible; when they are intense they produce a slight and diffuse luminous impression of a bluish colour.

Wave-lengths longer than 7,500 Å are still visible, if they are of sufficient intensity, but their luminosity rapidly decreases as the wave-length increases.

Two fluxes with equal energy but of different wave-lengths cause different sensations, since the colour is not the same. We can, however, more or less disregard the colour and say that one of these fluxes is "more luminous" or "less luminous" than the other. It is therefore possible to evaluate

for each wave-length a luminosity (or visibility) factor. Thus, the wave-length of 5,500 Å has the highest luminosity factor and is conventionally given the value of 1; to produce a similar luminous impression (although of a different colour) with the wave-length of 4,200 Å, 250 times more energy is required. The luminosity factor for this wave-length is therefore $1/250$ or 0.004.

Fig. I, 6. Mean curve of relative visibility factors for the human eye

The curve in Fig. I, 6 gives the luminosity factors for the different radiations of the spectrum; these factors have been adopted by photometry laboratories all over the world and have been ratified by international agreements. They are, as a matter of fact, rather arbitrary, for they depend on individuals, conditions of observation, etc., and it has been necessary, in order to reach agreement, to fix a mean conventional curve.

Composition of Solar and other Radiations

The study of radiations and of their quantitative composition, which is obviously of fundamental importance for all

experimentation on the properties of these radiations in relation to vegetation or any other kind of phenomenon, is undertaken by a few specialized laboratories possessing the necessary equipment and experienced personnel because it is extremely delicate work.

It is, however, desirable that manufacturers of sources of illumination, or those who use them for their experiments, should be able to determine easily and with reasonable accuracy the curve of spectral emission, from the ultra-violet to the infra-red, of their lamps or lighting units under the same conditions as those in which they will be used. The experiments would thus be much more informative.

Fig. I, 7. *Upper curve*: composition of solar radiation beyond the earth's atmosphere. *Lower curve*: composition of solar radiation at ground level, with the sun at the zenith and an atmosphere of average humidity

The light from the sun is the most important to human beings just as it is to plants. At ground level its power and its composition vary according to several factors; a special chapter of this book will be devoted to it. But, in order that it can be compared with other sources of light, we shall give the composition of solar radiation as it reaches ground level

when the sun is at the zenith and the atmosphere is pure and dry.

It is represented by the lower curve of Fig. I, 7. Note that the apex of this curve occurs in the middle of the visible region. On the ultra-violet side we find the limit imposed by the absorption of ozone, at 2,880 Å, which has already been mentioned in connection with the transparency of the air. The minima situated in the infra-red (the magnitudes of which vary with the angle of the sun's rays and therefore with the thickness of air traversed) are also due to atmospheric absorption. The absorption bands of carbon dioxide and of water vapour can be identified.

Taking this absorption into account, it has been possible to calculate the spectrum of sunlight before it has passed through the atmosphere. This spectrum is represented by the upper curve of Fig. I, 7. As we move towards the infra-red, the power of the solar radiation diminishes, but the radiation extends further than can be shown by the scale of the curve.

Although the apex of the curve is in the visible region, a little more than half of the solar emission is composed of infra-red radiations; the rest is radiated in the visible band except a little more than a hundredth part in the ultra-violet.

These results have enabled us to calculate the temperature of the sun's surface, which is about 6,000° C.

The electric arc used to be favoured for street lighting; it is a source of artificial light of high efficiency, that is to say, it converts into radiation a large part of the electrical energy which is used to supply it. The specially luminous part is the extremity of the carbon rod connected to the positive pole of the electricity supply, for it is there that the temperature is highest—about 3,400° C.

The curve giving the composition of the radiation from the arc resembles that for the sun, but it is displaced towards the long wave-lengths; the infra-red emission is proportionately greater, to the detriment of the visible and especially of the ultra-violet. Nevertheless, the arc is one of the sources which most nearly approaches sunlight and the possibility of making

it function in the free air, without a glass globe, allows its ultra-violet emission to pass unhindered.

The light from incandescent lamps is emitted by a tungsten filament, raised to a high temperature by the passage of the current, and enclosed in a bulb containing an inert gas. The filament is designed to remain at a lower temperature than its melting point, which is $3,117^{\circ}$ C. Its temperature is therefore lower than that of the electric arc; generally it lies between $2,600^{\circ}$ and $2,800^{\circ}$ C. The distribution in the spectrum of the energy radiated differs from the preceding by a displacement still nearer to the long wave-lengths; the energy emitted in the ultra-violet and the visible violet is very small. On the other hand, the greater part of the energy is radiated in the red and especially in the near infra-red.

Photometric Units

We have seen that all radiation can be decomposed, by means of a monochromator, into a series of pure radiations of known wave-lengths. In giving the power of the radiation of each wave-length, we can describe its physical nature in a complete and unambiguous fashion. A curve, continuous or discontinuous, is therefore necessary to characterize it and we have thus described the radiation of the sun.

When, for a definite purpose, only a small part of the spectrum is usable, it is not essential to know the other parts and a knowledge of the energy radiated in the useful part is then sufficient.

An example of considerable importance is that of the visible radiation applied to artificial lighting. The part of the usable spectrum lies between the wave-lengths of 3,900 and 7,500 Å approximately, but in this rather extensive band the same energy emitted in radiations of different wave-lengths has a lighting efficacy proportional to the very variable luminosity factor of these wave-lengths; the values of these factors are given in Fig. I, 6.

It has therefore been agreed to represent the "luminous" intensity ("luminous" this time being taken in the strictly

limited sense and meaning "capable of making an impression on the human eye and giving it the sensation of light") of a monochromatic radiation by the product of two factors, one being its energy and the other its visibility factor.

When the radiation is complex, like that of an incandescent lamp, the products thus obtained for each wave-length are added together. The sum calculated in this way is, by definition, the luminous intensity of the source and the units created specially for this purpose are photometric units.

These photometric units are used almost exclusively in the measurement of radiation because for a long time only lighting applications were considered.

The usual method of describing the radiation of a lamp by the number of lumens is therefore particularly incomplete and inadequate. It obviously has no value for those who wish to use infra-red or ultra-violet.

Long-wave Terrestrial and Atmospheric Radiation

Our planet receives a large quantity of power from the sun. Its emission contains visible and infra-red radiations of short wave-length and almost the whole of its spectrum is below $5\ \mu$. This is radiation, or light in the broadest sense, emitted by a star whose temperature is of the order of $6,000^{\circ}\text{C}$.

The property of emitting radiation is not peculiar to the sun; on the contrary, it is absolutely general. Every material body radiates round itself. We are bathed in the radiation of the objects which surround us and we send out our own radiation to them.

The intensity of the radiations increases with temperature; we feel it as our hand approaches a warmer object than our surroundings. We feel also, as a sensation of cold, the reduction of the radiation in the neighbourhood of a cooler body which is substituted for and masks the warmer bodies in front of which it is placed.

The ground therefore also radiates and grows cooler as it loses the energy that it emits. The pure atmosphere and the clouds behave in the same way; they send radiant energy

Fig. I, 8. General exchanges of radiant energy. The numbers inside the circles signify gram-calories per day per sq. cm. (mean values)

towards the sky and towards the ground. These complex exchanges of radiant energy are made by radiations whose spectrum is different from the solar spectrum; they are always electromagnetic and are situated in the infra-red, but their wave-lengths lie between 4 and 50 μ , the greatest intensity being in the neighbourhood of 10 μ . They are often called thermal radiations; actually a large part of the exchanges of heat between non-incandescent bodies is made by their intervention. But all radiations transport energy and are also, in that sense, thermal.

These exchanges can be summarized in the following way:

(1) The sun heats the ground directly through the atmosphere. In fact, of the 720 calories per day per sq. cm.—the average quantity that we receive—one half is sent back into space by reflection and does not affect us (unless it is to make our globe visible to the eyes of astronomers, if any, on other planets) while, of the half effectively used, 80 per cent is absorbed by the ground. The atmosphere, which is rather transparent to sunlight, absorbs the rest.

(2) The ground, heated by the sun, warms, in its turn, the atmosphere to which it yields 700 calories per day per sq. cm., more than double that which it receives from the sun. It does so, either in the form of water vapour, or, more particularly, in the form of long-wave radiations (5 to 50 μ) which are absorbed by the atmosphere to a large extent. Of the 700 calories lost by the ground, the atmosphere retains 560, letting 80 escape into space and reflecting 60 towards the ground.

(3) Because it is heated up by terrestrial radiation, the atmosphere, in its turn, radiates 340 calories towards the ground, sending it more radiant energy than the sun.

All these exchanges of energy are shown synoptically in Fig. 8. It can be seen that they balance one another; the ground, like the atmosphere, loses as much energy as it receives.

The numbers indicated are mean values. We see from the diagram in Fig. I, 8 that 360 (72 per cent) of the 500 calories of terrestrial radiation proper are absorbed by the atmosphere.

In reality, a hazy, cloudy, dust-laden or very humid, atmosphere absorbs 90 per cent and therefore radiates so much more into space and towards the ground. As a result, the temperature of the ground may be higher, since it will receive an increased atmospheric radiation.

Nocturnal Cooling by Radiation

The radiation from the ground is specially interesting, since dew, white frost, etc., are phenomena connected with it; it occurs particularly at night.

The cooling by radiation which is not compensated by the low radiation of a clear and dry atmosphere causes the condensation of water vapour into dew or its crystallization into white frost.

It is of great advantage if we can control this radiation; two methods are possible, either to reflect its own radiation on to the ground, or to increase the atmospheric radiation.

In the first case, the radiated heat is directed downwards, either by using taut screens (linen cloth, straw mats, glass) or by producing a smoke screen. These screens act by their reflection factor for the infra-red, and also by substituting their own radiation for that of the atmosphere, which they mask. This is all the more advantageous as their temperature remains higher.

Walls, heated up by the sun during the day and cooling slowly, form a partial screen for the area near to them; they mask a part of the sky and radiate abundantly during the night. In this way they are accumulators of energy.

In the second case—the increase of the atmospheric radiation—a very effective local action is obtained by lighting fires; the hot gases and particles proceeding from the combustion emit a radiation which is added to that of the atmosphere, even if the smoke produced is not abundant. Some fuels are shown to be more effective than others.

Glasshouses and glass-covered frames are a very interesting application of the properties of glass in the presence of radiations. It is very transparent to the visible and the near

infra-red, which constitute almost the whole of solar radiation. Clean glass, receiving the rays of the sun perpendicularly, allows about nine-tenths of their energy to pass through it; we can warm ourselves in the sun as well or better behind glass than in the open air. But the thermal radiation of bodies at ordinary temperature, with wave-lengths longer than $5\ \mu$, principally around $10\ \mu$, is totally absorbed by glass. Thus the heat produced in a glasshouse by solar radiation, which penetrates into it freely, is as it were imprisoned. We can say that, at night, the thermal radiation that the glass receives warms it. In its turn, it re-emits this absorbed energy, in the form of thermal radiation, from its two faces; half is therefore lost and the other half is sent back to the interior of the glasshouse. The protection of the glass has the effect of reducing by half the heat losses by thermal radiation without perceptibly reducing the contribution of energy from solar radiation. To this action is obviously added the suppression of cooling by movements of the air and by evaporation.

CHAPTER II

SOLAR RADIATION

THE solar radiation reaching the earth's surface is variable. Its composition, and particularly its intensity, are affected by its passage through the atmosphere. Even when the air is pure and the sky clear, certain parts of the radiation are absorbed; ozone suppresses the ultra-violet rays of short wave-lengths and other parts, situated particularly in the infra-red, are suppressed by water vapour.

The atmospheric absorption also depends on the height of the sun above the horizon, the luminous rays being obliged to pass through a greater and greater air mass as the sun sinks; in addition, the diminishing inclination of the rays reduces the illumination on the ground in proportion to the cosine of the angle that they make with the vertical.

Such are the principal factors which, with cloudiness, determine the nature and the intensity of the radiation on the ground. We shall study them separately and we shall also see how this radiation is distributed in time, according to the length of the day and night, for it is very important to plants that they should receive light in periods of a suitable length, even if the total quantity available remains constant. Finally, we shall study the diffused radiation which comes to us when the sun is hidden behind clouds and which also exists when the sky is clear.

Solar Constant

Although the atmosphere is in a continuously variable state, the solar radiation which reaches it appears to be very constant. The sun is an incandescent gaseous mass whose temperature at the surface is of the order of 6,000° C.

For this mass to be in equilibrium and to continue to radiate as it does, it is necessary, according to the calculations of physicists, that a central source of energy should maintain its interior at a temperature of about 40 million degrees Centigrade. This source of energy, which is nowhere near exhaustion, can be derived only from the transmutation of elements, the less stable being transformed into more stable ones, as hydrogen into helium and then into heavier elements.

The surface tends to cool by radiation and the heat lost in this way is compensated by a supply of heat from the interior.

As almost the whole of the energy available to man—solar heat, coal, petroleum, waterfalls, products of the earth, etc.—has been created at the expense of solar energy, we can say that we live by the transmutation of elements which takes place at the centre of the sun. Our globe receives an infinitesimal part of the enormous energy thus liberated. The transmutations are not chimerical; physicists know how to produce them in the laboratory, but their methods are very different from those by which the alchemists hoped to make gold. Extremely powerful apparatus has to be built, and, until uranium was successfully disintegrated to make atomic bombs, it was possible to produce only minute quantities of matter which could not be weighed by the most delicate microbalances.

At the temperature existing at the centre of the sun such transmutations take place naturally and matter is in a state indescribable in ordinary language and inconceivable to our imagination. Physicists can, however, calculate partially what happens there.

It is very easy to find the quantity of energy liberated, for it finishes by escaping in the form of radiation, which only needs to be measured. We can deduce what it must have been when it left the sun by measuring it on the ground and studying the properties of the atmosphere through which it has passed. Research stations, such as that at Montezuma in Chile, have been set up specially for this purpose.

It has been found that a surface of 1 sq. cm., exposed perpendicularly to the rays of the sun outside the earth's atmosphere, receives a power of 0.135 watts, or 1.94 calories per minute. This power per square centimetre is called the solar constant.

Is the solar constant really a constant? There is certainly one cause of variation, namely, the distance of our globe from the sun. While the earth is describing in the course of a year its elliptical orbit round the sun situated at one of the foci of the ellipse, the distance changes. We are nearer to the sun at the winter solstice than at the summer solstice. The maximum variation is 3.4 per cent, and the illumination, which is proportional to the inverse of the square of the distance, consequently varies by 6.8 per cent. The solar constant is therefore a mean value.

Effect of Latitude

It may seem surprising that we are nearer to the sun in the winter than in the summer, but the resulting difference in illumination is small and does little to diminish the preponderant influence of the height of the sun; the more its rays are inclined, the greater is the area over which the same flux has to be distributed.

Thus, at Bordeaux, at the medium latitude of 45° , the sun at midday at the equinoxes is at an angle of 45° from the vertical; at the winter solstice it is at 69° and at the summer solstice at 21° . Consequently, and without taking into account the absorption of the atmosphere which increases the differences still more, the flux of solar radiation for a given horizontal illuminated area is half as great in December, and 1.3 times greater in June, than it is in September and March. There is, therefore, at the confines of the atmosphere at this latitude, 2.6 times more solar radiation in summer than in winter over the same area, so that we can see that the 6.8 per cent which depends on the distance of the earth from the sun is trifling.

At higher latitudes the difference between summer and

winter is accentuated. At 60° N. (Stockholm, Leningrad) the sun's rays are inclined from the vertical at an angle between 84° and 36° , according to the season, and the ratio of the fluxes received is nearly 1 to 50. Within the polar circles, the flux received at the winter solstice is nil. On the other hand, in the equatorial regions, the differences between the seasons are scarcely perceptible.

It is interesting to note that the maximum illumination at the confines of the atmosphere in summer at the latitude of Bordeaux represents more than nine-tenths of the illumination at the equator. At the latitude of Stockholm it reaches nearly six-tenths and if, in addition, we remember that the days are much longer we can understand why some crops can be grown so successfully and in such a short time at high latitudes in countries which are reputed to be cold.

Atmospheric Absorption

We have discussed the nature and intensity of the solar radiation which reaches the upper atmosphere. In eight minutes it has travelled 93,750,000 miles through interplanetary space without undergoing any modification other than its flux density being diminished as the inverse of the square of the distance.

But during its passage through a few miles of gas of the terrestrial atmosphere it is weakened—sometimes considerably—and its composition is changed because the radiations of different wave-lengths are differently affected.

The degree of this weakening depends on the state of the atmosphere and on the thickness of air traversed, i.e., on the height of the sun. This explains why our eyes can bear the light of the setting sun and why it is red in colour.

The thickness of air traversed is expressed by what is called the "air mass" (abbreviated symbol m); when the sun is at the zenith, by convention $m=1$.

When the rays of the sun make with the vertical an angle called the zenith distance, they pass through a larger air mass. This mass is doubled for a zenith distance of 60° , that is,

when the sun is at 30° above the horizon. The following table gives the relation between m and the zenith distance.

Zenith distances in degrees	Air mass m
0	1
10	1.01
20	1.06
30	1.15
40	1.30
50	1.55
60	2.0
70	2.9
80	5.6
85	10.3
88	19.5
90 (horizon)	30 (approximately)

There are three reasons why solar radiation is weakened by its passage through the atmosphere.

1. Molecular diffusion, which removes from the direct radiation a part varying with the wave-length and which disperses it in all directions. As this effect varies inversely as the 4th power of the wave-length, it is particularly perceptible, as far as the rays of the visible spectrum are concerned, in the blue; it is this diffused blue radiation which gives its colour to the sky. All the gases in the atmosphere contribute to the diffusion.

2. Absorption, properly speaking, by gases, principally by ozone and water vapour; the energy thus absorbed is transformed into heat. Each gas selectively absorbs well-defined spectral bands which characterize it. As water vapour exists in very variable proportions in the atmosphere, its absorption is also variable.

3. Weakening, particularly by diffusion, due to particles of all sorts—dust, smoke and droplets—in suspension in the air; this is also very variable and is often very important in certain regions.

Molecular Diffusion

Molecular diffusion disperses the direct radiation of the sun just as a turbulent medium would do. We shall consider

this phenomenon as it occurs in pure, dry air, containing neither dust nor water vapour.

It is caused by the molecules of nitrogen and oxygen in the atmosphere. The weakening of the direct rays by diffusion can be calculated exactly; it is quite negligible for the infra-red but it increases rapidly as the radiations become shorter.

In their vertical passage through a pure and dry atmosphere, the red rays would lose one-tenth of their intensity, the blue rays of wave-length 0.45μ two-tenths, the ultra-violet rays of wave-length 0.3μ nearly seven-tenths.

If the thickness of air traversed is greater, the quantity transmitted becomes smaller. Thus, the blue radiation, which is reduced to 0.8 of its initial value after the vertical passage through the atmosphere or, in other words, through an air mass $m=1$, is further reduced in the same ratio if it has to traverse an equal thickness again, so that its intensity becomes $(0.8)^2=0.64$ for $m=2$; it falls to $(0.8)^3=0.512$ for $m=3$; and, in general, it becomes $(0.8)^m$ times its initial value.

When the sun is very low on the horizon, m assumes large values and the blue is almost completely diffused; since only radiations of long wave-length are transmitted, the sun appears red.

For the ultra-violet the diffusion is still greater; at a high altitude, the reduction of the thickness of air to be traversed enables the ultra-violet rays to be felt with more intensity. On the other hand, the sinking of the sun on the horizon and the consequent increase of the air mass m rapidly reduces the quantity of ultra-violet reaching the ground. If for $m=1$ the transmission is 0.3 , for $m=2$ it will be $(0.3)^2=0.09$, for $m=3$ it will be $(0.3)^3=0.027$, and so on.

Absorption by Gases

Molecular diffusion disperses the radiation but does not absorb it; only a part of the diffused light, which returns to the space beyond the atmosphere, is lost. The rest reaches the ground after diffusion; this is the blue light of the clear sky, light whose spectrum includes all the solar radiations although

the short wave-lengths are markedly predominant and produce its blue colour.

By contrast, we shall now discuss real absorption. Ozone and water vapour (by water vapour, we mean an invisible gas, and not droplets which forms clouds) are the two principal gases of the atmosphere capable of absorbing a large part of the solar radiation.

Ozone exists in a proportion which is nearly constant; the quantity of atmospheric ozone is evaluated by the thickness of the gas layer, this gas being assumed to be collected in a uniform pure layer at atmospheric pressure and at a temperature of 15° C. The thickness of ozone is of the order of 3 mm. (the thickness of the atmosphere expressed in the same way would be 10 km., i.e., 3 million times more).

Water vapour exists in a proportion which is very variable with place and time; its quantity is measured by the thickness of the layer of liquid water that would be produced by condensing all the vapour at the surface of the ground. In Paris, the average is 1.84 cm.

We have seen already that ozone stops completely all the solar ultra-violet radiation of a wave-length less than 2,900 Å. This is by far the most important characteristic of atmospheric absorption and will be discussed in the chapter concerned with the properties of the ultra-violet. All vegetation, if it were still able to survive, would be profoundly different from the vegetation that we know if this thin screen of ozone did not protect it from the fatal action of ultra-violet rays of short wave-length; our skin and eyes would also suffer grievously from it.

It is estimated that about 5 per cent of the solar energy is thus absorbed by ozone in the ultra-violet. This proportion is rather small because the sun radiates relatively little in that spectral region.

Ozone also absorbs 0.5 per cent of the visible radiation and 0.1 per cent of the infra-red.

The atmosphere contains a very variable proportion of water vapour which absorbs certain radiations situated in narrow bands of wave-length, especially in the infra-red.

In Paris, about 20 per cent of the solar energy is absorbed by water vapour, i.e., nearly as much as is affected by atmospheric diffusion. These figures relate to an air mass of 3.5, when the sun's rays arrive obliquely at an angle of $73\frac{1}{2}^{\circ}$ from the vertical and the thickness of precipitable water is 1.5 cm., which are average conditions.

But whereas diffusion particularly affects the radiations of short wave-length—blue, violet and ultra-violet—absorption by water vapour suppresses more especially the infra-red radiations.

Absorption by Particles in Suspension in the Air

Particles of all kinds, solid and liquid, are suspended in the air; without them, a cloudless sky would always be very blue. They act by diffusion, more than by true absorption, and as they diffuse almost equally the radiations of different colours they give the sky a whitish or greyish tint which is superposed on the blue caused by molecular diffusion.

The particles vary greatly in kind: there are microscopic droplets of water which seem to remain liquid even when the atmosphere is not saturated, dust of all sorts, smoke from towns, spores, pollen, volcanic ash, dust raised by the wind and carried sometimes over long distances, and small grains of salt from the evaporation of droplets of sea-water in coastal districts.

Their linear dimensions seem to be of the order of a few tenths of a micron and the viscosity of the air is sufficient to prevent them from falling more than the small particles in tobacco smoke.

We do not know how to calculate directly the energy lost by direct radiation through the diffusion caused by particles. But as we know how to calculate the loss due to the two other factors, atmospheric diffusion and absorption by gases, we can deduce this unknown quantity by the difference between the measured total absorption and that calculated. In winter at Saint-Maur, near Paris, this loss is nearly equivalent to that due to absorption by water vapour; in summer it is a little less.

In Paris, on an average, the three principal factors in the reduction of the direct radiation of the sun by the atmosphere are therefore of almost equal importance in their effect on the total energy.

After forest fires or fires affecting highly combustible material, or after volcanic eruptions, an abnormal reduction of the radiation, exceeding 20 per cent, has been observed to last for a long time.

On the other hand, in the pure atmosphere of the Jungfrauoch, particles absorb only 6 to 16 per cent.

Day Length

We shall see in connection with photoperiodism that to receive the same radiation, in the same quantity, but spread over a short or a long day, is not a matter of indifference to a plant. The lengths of the day and the night often have a considerable influence on the vegetative growth. Then again, growth and assimilation depend on the total quantity of light received, that is, not only on the intensity of this light, but also on the number of hours for which it lasts. It is therefore important to know the variation of the day length according to the latitude and the season.

Fig. I, 9. The earth at the summer solstice. The northern hemisphere has long days, the southern hemisphere short days

The day length, or the time which separates sunrise from sunset, is constant at the equator—it is always twelve hours.

At two seasons of the year, the equinoxes, the length of the day is also twelve hours over the whole surface of the globe. In all other cases, the days and the nights are unequal.

Our globe is constantly bathed in sunlight over one half of its surface, while the other half is in shadow; as a result of the diurnal rotation of the earth about its axis, each point on its surface, except those in the polar regions, passes successively in twenty-four hours through the light and dark spaces, thus creating the alternation of day and night at that point (Fig. I, 9).

The speed of rotation is uniform; the length of day and night at one point depends on what fraction of its circular path is illuminated. As a result, all the places situated on the same parallel—or, which is equivalent, at the same latitude—have days of the same length.

If the boundary of the shadow passed through the poles, which happens only at the equinoxes, it would divide all the parallels into two equal parts and the days would everywhere be equal to the nights. But the axis through the poles makes an angle with the plane of separation of the shadow and the light which varies in the course of the year and reaches its maximum value, $23\frac{1}{2}^{\circ}$, at the time of the solstices.

Let us consider the season of the summer solstice. The North Pole is in the illuminated hemisphere at $23\frac{1}{2}^{\circ}$ from the circle of separation. The day there is continuous; it is the same for all the parallels of latitude situated in the neighbourhood of the Pole, including the one which is separated from it by $23\frac{1}{2}^{\circ}$ and which is called the Arctic Circle. All the polar region within this circle performs its daily rotation without passing into the shadow so that there the sun does not set.

Round the South Pole, the region within the Antarctic Circle remains, on the contrary, constantly in shadow and there the sun does not rise.

Between these two polar circles, the lengths of day and night vary progressively and are equal at the equator.

It remains to be explained why the earth's axis makes a variable angle with the plane of separation of shadow and

light. This is a result of the revolution of our planet round the sun; the ellipse described during this revolution is in a plane to which the axis of rotation of the earth is not perpendicular but is inclined at an angle of $23\frac{1}{2}^{\circ}$ from the normal.

The movement of the earth has been compared to that of a top which spins rapidly on its point (this represents the diurnal rotation) while its point describes circles on the ground (this represents the annual revolution); the axis of the top is also inclined, but here the analogy ceases, for the axis of the earth remains always parallel to the same fixed direction, while that of the top describes a cone.

Because its axis retains this fixed direction in space, the earth turns its north pole towards the sun at the summer solstice; then, six months later, when it is at the opposite point of its orbit, it turns its south pole towards the sun. At the equinoxes, when it is half way between these two positions, the two poles are at equal distance from the sun and they are situated on the contour of the shadow.

This geometric description takes into account, not only the unequal length of the days, but also the different inclinations of the sun above the horizon at the different seasons, which, as we have already seen, cause variations in the solar illumination received on a horizontal surface.

The table below gives the length of the longest day and of the shortest day for different northern latitudes not included within the Arctic Circle.

Latitude North	Longest Day	Shortest Day
0°	12 h. 05 m.	12 h. 04 m.
10°	12 h. 40 m.	11 h. 30 m.
20°	13 h. 18 m.	10 h. 53 m.
30°	14 h. 2 m.	10 h. 10 m.
40°	14 h. 58 m.	9 h. 16 m.
45°	15 h. 33 m.	8 h. 42 m.
50°	16 h. 18 m.	8 h. 00 m.
55°	17 h. 17 m.	7 h. 05 m.
60°	18 h. 45 m.	5 h. 45 m.
65°	21 h. 43 m.	3 h. 22 m.
65° 59'	24 h. 00 m.	2 h. 30 m.
67° 07'		0 h. 00 m.

Inside the Arctic Circle the sun remains visible for several days in succession in the summer and is hidden for several days in succession in the winter.

The following table gives the length of this polar "day" and polar "night" for different latitudes:

Latitude North	Polar Day	Polar Night
70°	70 days	55 days
75°	107 "	93 "
80°	137 "	123 "
85°	163 "	150 "
90°	189 "	176 "

Energy Received per Day

Let us assume, for the sake of simplicity, that the atmosphere is perfectly transparent. The daily quantity of solar energy received on a given horizontal surface, for example, 1 sq. cm., depends both on the zenith height of the sun, which varies in the course of the day, and on the length of the day.

At the equator, the days are always twelve hours long and the daily energy received varies little in the course of the year. It is a little greater at the equinoxes, when the sun is at the zenith, than at the solstices, when the zenith distance at midday is $23\frac{1}{2}^{\circ}$.

At higher latitudes, the solar illumination is generally weaker, but the days are longer in summer and shorter in winter. As a result, the differences between summer and winter become more and more accentuated. In summer the greater length of the days compensates for the diminution of illumination and the total energy received in a day may be more than that received at the equator.

A striking fact is the large quantity of solar energy which reaches regions of high latitude in the summer; this explains the surprisingly rapid growth of northern vegetation, caused by a daily quantity of solar energy almost equal to that at the equator and spread over very long hours of daylight.

Diffused Solar Radiation

So far in this chapter we have been considering the direct radiation of the sun. But even a pure atmosphere diffuses this radiation and clouds diffuse it still more.

This diffused light sometimes constitutes almost the whole of the light available; thus Stockholm, in December, receives, on an average, 93 per cent of diffused light, against 7 per cent of direct sunlight.

In Paris, the fraction of the sky covered by clouds in the course of the year is greater than the fraction of blue sky, 58 per cent against 42 per cent. Thus, first, the duration of illumination by diffused light, and, second, the quantity of energy received from it, have an importance that should not be forgotten.

The general average, calculated over a year, of the energy received on the ground and coming from a blue sky, or from a cloudy sky in the form of diffused radiation, represents in Paris about 40 per cent and in Helsinki 44 per cent of the total radiation; the rest comes directly from the sun without diffusion.

CHAPTER III

PHOTOMETRY OF THE LEAF

THE fundamental role of light in the life of plants can often be seen by the arrangement of their leaves spread out horizontally as if to expose as much of their surface as possible. Sometimes there may be too much light so that beans under the blazing summer sun turn their leaves edgewise to offer the minimum surface to its rays and allow the light to pass to the ground almost without causing any shade. Even the internal structure of the leaf is adapted to the illumination that it receives.

Measurement of the Absorption, Reflection and Transmission Factors

Before studying the complex phenomena which occur in the plant under the influence of light—phenomena of which we still know very little considering the immense importance that we suspect them to have—there is a preliminary question which must be answered: How can we measure the fraction of light absorbed by the leaf, for only that fraction can have any effect? It is a physical problem which is not easy to solve completely, but we know the correct methods by which to approach it.

Unfortunately, many measurements have been made in ill-considered conditions and have given results which cannot be accepted without reserve. But we may take the opportunity, as this is a matter on which we can speak with some certainty, of explaining the physical relations between radiation and the plant, the latter being more particularly represented by its leaves since their surface is generally greater than its other parts.

What becomes of the light which strikes a material surface, such as a leaf? It is divided into three parts: the first is reflected, usually in a diffused way; the second is transmitted after having traversed the thickness of the leaf; the rest ceases to exist in the form of light, its energy being used and changed into another form (Fig. I, 10). Only this third part entering into the physical and chemical processes of the vegetable tissues is of interest to us, but we have no means of measuring it

Fig. I, 10. Interaction between light and leaf. Part of the light is transmitted or reflected; the difference between that part and the incident light gives the part absorbed by the leaf

except by finding the difference between the incident light on the one hand and the sum of the reflected and transmitted parts on the other.

That is why it is important to measure exactly the light which is reflected and transmitted by the leaves, whether their surface is left naturally uncovered or is coated with chemicals or powders modifying, intentionally or not, the proportion of light absorbed.

To calculate the fraction of light reflected we need to know: (1) the composition of the incident light; (2) the reflection factor for each of its monochromatic radiations.

The same facts are required for the calculation of the fraction of light transmitted or absorbed. The corresponding factors must be known for each wave-length and their measurement must be made in monochromatic light—in the ultra-violet, as well as in the visible and the infra-red. This is the first condition to be fulfilled.

In the second place, care must be taken to include in the measurement of the flux reflected (or transmitted) all the rays diffused in various directions so that the total is measured. If only a part is included, the proportion that it represents remains unknown, for that proportion is certainly variable with the wave-length and with the nature of the leaf studied.

It has been observed that the light transmitted and collected on the underside of the leaf is “completely diffused”. It is therefore possible in this case, without too gross an exaggeration, to compare the leaf to a “perfect diffuser”. This enables us to limit the measurement of the flux transmitted to a measurement of brilliance (or some other equivalent), but it will be only an approximation and we do not know *a priori* its value.

For reflection, such a comparison is generally impossible; the distribution of the light diffused by reflection is too variable with the nature of the surface of the leaves. This is obvious, for example, if we compare the surface of an ivy leaf, which is smooth and glossy and reflects rather like a mirror, to that of a hairy leaf, which is much more diffusive.

It is therefore necessary, in measuring the reflected flux, and preferable in measuring the transmitted flux, to be able to measure the total of each of these fluxes.

The following method is generally used for the measurement of the diffused fluxes. They are made to penetrate into an enclosed (or nearly enclosed) chamber the inside walls of which are white and diffusive and which is preferably of spherical shape. The illumination of the wall is then measured, in a region protected against the direct flux by a small white screen but receiving the diffused flux from the rest of the walls (Fig. I, 11).

This measured illumination is proportional to the flux entering into the enclosed chamber, whatever its distribution in direction may be, but the inner walls must be covered with a coat of paint, perfectly mat and diffusive, very white and having a high reflecting power.

Some laboratories are equipped with apparatus for making these measurements, adapted either to the visible or to the ultra-violet wave-lengths.

For the infra-red, the low sensitivity of the thermocouple,

Fig. I, 11. Diagram of a method of measuring the reflection factor of a leaf for monochromatic light and a certain angle of incidence

the receiver generally used, renders the problem almost insoluble.

We can see, therefore, that the problem of making photometric measurements on the leaf is clearly posed and that the most effective methods are known. On the other hand, the monochromator and the diffusive sphere are great wasters of light and the illuminations to be measured are so small that it is difficult to evaluate them correctly.

That is why results have sometimes been obtained for a few isolated wave-lengths that can be produced with sufficient intensity like those of the spectral lines of mercury; sometimes it has been decided to abandon the use of purely monochromatic light or to measure the diffused light with less

precision, or to adopt both courses at the same time. Let us now consider some of these approximate methods.

We may try to replace the monochromator by a filter of glass or coloured gelatine, or a vessel containing a coloured liquid. The spectral bands thus isolated are always rather large, with shaded edges, and infra-red transmission bands, often unsuspected, are particularly misleading (see, for example, the blue filter in Fig. I, 4). It is nearly always necessary to have several filters superposed.

Also, to avoid the very low light efficiency of the diffusing sphere, several experimenters have used spherical or elliptical polished mirrors, of very large aperture, which collect all the rays reflected by the sample placed near the centre, or at a focus, and send them to the conjugate point, which is the other focus in the case of the elliptical mirror.

The principle appears to be unassailable, but all receiving systems sensitive to light—cells or thermopiles—have a different sensitivity for differently inclined rays; in general, rays with an incidence too far from the perpendicular are much less effectual, so that the more the light is diffused, the less intense it appears with this method, which suffers also from other defects.

On the other hand, the apparatus thus receives much more energy, since the flux reflected by the sample is concentrated on the receiver instead of being dispersed over the whole surface of a diffusing sphere.

Possible errors are much reduced by comparing the leaf with a white diffuser of magnesia or magnesium carbonate.

It is, therefore, to avoid the difficulties of measuring very small quantities of light that the use of truly monochromatic light and of a diffusing sphere have been abandoned.

Even if a really practical solution were found to this purely technical problem, one would still have to remember that the reflection factor depends on the way in which the flux of incident light is presented. It may be projected in nearly parallel rays, and in this case the angle of incidence may vary from 0° to 90° . It may also be projected in a more

or less diffused fashion. In the first case, the light is like direct sunlight; in the second, it is like the diffuse light from a blue or cloudy sky, and we may remember in this connection that the sky is more often covered than clear.

In each case the measured reflection factor is different. Fortunately, the differences are not great, either for reflection or for transmission; according to the measurements made by Seybold, they have a maximum value of 2 per cent in the transmission factor.

Finally, everyone knows that different species of vegetation have differently coloured leaves and that a very young leaf differs from an adult leaf and from a withered autumn leaf. It is therefore necessary to work, not only with the correct methods but also on well-specified samples, so that even this question—undoubtedly the simplest that will be treated in this book—appears complex enough when it is examined in some detail.

Results

To show how little confidence can be placed in measurements made under conditions which are not absolutely correct, we may quote the results obtained by two experimenters using yellow light with the leaves of *Fraxinus excelsior*; one gives a transmission factor of 5 per cent, the other of 10 per cent; for *Tilia parviflora*, one gives 1 per cent, the other 17 per cent. This is an extreme case but is taken from the measurements generally considered as being the best.

It seems probable that the most serious errors were not due to the nature of the light, which was sufficiently monochromatic, but rather to a defective method of measuring the diffused light; even today, and in many fields of work, too many experimenters underestimate the dangers of an imperfect method in the study of diffusing surfaces.

In the visible region, as we might expect simply because the leaves are green by reflection and by transparency, the transmission and reflection factors are both maximum in the middle of the spectrum, in the green, at the wave-length of

5,500 Å; both decrease towards the edges of the spectrum, particularly towards the violet and the ultra-violet.

The opposite is true for the absorption factor, which is deduced from the preceding factors; it is greater at the ends of the visible spectrum than in the green region; it is particularly high on the side of the short wave-lengths, towards the blue and the violet (Fig. I, 12).

Amateur photographers who remember the time when the plates used were not orthochromatic and were particularly sensitive only to the short wave-lengths (blue and violet) know that foliage always appeared very dark on the proofs because of the small quantity of light reflected by the leaves in that spectral region.

On the contrary, photographs obtained with plates sensitive to the infra-red and with an infra-red filter before the object show very light foliage. This confirms the result of measurements made at the Institute of Optics by quite a different method. These show that the reflection factor, which is small in the red, increases rapidly towards the infra-red.

In this spectral region at the beginning of the infra-red, the pigments of the leaf, chlorophyll in particular, are transparent; nor has parenchyma any more marked selective absorption. The leaf therefore acts like a diffuser and its superficial layers disperse in all directions the light that they receive. About half is returned; that is the reflected part. The other half is diffused towards the interior of the leaf; part of this, depending on the thickness of the leaf, passes through it. Here the optical phenomena are the simplest.

The red and blue radiations that chlorophyll absorbs strongly are for the most part absorbed by the green chloroplasts. The radiations of shorter wave-lengths, violet and ultra-violet, are absorbed by yellow substances, such as carotene, xanthophyll, etc., which are extremely opaque to them.

The infra-red rays of longer wave-length are absorbed by water and it is certain that for radiations of wave-length

Fig. I, 12. Curves showing (diagrammatically) the composition of solar radiation and the proportion absorbed by a leaf in each spectral region. Compare Fig. I, 13, page 64.

longer than $2\ \mu$ the leaf becomes more and more "black" (Fig. I, 12).

Light-coloured leaves, deficient in chlorophyll, behave very differently from green leaves. The explanation given in the preceding paragraph would lead us to expect that the absence of chlorophyll will have the effect of extending, from the near infra-red to the green blue in the visible, the range of the high reflection factor, about 50 per cent, which is manifested when chlorophyll does not absorb. This is actually what takes place.

The transmission factor also remains rather high because the absorption in such leaves is low. But at the violet end of the spectrum as the yellow pigments come into operation and absorb the radiations of short wave-lengths the absorption becomes nearly as great as it is in green leaves, while the transmission and reflection are greatly diminished.

The properties of the leaf are modified by age. In the region of the visible radiations, where these properties are best known, the changes correspond to the enrichment in chlorophyll of the young leaf, during which time the reflection and transmission diminish, while the absorption increases. They are halted during the adult period when the concentration in chlorophyll is stationary. In the autumn, the destruction of the chlorophyll causes an increase in the reflection factor in the yellow and the red, while the yellow pigments, which are always present, maintain the strong blue-violet absorption.

These variations are slow, but there are also rapid variations which take place under the influence of the light itself; the chloroplasts are displaced and oriented according to the illumination so as to reduce the variations of the light absorbed. When it is weak, they arrange themselves in such a way as to lose as little of it as possible; on the other hand, when it is strong, they are prepared to absorb a much smaller proportion.

The leaves of *Tradescantia viridis* (and also *Pelargonium zonale*, *Adiantum cuneatum*, and *Coleus hybridus*) show this phenomenon particularly clearly. For a period of the order

of ten to forty minutes, in full sunlight, the average transmission factor can increase by 40 per cent; at the blue-violet end of the spectrum it can increase threefold. This seems to indicate that all the absorbing coloured pigments, and not only chlorophyll, are involved in the movements taking place inside the tissues of the leaf under the influence of light.

The starch produced by photosynthesis and accumulating in the tissues can also reduce the transmission factor.

All these variations, the diversity of species and the different structures of the same plant when raised in shade or in sunlight make it very difficult to estimate the average factors for reflection, transmission and absorption.

Thus Schanderl and Kaempfert studied the transmission factor of the epidermis detached from the upper face of various leaves. The differences between shade plants, growing in poor light, and desert or mountain plants, growing in intense light rich in ultra-violet, are enormous and show how the plants are adapted to the conditions of illumination. The transmission factor of the epidermis in the first case may reach 98 per cent, while the thick epidermis of the plants in the second category can transmit only 15 per cent to 20 per cent of the incident flux. Often the colouring matter and resinous material of the epidermis greatly reduce the part of the spectrum of short wave-length, thus protecting the internal fragile tissues against the injurious ultra-violet.

Utilization of the Light Absorbed

Some scientists estimate that an average of 80 per cent of the light is absorbed by the leaf, but if we take into account the solar infra-red it appears that this estimate is exaggerated and that only 70 per cent is really absorbed, the remaining 30 per cent being transmitted or reflected.

In any case, the greater part of the direct or diffused solar radiation received by the leaf is absorbed by it and transformed into energy of a different kind. What are these transformations and for what purpose is the absorbed energy

used? It is to these questions that we shall give an approximate answer.

Taking as a basis the estimates made some years ago by Brown and Escombe, who appear to have studied the question fairly thoroughly, we may assume that in the conditions of illumination generally prevailing in agriculture the 70 per cent of light absorbed is distributed in the following way:

Energy used for photosynthesis	.	.	.	.	1 per cent
Energy used for evaporation	.	.	.	.	49 „ „
Energy transformed into heat and re-emitted by radiation	.	.	.	.	20 „ „

Photosynthesis transforms the light into chemical energy, which is stored in the chemical products made by the plant with water and carbon dioxide as the principal raw materials. These products—wood, cellulose, starch, sugars, fats, etc.—are capable of restoring later the energy that they contain. This happens during their combustion, i.e., their destruction and oxidation, which re-creates the water and carbon dioxide from which they were originally formed. They constitute, therefore, a store of solar energy.

In particular experimental conditions it is possible, as we shall see in the chapter on photosynthesis, to transform a much greater proportion of the light into chemical energy. In agriculture, it is this hundredth part of the luminous energy which constitutes the value of the crop. If we succeed in doubling the proportion of light used by photosynthesis, we shall double the profit.

We can verify the amount of this proportion by comparing the weight of dry matter of the crops from one acre with the total solar energy received by the same area during the period of their growth. Let us assume that during the summer the average power supplied by the sun is 1,200 kW. per acre; 1 per cent, i.e., 12 kW., would be used for photosynthesis. This power corresponds to the synthesis of 0.8 grammes of carbohydrates per second; for a period of six months at eight hours a day, totalling five million seconds,

the production should therefore rise to 4 tons of carbohydrates. Now, one acre of lucerne can provide a crop of about 4·8 tons of dry matter. We can see therefore that the preceding calculation leads to a correct estimate of the proportion of the energy used for photosynthesis.

As regards the part of the incident energy used for the evaporation of water by the leaf, we can make a similar attempt to check it by calculating the total quantity of water thus evaporated per acre and comparing it with the annual rainfall. As we have indicated, about half of the power of solar radiation would be used for evaporation. Now, 600 kW. is equal to 140,000 calories per second and can vaporize 240 grammes of water per second. In five million seconds, 1,200 tons of water are thus evaporated. The annual rainfall in France averages 29·5 inches, corresponding to 3,000 tons of water per acre. In six months our crop of lucerne would therefore have taken nearly half for the needs of transpiration. The rest is evaporated directly from the soil or soaks away. There, again, our calculation leads to a reasonable conclusion which confirms the estimates on the utilization of radiation by plants.

Returning to the efficiency of photosynthesis, even if we assume, as we have done, that a hundredth part of the luminous energy received by the leaf is stored in the plant in the form of the chemical energy of the products of synthesis, we cannot conclude that one-hundredth of the energy received on a cultivated field will be effectively used. In fact, especially when the plants are young, a part of the light, passing between the leaves, strikes the ground directly. As the earth is more often bare in winter and vegetation is produced only during part of the year, the *overall efficiency*, that is to say, the fraction of the annual total solar energy which is effectively recovered in the crop, is much less than one-hundredth.

It must also be remembered that, in order to live, the plant uses part of the substances that it has created; their waste products in the form of carbon dioxide are given off in respiration.

Here are some examples of these overall efficiencies:

At the observatory of Saint-Maur, the luminous energy received per year from the sun is about 100,000 calories per sq. cm., energy theoretically sufficient to effect the synthesis of 25 grammes of carbohydrates. For one acre this quantity becomes 1,000 tons. This would be the dry weight of the crop if the efficiency were 100 per cent. Now, the annual production of dry wood from a forest of beech trees is 1.6 tons per acre; the overall efficiency is therefore 0.16 per cent.

A field of wheat makes better use of the light; its efficiency, calculated in the same way, is of the order of 0.3 per cent.

CHAPTER IV

THE ROLE OF INFRA-RED RADIATION

INFRA-RED light comprises all the radiations of wave-length greater than $8,000 \text{ \AA}$ and these are invisible. Here we are considering only the near infra-red, i.e., of wave-lengths between $8,000$ and $20,000$ or $30,000 \text{ \AA}$. A little more than half of the solar radiation is in this region, most of the remainder being in the visible range.

Incandescent lamps, which are the most common artificial light sources, radiate about nine-tenths of their power as infra-red radiation.

It is therefore important to know the particular action of these radiations, both for plants grown in natural daylight and for those—which are bound to increase in number—cultivated wholly or partially in artificial light.

Properties of the Infra-red

In comparison with visible light, infra-red is characterized by a smaller quantity of energy in each of the quanta, or grains of energy of which it consists. In fact, each quantum carries an amount of energy $h\nu$, proportional to the frequency ν , which is the number of wave-lengths contained in $300,000 \text{ km}$. Compared with a quantum of green light of wave-length $5,000 \text{ \AA}$, a quantum of infra-red light contains half the energy at double the wave-length, i.e., $10,000 \text{ \AA}$, one-third at $15,000 \text{ \AA}$, and so on. The chemical activity of the infra-red is therefore much less.

In the language of chemistry, the absorption of a photon of wave-length $5,000 \text{ \AA}$ by a molecule corresponds to a "heat of activation" of $56,900$ calories. At the wave-length $15,000 \text{ \AA}$, this heat would be reduced to one-third, i.e., $18,966$ calories.

In practice, the chemical activity of infra-red radiation is not strong enough to disturb chemical structures; it causes oscillations of the atoms round their positions of equilibrium without destroying the molecules. These oscillations are solely heat manifestations and we may expect that the special action of infra-red will be to heat up the bodies that absorb it.

On the contrary, although, by the same process, the visible and the ultra-violet also have a heating effect on the substances that absorb them, these radiations can, in certain cases, particularly the ultra-violet, transmit to the molecules enough energy of excitation to make chemical reactions possible.

We shall see to what extent experiments on the action of infra-red confirm this estimate concerning the whole of the chemical phenomena in the life of plants.

Absorption by the Leaves

Since only the absorbed radiation can have any action, it would be interesting to know the absorption factor of leaves for the various infra-red radiations. Unfortunately, scarcely any measurements have been made on this subject. The fraction absorbed is determined by the difference between the incident energy on the one hand, and the energy not absorbed, that is, reflected or transmitted, on the other.

The reason for this lack of data is undoubtedly the difficulty of measuring the radiation diffused and dispersed by the leaf. The only instrument that can be used in all the infra-red is the thermopile, which, not being very sensitive, is inadequate to measure the small quantity of illumination that it receives in diffused light, while the incident energy cannot be increased to excess without drying up the leaf that is being studied. Measurements are therefore difficult, but nevertheless it is possible to make them with suitable methods.

In 1913, Coblentz attempted to measure the reflection factor up to 30,000 Å. He found that the values were rather small; the highest related to the leaves of red oak. The reflection factor would be 18 per cent at 8,000 Å, at the red

limit of the visible, and would gradually diminish in the infra-red, to 8 per cent at 30,000 Å. Unfortunately, this result, at least for the near infra-red accessible to special photographic plates, is contradicted by photographs of trees taken in infra-red light, where the leaves appear as if they were white.

For the single wave-length of 11,000 Å, one investigator measured, certainly with a more correct method, the reflection factor of a vine leaf and of a potato leaf; it is about 45 per cent. This high value confirms the indications given by the photographs.

It is therefore extremely probable that, at least in this region of wave-length, leaves reflect about half the infra-red that they receive.

It is precisely in this region that the sun sends most radiating power and the more extreme radiations are less important.

We can expect, as Coblentz indicated, that the reflection will become less and less intense towards the long wave-lengths, for this diffuse reflection is caused by the thickness of the leaf, and beyond 14,000 Å the large quantity of water contained in the vegetable tissues absorbs strongly.

We shall therefore assume, until more precise measurements have been made, that the reflection factor is 45 per cent at the beginning of the infra-red and lower than this in the more extreme range.

As regards the transmission factors, all the data that we have relate to some measurements made by John M. Arthur by a very simplified method, but he assumed that the reflection factor was 20 per cent, which is certainly too low.

The only result to be retained is that the transmission factor is notably higher in the infra-red than in the visible. We can estimate that it is of the order of 20 per cent to 25 per cent.

To sum up, in the near infra-red, which is the most important region, half the incident radiation is reflected, a

quarter is transmitted, and therefore only a quarter is absorbed by the leaf.

Although this conclusion cannot be final, it seems certain that the proportion of infra-red energy absorbed by leaves is lower than it was at one time supposed, being relatively small—smaller than the proportion of absorbed visible radiation.

In the more extreme infra-red, i.e., at wave-lengths greater than $14,000 \text{ \AA}$, it is probable that all leaves become very opaque, reflecting very little, and absorbing the greater part of the radiant energy.

It is necessary then to distinguish two principal zones in the infra-red: the first, of wave-lengths shorter than $14,000 \text{ \AA}$, which represents the major part of the solar infra-red and is relatively little absorbed by the leaf; the second, of wave-lengths greater than $14,000 \text{ \AA}$, relatively less abundant in solar radiation but, proportionately to the visible, very abundant in the radiation from incandescent lamps. This second zone is strongly absorbed by leaves.

As a result, when plants are cultivated under incandescent lamps, the action of the infra-red is inordinately increased for two reasons: first, because the incandescent lamp supplies, for the same power in the visible, much more infra-red than the sun; secondly, because this infra-red is situated particularly in the region where it is most strongly absorbed by the water vapour in the leaf (see Fig. I, 13).

Effect on Transpiration

What becomes of the absorbed energy? Before answering this question, it is interesting to note a fairly recent industrial application of incandescent lamps. Special lamps, which are very little different from lighting lamps, except that the filament is run at a slightly lower temperature so that they radiate particularly in the near infra-red, principally between 1μ and 2μ , are sold for drying purposes. In fact, experience shows that the substances exposed to this radiation become heated and lose moisture, if they contain any, as they would

Fig. I, 13. Curves showing (diagrammatically) the composition of radiation from an incandescent lamp and the proportion absorbed by a leaf in each spectral region. Note the excessive absorption of infra-red and the small absorption of blue-violet. Compare Fig. I, 12, page 54-

do in an oven. But drying in an oven, for the same maximum temperature attained, takes five to ten times longer, because the heat has to be transmitted from the surface towards the interior, while the infra-red radiation more or less penetrates before being absorbed and produces heat at a depth.

It is possible also that evaporation is favoured by the fact that the molecules of water are themselves capable of absorbing the infra-red energy.

The leaf submitted to infra-red radiation finds itself in exactly the same conditions as the substances exposed to the drying lamps, and one of the results must certainly be an evaporation of water or a transpiration in proportion to the illumination received or, more exactly, absorbed. We must not forget, however, that visible radiation can also have the same effect.

The precise experiments made by Arthur and Stewart at the Boyce Thompson Institute for Plant Research in New York showed that this is the case.

Potted tobacco plants were used for the tests; the pot was watertight and covered with an impermeable paraffin paste so that the measured loss of water was entirely due to the leaves and stems.

For example, under the infra-red light of incandescent lamps fitted with filters opaque to the visible and giving a power of 0.65 cal./sq. cm./minute (compare this with the maximum power of sunlight on the ground, which is about 1.8 cal./sq. cm./m.), the loss of water was 0.34 grammes per sq. cm. in twelve hours. The heat necessary to evaporate this quantity of water is $585 \times 0.34 = 200$ cal., so that in one minute the evaporation uses 0.28 cal./sq. cm., i.e., 43 per cent of the incident energy.

It would be of great interest to know what this energy represents in relation, not to the incident energy, but to the absorbed energy. From experiments made with infra-red light from incandescent lamps, we know that there is a considerable absorption of these radiations and that most of the absorbed energy serves to stimulate transpiration.

Arthur and Stewart also found that the transpiration was still more intense when the same incident energy comprised not only infra-red but also visible radiation.

The heat used in vaporization therefore accounts for nearly half of the incident energy. This increase may be due to a stronger absorption of the visible than of the infra-red. It should probably be related to another phenomenon: the opening of the stomata which facilitates the interchange of gases between the tissues of the plant and the atmosphere. The stomata open in visible rays, but they remain closed when the incident radiation comprises only infra-red. It is rather surprising that the opening of the stomata increases the transpiration by only 14 per cent.

In open-air cultivation in natural daylight, when the visible always accompanies the infra-red, the opening of the stomata coincides with the arrival of the whole range of radiation and the beginning of the phenomenon of transpiration. It has, in fact, long been known that transpiration in natural conditions is very small at night; it occurs, and passes through a maximum, during the day.

We may conclude that the preponderant action of infra-red radiation (and the same could be said of the visible) is to provide heat inside the leaf and thus to stimulate the evaporation of water.

Is this transpiration beneficial? What is its use and in what circumstances can it be harmful? The quantity of water lost by plants in transpiration is very large; an annual plant evaporates several hundreds of times its weight in water.

This current of liquid is indispensable to good growth. Thick-leaved desert plants, offering a small surface to radiation and adapted to a severe economy of water, show only very poor growth, undoubtedly because photosynthesis is checked through the lack of absorbed energy, and perhaps also because they cannot pump water from the soil in sufficient quantity.

The simple physical fact that a small, but not negligible, quantity of elements such as calcium, potassium, sulphur, etc.,

are found in plants shows the importance of intense evaporation.

Here, for example, is the composition of a crop of lucerne from one acre, its total dry weight being 4·8 tons.

	<i>lb.</i>		<i>lb.</i>
Carbon	4981·68	Sodium	17·6
Oxygen	4541·68	Silicon	6·16
Hydrogen	608·96	Boron	4·4
Nitrogen	358·16	Iron	1·76
Calcium	246·4	Silver	1·76
Potassium	94·16	Manganese	0·176
Sulphur	45·64	Caesium	0·176
Magnesium	33·44	Copper	0·176
Chlorine	29·92	Titanium	0·0616
Phosphorus	29·92		

All these elements, except those which are present in the atmosphere, are derived from the soil and conveyed in the water sucked up by the plant. Some are in the form of almost insoluble combinations and can accumulate in the plant only when a sufficient quantity of water, drawn from the soil with traces of dissolved salts, has passed through it and evaporated, leaving the elements behind. There is no doubt that they are beneficial, as numerous investigations have proved.

Taking again the example of one acre of lucerne, it can be calculated that transpiration displaces 1,920 tons of water. Calcium, which is the metal found in the largest quantity in the plant, must be contained in this water at a concentration

246·4 0·6

higher than ————, i.e. ———— (approx.).

4,300,800 10,000

The proportion of these elements contained in the soil varies with its composition and the roots are capable of filtering to some extent those which may be too abundant and preventing excessive quantities from penetrating into the plant. But obviously it cannot receive more than is contained in the water evaporated, so that if their presence is necessary

in the proportions indicated, which seems certain in many cases, then the evaporation of a large quantity of water is vitally important.

The abundance of infra-red radiation normally provokes intense transpiration, but what happens when the quantity of water available to the plant is insufficient, or when the air surrounding the leaves is so charged with moisture that evaporation is checked?

The leaves then become damaged and the plant withers; experiments have given this result in conditions of high temperature, strong infra-red illumination and very moist air existing simultaneously.

Gathered fruit and melons deprived of their leaves as a result of disease, and therefore incapable of evaporating water, suffer from scorching under the action of intense radiation.

These effects have been observed, but it is not known whether intense visible radiation deprived of infra-red would not be capable of causing the same disorders, since, in ordinary natural conditions, the visible and the infra-red always come together.

CHAPTER V

THE ROLE OF ULTRA-VIOLET RADIATION

Ultra-violet

IF we asked a physicist the properties of ultra-violet rays, he would reply that, since their quantum of energy is greater than that of the visible and the infra-red rays, the absorption of ultra-violet will more easily disturb the delicate chemical structures of plants by provoking various "activations". We must therefore expect intense chemical action to be stimulated by the ultra-violet part of solar radiation, which is of vital importance to man on account of its anti-rachitic potency.

Now, this ultra-violet part is not very abundant and, in our present state of knowledge, it seems that plants have rather disdained the small proportion of solar ultra-violet, since no really important action which could be attributed to it has been completely proved; they have adapted themselves so that they are capable of using the visible rays, which are reputed to be less chemically active but which are incomparably more abundant in sunlight.

The action of ultra-violet on plants becomes important only if radiations of very short wave-length are produced artificially—radiations which, owing to atmospheric absorption, are absent from the solar spectrum and have wave-lengths lower than its limit of 2,890 Å. They have a clearly injurious effect.

But on the near side of this harmful region, it does not seem that any chemical action caused by radiations situated between it and the visible has been observed with certainty. Perhaps suitable methods of observation have not been found. In any case, it is unlikely that any very important effect will be discovered in the future, since plants can be cultivated for

several generations under glass screens which are an insuperable obstacle to ultra-violet.

Absorption by the Epidermis

The insensibility of plants to this ultra-violet spectral region of wave-lengths longer than 2,890 Å may have a very simple explanation. We know that a radiation is active only to the extent that it can be absorbed; a body which reflects it, or is transparent to it, cannot suffer any effect from it. How do the vegetable tissues behave, from this point of view, in the presence of ultra-violet? As the photographic plate provides a sensitive and easily used means of detecting it, many investigations have been made on the subject.

But although the presence of these rays can be revealed by photography, quantitative measurements require an extremely precise technique. Consequently, the various experimenters have been able to give only qualitative information, but they all agree in stressing the opacity of the epidermis and of the cell walls. The observations are made with a special microscope for ultra-violet.

As a result, it appears that the ultra-violet cannot penetrate to the interior of the plant, like the visible and the near infra-red, which are even capable of traversing the entire thickness of a leaf. Obviously, therefore, it is less important and its action, if it has any, is confined to the most superficial and directly exposed cells.

It would be interesting to know whether this ultra-violet, which is not transmitted, is reflected or absorbed. The appearance of photographs of vegetation taken in ultra-violet radiation lead one to believe that the reflection factor is small. This observation confirms the intuitive impression of the physicist accustomed to encounter infinitely more substances capable of absorbing ultra-violet than of reflecting it. In conclusion, and in the absence of direct investigation and clear results, we may say that in all probability the greater part of the ultra-violet radiation which strikes the surfaces of plants is absorbed by the superficial layers, that the reflected

part is rather small and that none, or very little, can penetrate inside the thickness of the tissues.

The immediate action of ultra-violet cannot be other than principally superficial, but it is possible that profound repercussions are ultimately manifested.

The effects observed differ widely according to whether the wave-length is longer than 2,890 Å, or shorter. This is precisely the limit of the solar spectrum; the solar radiation received at ground level does not contain wave-lengths shorter than 2,890 Å.

The Near Ultra-violet

We shall call the spectral region between 2,890 Å and 4,000 Å the near ultra-violet and all the radiations of wave-length shorter than 2,890 Å the extreme ultra-violet.

Experiments bearing on this question have been made, both with sunlight and with sources of artificial light.

In the first case, the vegetation directly exposed to the sun is compared with that protected by glass screens; the screens used are made of special glass, chosen for its transparency or the degree to which it is opaque to wave-lengths in the ultra-violet. Obviously only the possible influence of the near ultra-violet can be shown in experiments of this kind, since the extreme ultra-violet is not present in the solar radiation, which has already been filtered by the atmospheric ozone.

We shall describe some of the observations that have been made with this method, but the results obtained cannot be accepted without a good deal of reserve. Most of the experimenters omitted to examine the properties of their screens in the infra-red. The conditions of ultra-violet irradiation were considerably affected, in the way that one would expect them to be, by the different screens, but other conditions, such as infra-red irradiation, and even visible irradiation and temperature, varied at the same time. These last factors are extremely active and greatly modify the manner and rate of growth. To prove that an observed effect is attributable to the action

of ultra-violet, it would therefore be necessary to check by very precise and complete measurements the nature of the conditions other than the ultra-violet irradiation, both for the controls and for the subjects of the experiments.

Here, however, are some of the results obtained from different experiments. Ultra-violet tends to make plants dwarf and hairy with small thick leaves and brightly coloured flowers. A natural example of this is furnished by alpine vegetation at high altitudes; there, the ultra-violet is more abundant than it is at sea level, since molecular diffusion, which disperses principally the short wave-lengths, has not yet diminished its proportion.

It may be remarked that light of all wave-lengths is also more intense at high altitudes and that very intense light tends to produce small plants.

Very many experiments, intended to provide practical information for the cultivation of vegetables or flowers, have been carried out in glasshouses in which ordinary glass has been replaced by special glass. The results obtained are contradictory; sometimes the crops are more abundant, sometimes less, than in ordinary conditions. Chemical analysis shows, in general, a higher percentage of lipide in plants cultivated under glass which is more transparent to ultra-violet. This is undoubtedly the clearest result, but it does not appear to be established that ultra-violet is the only cause of it.

On the other hand, a very marked effect is observed in plants which are deprived of visible violet, and particularly blue, radiations, i.e., those which are nearest to the ultra-violet but which still appear to our eyes to be coloured. The plants are clearly abnormal. The absence of the violet and blue rays gives rise to etiolation and the growth, measured by the weight of dry matter, is reduced. But this action is related to visible and not to ultra-violet radiations.

In experiments with artificial light, arcs between iron or carbon electrodes are used as the source, or more often mercury arcs in a quartz envelope; the latter are ordinarily manufactured for numerous photographic, chemical and

medical applications. They are particularly convenient, being as easy to use as incandescent lamps. Their radiation includes both the near ultra-violet found in sunlight and the extreme ultra-violet. By interposing suitable filters, it is possible to isolate any region of ultra-violet and submit the plants to investigation.

These artificial sources have enabled the region of the near ultra-violet, between the wave-lengths 2,900 Å and 3,130 Å, which are present in sunlight with only a very small quantity of energy, to be studied with stronger illumination. The experiments of Withrow and Benedict (1931) were carried out in well-defined radiation, but unfortunately on too small a number of plants (coleus and tomato) and they have not been repeated. Since these radiations are vitally important for animal life, we may reasonably wonder whether they are just as important for the vegetable kingdom.

The conclusion reached by the investigators, which they themselves give as only provisional, is that there are some indications that wave-lengths between 2,900 Å and 3,100 Å have a favourable effect on vegetation; the plants are taller, the stems are thicker, the leaves larger and more numerous, and the weight, in the fresh state and after desiccation, is heavier.

A very small proportion of ultra-violet of shorter wave-length neutralizes the beneficial effect observed; we shall see later that this extreme ultra-violet is, in fact, very injurious.

The general illumination in these experiments was so small that the conditions of normal vegetation were not assured, so that the slightest difference between the illumination in visible light was capable of reacting intensely on the activity of growth. In fact, the individual differences between plants cultivated under the same conditions were too great for the results to be clear.

We must therefore conclude that the near ultra-violet has no perceptible action on vegetation. Numerous experiments, both in sunlight and in artificial light, give only contradictory or rather unconvincing results. Some of them, conducted

with the greatest care and in well-controlled conditions, as they were at the Boyce Thompson Institute in New York, showed no observable difference between cultivations under ordinary glass and under glass specially transparent to ultra-violet. Lamprecht, in Sweden, drew the same conclusion from his practical experiments.

There is therefore no reason to recommend other than ordinary glass for the construction of glasshouses, since the much more expensive special glass transparent to ultra-violet would not have any indisputable advantage.

The Extreme Ultra-violet

If we pass on to consider the influence of the extreme ultra-violet of wave-lengths shorter than 2,890 Å, we find unanimous agreement among all the experimenters. Extreme ultra-violet causes severe damage, especially to the superficial parts—a fact that has been known for a long time. The outer layers of cells become discoloured and die; the depth to which they are affected depends on the nature of the radiation and on the quantity received. Different tissues are sensitive in different degrees to this action.

Since radiations of wave-length very little shorter than the limit of the solar spectrum begin to be dangerous, we see the importance of the thin layer of atmospheric ozone which suppresses by absorption all the solar radiations on the far side of this limit of 2,890 Å. The shorter the wave-length of the radiations used, the more intense is their destructive action.

A prolonged action may kill the whole plant. Otherwise, the plant recovers after a length of time depending on the seriousness of the injuries.

A daily exposure of ten minutes to radiation from a mercury arc is sufficient to cause the death of young plants. Subjects raised under a subdued light are all the more sensitive, which shows that light makes the epidermis of the leaves more robust and more opaque to ultra-violet.

When the first layers of cells are dead as a result of these destructive radiations, they form a screen which protects the

lower layers. But as the plant grows, this protective envelope is torn away and the radiation can penetrate more deeply.

Even inside the leaf, the growth of the cells appears to be slowed down; there are fewer small cavities and differentiation is checked.

Anthocyanins, the colouring matter found for example in begonia leaves, resist the action of ultra-violet, but nevertheless they disappear in the living leaves submitted to this radiation.

Finally, it is worth noting that no beneficial effect of these radiations has ever been proved.

Fluorescence

Ultra-violet light is more apt than any other to make certain substances fluorescent. Fluorescence is the phenomenon by which absorbed radiant energy is in part immediately re-emitted in the form of light; the most striking case is that in which the light is visible, for the fluorescent substance, lit by invisible radiation, seems to be independently luminous and sometimes shows a brilliantly coloured light.

Many instances of fluorescence have been observed in the vegetable world. Green leaves and some kinds of flowers show intense fluorescence under the action of radiations between 3,400 Å and 3,800 Å. Radiations from 3,000 Å to 4,000 Å are capable of producing fluorescence in certain seeds during their germination, and it has sometimes even been possible to distinguish breeds or varieties by the differences in the light emitted.

These phenomena are very striking to observe, but their scientific interpretation is too complex to enable us to draw practical conclusions from them. We know, however, that the fluorescence of a substance is proof that it has absorbed ultra-violet and is momentarily in an excited state; it returns to its normal state by emitting its energy of excitation in the form of light.

The addition of another substance may extinguish the fluorescence; this proves that the energy of excitation has

been transferred to the other substance instead of being used for the emission of light. It is therefore possible in a few exceptional cases to follow part of the mysterious destiny of the energy of the radiation absorbed by a plant.

It is obvious that fluorescence cannot be observed under the action of sunlight, for the emission of light that results from it is extremely small and can be seen only in complete darkness; it is necessary to work with an artificial source, a mercury arc, for example, and filters opaque to the visible and transparent to ultra-violet, or with a monochromator.

To summarize this chapter briefly, we may say that ultra-violet radiations, according to their wave-length, are either harmful or inactive. In the first case the wave-lengths are shorter than $2,890 \text{ \AA}$; in the second they are longer and therefore nearer to the visible. The first are absent from solar radiation, which is therefore not harmful; the second are present with a power rapidly increasing as a function of the wave-length, but at the same time the entire solar ultra-violet represents only 1.3 per cent of the total radiation.

The chemical activity of ultra-violet is well known. We should expect to see it used by nature for many syntheses of vegetable life. We see, on the contrary, that plants cover themselves with cells more or less opaque to these radiations as if to protect themselves from them. Their activity would undoubtedly be too intense and dangerous for the complex substances of the cells.

Plants are adapted, on the other hand, as we shall see in the following chapters, to make use of less active radiations, situated in the visible spectrum and abundantly provided by the sun.

CHAPTER VI

THE ROLE OF VISIBLE LIGHT

The Particular Importance of the Visible

IT is in the region of the visible radiations that light has the most important effects on plants, the chief being the stimulation of photosynthesis. By this process the energy of the light is "eaten" by the plant to promote its own growth and to maintain its life and that of every living thing. Light also has many other effects on growth, flowering, tuberization, hibernation and the opening of the stomata.

All these phenomena, which are certainly not due to light alone although it is often of fundamental importance, undoubtedly begin by a photochemical reaction, i.e., a chemical modification caused by light.

The most interesting characteristic of the effects of visible radiations is therefore linked with their power of chemical activation. We know that this activation, which is an excitation of the chemical molecule capable of absorbing light, is a contribution of energy in quantities equal to the energy quantum $h\nu$, which is proportional to the frequency of the luminous vibration.

This quantum, or photon, transports an increasing amount of energy as we go from the infra-red towards the ultra-violet, passing through the visible. In the infra-red, the quanta are individually weak but numerous; they make the molecules vibrate without chemically activating them, heat them up and provoke the evaporation of water. In the visible, the heating up and the evaporation are produced in the same way, but in addition the quanta are now capable of chemical actions, which become extremely important; the visible radiations are unique in being absolutely indispensable to

plant life. In the near ultra-violet, we should expect an increase in the chemical activity of photons of more and more concentrated energy, but the plant seems to defend itself from this action by confronting them with an opaque epidermis. In the more extreme ultra-violet, the chemical activity becomes so great that the photons destroy the molecules of the epidermal cells and cause injury to the plant.

If we compare these actions, and their character, which may be beneficial to a greater or less extent to the health of the plant, with the composition of sunlight in the corresponding spectral regions, we cannot but admire the perfect adaptation of the plant to the radiation which is offered to it. The essential visible is the most abundant in solar radiation, which has its maximum energy in that region; the infra-red, which ensures transpiration, the circulation of water and the provision of indispensable mineral salts, is also quite abundant; the near ultra-violet, whose use is doubtful, is present in a proportion of about only 1 per cent; the extreme ultra-violet, which is mortally injurious, is eliminated exactly at the limit imposed by the atmospheric ozone. And this limit is such that it still permits the passage of certain radiations of the near ultra-violet which, if they are perhaps useless to the plant, are vitally necessary for men and animals.

The part played by visible light, of wave-lengths between 4,000 Å and 7,500 Å, is certainly more complex than that of all the other radiations. It has also been the most studied, if only because the visible quality of this light makes it more interesting and easier to use for experiment.

Three phenomena, in which light plays a particularly active part, are so important that special chapters have been devoted to them. They are:

1. *Photosynthesis*, or assimilation through chlorophyll. Chlorophyll, the substance in plants which gives them their green colour, has the property of absorbing light and transforming the radiant energy thus captured into chemical energy. This energy is used to reduce carbon dioxide and water, liberating a part of the oxygen and making the carbon

enter into organic compounds which constitute, with water, almost the whole of vegetable matter. By what mechanism are these syntheses accomplished? Many investigations have been made to try to find the answer to this question and some of them will be described in the three following chapters.

2. *Phototropism*, or the action of light on the form of growth. Plants, in general, grow towards the light. Recent research on this phenomenon has shown that the curvature of a stem towards the light is due to unequal elongation of the parts that receive more or less illumination. It has led to the discovery of substances called hormones, or auxins, which influence growth and which are dependent on illumination.

3. *Photoperiodism*, or the effect of the daily period of illumination. A plant needs a certain quantity of light each day, but the way in which it receives that light is extremely important. The effect of intense illumination for a short time is quite different from that produced by weaker but more prolonged illumination. The artificial lengthening of the day by means of even very low-powered lamps, the action of which must be negligible from the point of view of energy, can profoundly modify the development of the plant, for example, by stimulating flowering or by preventing it.

Many phenomena of this kind have been discovered and studied only comparatively recently, but they are very important when we come to consider the adaptation of different species of plants to a particular latitude and climate. Besides these three main questions, there are numerous other actions known to be due to the visible part of light, and these have been grouped together in the present chapter. The small amount of space devoted to them does not necessarily imply that they are of secondary importance, but often simply that they have not yet been completely investigated.

It is quite possible that in the future, among the phenomena that we shall now describe in a few lines, a discovery of a process of luminous action of great theoretical interest will

reveal a hitherto unsuspected secret of the mysteries of plant life. The more science advances, the better we shall be able in agriculture to use our knowledge to increase production and improve quality.

Opening of the Stomata and Transpiration

Transpiration is stimulated by visible radiation, as it is by infra-red, but while in infra-red alone the stomata of the leaves remain closed and evaporation must thus take place through the epidermis, visible radiations, blue in particular, have the effect of opening the stomata. As a result, it appears that transpiration is still further stimulated.

A very thorough study of the opening of the stomata was made by Sierp in 1933. He had no difficulty in confirming the already known fact that under infra-red light the stomata remained closed. Working on the leaves of *Helianthus annuus*, grown in a pot, and without detaching them from the plant, he examined their lower surface under the microscope. A few stomata were chosen and their area was measured. The same stomata were observed throughout the experiments. This was necessary because different stomata behave differently, even on the same leaf.

The variation of the area, with time, was measured while the plant was being submitted to a given illumination, supplied by the filtered radiation from an incandescent lamp. A vessel containing a 6 per cent solution of copper sulphate, 1 cm. thick, served as a screen opaque to the infra-red; then coloured glasses allowing only spectral bands to pass were used; these bands were rather wide, but they presented a maximum of energy in the blue, the green, the yellow, the orange or the red. With the blue filter, the power transmitted was rather small, as the incandescent lamp produces little radiation of that colour; the power of the illumination varied, in different cases, from 0.1 cal./sq. cm./minute to half that figure. Sierp reduced the luminous flux transmitted by the other filters to bring the illumination obtained with them to the same level, so that the plant should always be submitted to the same

energy of illumination, measured with the thermocouple, although its composition was changed.

These details give some indication of the care that must be taken in the comparative study of the influence of different colours. Note in this connection that to equalize the energies corresponding to the different colours the illumination must be reduced. Experiments of this kind always have one fault in common; they are made only in much worse conditions of illumination than the normal conditions of existence of the plant. The coloured illumination in Sierp's experiments is ridiculously low when compared with the brilliance of full sunlight. Nevertheless, these experiments, following many which had not been so thoroughly carried out by other investigators, were the first to give conclusive and certain results.

In short, the stomata open under visible light. Since the spectral compositions are very complex, it is impossible to state precisely the limits of the range of wave-lengths in which this action is produced. In addition, the blue causes a more rapid and wider opening than the red—the open surfaces are in the ratio of 5 to 3.

Other investigators, before Sierp, had stated the contrary—that the red was more effective than the blue—but this was because they had omitted to measure the energy of the illumination in the two cases. Their observations were made in very low blue illumination and very intense red; the conditions were not identical and the intensity of the red largely compensated for its lower efficacy. In reality, with equal energy, blue light stimulates the opening of the stomata to a much greater extent.

One effect must be that the gaseous exchanges between the leaf and the atmosphere, and particularly the evaporation of water, are facilitated. If we also remember that the blue and the violet are absorbed in greater proportions in the tissues of the leaf than any other visible radiations, we see that there are two convergent causes tending to favour transpiration under the influence of blue light. This is precisely

what the most carefully made direct measurements have shown.

Ivanoff and Thielmann exposed plants to the filtered radiation of an electric arc and ensured the equality of the energy from the illuminations by means of a thermocouple. They measured the variations, in the weight of water evaporated in a given time, with the composition of the visible radiation to which the plant was submitted, and found that the blue-violet radiation causes more rapid transpiration than the yellow-red.

These experiments were made before those of Sierp on the opening of the stomata, but they agree well with his, in spite of the different interpretation that Ivanoff and Thielmann had originally given to their results.

With equal energy, the blue stimulates a rate of transpiration exceeding by 20 per cent to 60 per cent that observed in red light.

Thus, both the visible radiation and the infra-red, absorbed by the leaf, provide it with a quantity of heat which causes the evaporation of water, but what is peculiar to the visible, and more particularly to its blue radiations, is the faculty of stimulating the opening of the stomata, by a process which is totally unknown to us.

This process cannot be purely physical and is not, for example, simply one of heating, for that would not explain the specific character of the action of the blue and, more generally, of the visible radiation. It is probably, at least in origin, photochemical; certain substances in the leaf, capable of absorbing the active radiations, are subjected to a chemical excitation which has the effect of modifying their composition, or of putting them into a state in which they are ready to react with other substances. In this way the opening of the stomata would be produced by a chemical action.

This is only an hypothesis, but it is supported by analogy with other better known phenomena, also connected with an action of light. It is very probable that the action of light, apart from cases of simple heating, most frequently consists,

in its initial phase, in a photochemical excitation of certain molecules.

Thus the physicist alone cannot be expected to analyse these phenomena completely; he will need the results of modern chemical research in which further progress has still to be made.

The rapid advance of knowledge in organic chemistry and the introduction of exact methods of measuring and defining the radiation are the two essential requirements in research on the effects of light on vegetation.

Equilibrium of Development

It has long been known that the radiations of the shortest wave-lengths in the visible spectrum, the blue and the violet, have a particularly marked influence on the regulation of the growth and development of plants. If these radiations are absent and the illumination consists of only yellow and red light, photosynthesis appears to proceed normally. The plant remains green, but it takes on the characteristic appearance of plants which have developed in obscurity or in insufficient illumination and are suffering from what is called etiolation.

The most obvious effects of the lack of blue light are: long, thin and weak stems, imperfectly developed leaves, internodes which are too long and tissues which are only slightly differentiated.

The greater height, or length of stem, has often been interpreted as a favourable indication and a desirable effect. Nevertheless, the total weight, and especially the weight of dry matter, is always lower in the absence of blue light; the plant shows unmistakable pathological signs.

The best experiments have been made with coloured glasses filtering the sunlight. They are chosen so that they abstract from the solar spectrum larger and larger portions, starting with the short wave-lengths. Under the glasses which transmit the largest part of the spectrum, muslin is fitted to reduce the illumination to the same value as it is under the glasses which transmit only a part of the spectrum. The

differences observed are therefore imputable not to the differences of illumination, which are suppressed, but to the differences in the composition of the light.

Popp's experiments, in 1926, were conducted in this way. Under glasses allowing only radiations of wave-length greater than 5,290 Å to pass, the stems were often longer, and always thinner and weaker; the leaves were rolled up and the tissues badly differentiated; the cells had thin walls; flowering was retarded and the production of fruits and seeds much reduced in comparison with the controls which had received light of the same intensity but containing all the solar radiations. The tissues were abnormally swollen with water, although the total weight, even with this water, was less than the weight of normal plants. Chlorophyll formed well.

Note again that glasses opaque to the ultra-violet, but allowing the blue and the visible violet to pass, do not produce any of these effects on the plants that they screen. This result, therefore, is not an effect of the ultra-violet but of visible radiations of short wave-length, whose beneficent action is indispensable for the formation of robust and well-grown plants.

Popp's experiments confirmed, under better operating conditions, the observations which had been made previously. They lead us to think that cultivation in purely artificial light would be difficult with incandescent lamps, since these lamps, unless they are very much overrun, emit a radiation which is rich in red light and poor in blue. They would probably have to be combined with supplementary sources of radiation capable of providing the blue light necessary for the balanced development of the plant.

This regulating action of visible light of short wave-length is no doubt of photochemical origin, but its mechanism is certainly very complex and completely unknown to us. One of its effects, which is of the greatest practical importance, is to increase photosynthesis.

Other effects are probably connected with this. For example, light appears indispensable for hardening the plant

against the cold and the wind, especially when the nights are cold and the days hot; the same alternations of temperature, without light, are incapable of increasing the resistance of the plant. Reserves of carbohydrate also appear to be necessary to promote this action. Thus several factors are combined, each being indispensable. This is a very common case.

Chemical Composition

The action of different radiations on the chemical composition of the plant is very imperfectly understood. Thus, Dumont stated that wheat ripened under red glasses contained less nitrogenous substances, and he concluded that the radiations of shorter wave-length favoured the formation of albuminoids. Popp, on the contrary, in the experiments already mentioned, showed that the suppression of these radiations caused an increase in the total quantity of nitrogen. These two observations seem to be contradictory; the most probable explanation is that light is not the only factor involved and that other factors manifested themselves in a different fashion in the two experiments.

In the particular case of very young wheat seedlings cultivated in artificial light with incandescent lamps, it has been observed that supplementary illumination by carbon arcs to supply the blue radiation which otherwise would have been only very slight, favours the absorption of nitrates, and more particularly of potassium nitrate; sodium nitrate is not so well utilized.

This example shows that there is a relationship between the illumination, in quality and in quantity, and the utilization of the mineral substances that the plant draws from the soil. Thus the question of fertilizers is perhaps connected very closely with the action of light.

The synthetic production of organic substances by the plant is also dependent on the nature of the illumination. It has been observed, for example, that tobacco leaves grow larger and more abundantly under slightly lower illumination than they receive in the open air, but their yield in nicotine

diminishes. However, investigations do not seem to have been made to determine whether certain regions of the spectrum are more particularly active in stimulating this production.

The formation of anthocyanins has been studied in more detail. Some plants effect their synthesis in darkness, but it seems certain that light, if not always indispensable, is at least a very active supporting factor.

The reddening of MacIntosh apples can be produced, according to experiments made in natural light or in artificial light coloured by optical filters, under the action of all the visible radiations of wave-length shorter than 6,000 Å. But the blue and violet rays are the most efficacious; the optimum is situated in the neighbourhood of 4,100 Å, i.e., in the extreme violet.

Similar results have been obtained in other cases; thus flowers, whose colour is often partly attributable to anthocyanins, lose their brilliant colouring proportionately as the rays of short wave-length are suppressed from the illumination received during their formation.

Red lettuce, red-leafed beetroots and begonias tend to lose their colour in the same conditions and redden again when they are re-exposed to complete solar radiation. This is one of the rare examples which apparently demonstrates the action of the ultra-violet near the visible; this radiation of short wave-length is useful for the formation of anthocyanins.

These few examples prove that the action of light is not confined to photosynthesis. It extends more or less directly to all the chemical processes of the plant, both for the utilization of the mineral substances in the soil and for the elaboration of the infinitely varied organic compounds whose mysterious operation enables the plant to live.

In the field of organic chemistry, we have mentioned some experiments on the formation of anthocyanins. In the chapter on phototropism we shall discuss other studies on auxins—substances whose chemical nature and composition are now fairly well known and whose striking effects on growth have

been the subject of numerous experiments. The formation of auxins and their movements in the plant are directly dependent on light, and the wave-lengths of the active radiations and of those to which the plant is indifferent are known.

Other examples could be taken from the chapter on photoperiodism.

This collection of more or less well-known facts reveals an infinitely small part of the chemical processes which we have to conjecture in order to interpret a large number of observations.

CHAPTER VII

PHOTOSYNTHESIS

IN this chapter we come to the most important effect, from both the practical and scientific points of view, of light on vegetation, namely, photosynthesis or synthesis by light. Briefly, the process is that, through the absorption of luminous energy, green plants are capable of combining water and carbon dioxide and, with the liberation of oxygen, of producing carbohydrates such as starch.

This synthesis is only one example of the numerous syntheses in the interior of the plant which are promoted or conditioned by light, but it is the oldest known and its importance, both by the quantity of the products thus created and by their value, has caused it to be regarded as the supreme example of photosynthesis.

General Characteristics of Photosynthesis

It is also called assimilation through chlorophyll; in fact, the assimilation of carbon from the air, of which green plants have almost the exclusive monopoly, can be effected only through the intermediary of chlorophyll.

But, although chlorophyll is indispensable, it is only an agent which is able to capture and transform luminous energy and to fix it in the form of chemical energy in endothermic compounds; it is therefore powerless in the dark.

Moreover, its function can be fulfilled only in the living plant. Chlorophyll can be extracted and isolated, but when it is exposed to light *in vitro* it decomposes and is useless for photosynthesis.

Aquatic plants find carbon dioxide in solution in the water, but plants growing on land find it in the air, which

contains a very small proportion—1 litre of carbon dioxide in 3,300 litres of air.

The following table gives the composition of dry air at ground level:

Nitrogen	.	.	0.7803
Oxygen	.	.	0.2099
Argon	.	.	0.0094
Carbon dioxide	.	.	0.0003
Hydrogen	.	.	0.0001
Neon	.	.	0.000015
Helium	.	.	0.0000015

Thus argon, although it is classed among the rare atmospheric gasses, is 31 times more abundant than carbon dioxide, but it has no chemical activity.

Most plants spreading their leaves over a considerable area are well adapted by their shape to capture a sufficient quantity of carbon dioxide and to absorb the luminous energy which they need for many purposes, and particularly for photosynthesis.

Without making any hypothesis on the process of photosynthesis or describing any of the certainly complex intermediate reactions, we can write the overall result in the form of a very simple chemical equation. The products of photosynthesis—starch, sugars, etc.—all have a composition expressed by the formula CH_2O . Assimilation through chlorophyll is therefore represented by:

Thermochemical data show that such a reaction is endothermic, which means that it cannot take place without energy. C represents 12 grammes of carbon, H 1 gramme of hydrogen, O 16 grammes of oxygen, and the energy necessary to produce the quantities shown in the formula is 112,000 calories (equal to 460,000 joules, or 128 watt-hours).

The plant draws this energy from the light absorbed and

produces with it 30 grammes of starch or substances of similar composition.

Respiration

Photosynthesis has the reverse effect to that of respiration. In respiration, the oxygen of the air combines with organic substances and this combustion produces carbon dioxide and water vapour, which are given off.

Like all other organisms, plants breathe, day and night. Even the green parts, while they are receiving light and are assimilating through photosynthesis the carbon dioxide of the air, are, at the same time, performing the opposite function of respiratory combustion.

At night, only respiration takes place, but during the day photosynthesis predominates. There is a level of illumination at which respiration and photosynthesis compensate each other exactly and at which the overall gaseous exchanges balance. This point, called the *point of compensation*, gives an idea of the relative intensity of the two processes. It is generally reached at a much lower illumination than that of a dull day; the highest is at 4,200 lux for a lichen, *Pelligera canina*, but this is exceptional. For shade plants, compensation occurs at less than 100 lux, for plants which grow in full sunlight, at a few hundred. These illuminations are 100 or 1,000 times lower than those of full daylight. We may therefore conclude that at a medium latitude photosynthesis generally predominates from dawn to dusk. In July, at 69° N., it continues without interruption for twenty-four hours a day.

The Influence of Illumination

Certain species of plants, for example deep-water algae, can maintain life, and therefore effect photosynthesis, in extraordinarily low illumination—no higher than moonlight. One green moss, *Schistostega ormundacea*, living in dark caves where the illumination is of this order, is adapted to such conditions and possesses a layer of superficial cells in

the form of lenses which are said to concentrate the light on the chloroplasts containing chlorophyll.

Other plants are adapted to very high levels of illumination. In fact, plants have been classified, according to observations, as sun plants and shade plants. Cereals are examples of the first category, woodland plants of the second.

Each species is therefore adapted to an optimum illumination. But rapid adaptations to changes of light intensity have also been observed in the same plant in the course of the same day.

Besides the eucalyptus, which turns its leaves parallel to the rays of the burning sun so that they make no shade, the common bean is a striking example of this adaptation. In the morning, the leaves are spread to capture as much luminous energy as possible, but at midday, if the weather is fine, they all turn on their petioles to present themselves edgewise to the sun's rays, like the eucalyptus leaves. The illumination of the leaf surfaces thus remains moderate.

Moreover, inside the leaf, the chloroplasts—green centres, charged with chlorophyll, in which photosynthesis is effected—change their position. In moderate light they spread out parallel to the surface of the leaf, but in strong light they arrange themselves at right angles to the surface so that those nearest to it provide shade for the others.

This internal modification can be observed, not only by examination under a microscope, but also by the measurement of the transmission factor; the quantity of light transmitted increases in strong illumination because the absorbing green particles are arranged in such a way that they allow the luminous flux to pass more freely. This fact has already been mentioned in the chapter on the photometry of the leaf.

These reactions of certain plants to strong variations of illumination are superposed on the variations of the performance of photosynthesis itself; they have the effect of reducing, without suppressing, the variations of the quantity of light available to the chloroplasts.

How does photosynthesis depend on this quantity of

light? In laboratory experiments, its activity is generally measured either by the absorption of carbon dioxide or by the liberation of oxygen. The action of light is known to depend on other factors, such as the carbon dioxide content of the air and the temperature, and this dependence is governed by complex rules.

The simplest and most useful indication in these phenomena is the *law of the minimum*, according to which the lowest factor regulates the rate of assimilation.

Suppose, for example, that the light is poor but that the temperature is favourable and the atmosphere is artificially enriched with carbon dioxide. The plant will have an abundance of everything except light. It is light, therefore, which will check the photosynthesis and regulate its speed.

In these conditions, and within a limited range of variation, the rate of photosynthesis is proportional to the illumination. Then, as the light becomes more abundant, the rate increases more slowly and is finally stabilized. A further increase of illumination is useless because the rate is checked by another factor.

In ordinary conditions, and for the majority of plants, photosynthesis reaches its maximum with relatively low illuminations; for wheat, for example, the value is ten times lower than that of full sunlight. That is why crops can be grown with record rapidity in the summer in high latitudes with very long days, in spite of the considerable atmospheric absorption due to the sun remaining low on the horizon; photosynthesis takes place at the same rate as it does in districts where the light is stronger, but it continues without interruption, while in lower latitudes the nights are longer.

Adaptation also plays an important part; a plant raised in poor light makes much better use of it than a plant raised in full daylight.

The Influence of the Pressure of CO₂

When the illumination is adequate, it is therefore necessary to control another factor which limits the rate of photo-

synthesis—the proportion of carbon dioxide in the air must be increased.

In experiments at the Smithsonian Institution in the United States, the carbon dioxide content of the air in a glass chamber was increased from 0.04/1000 (nine times less than the normal concentration) to 5/1000 (fourteen times more than the normal concentration) and the rate of photosynthesis of plants inside the glass chamber was measured.

The experiment was made first with wheat in artificial illumination of 4,000 lux supplied by incandescent lamps and deprived of its excess of infra-red by a solution of copper sulphate. This illumination is sixteen or seventeen times lower than full sunlight, but to enable it to be used to the best advantage it is necessary to increase the concentration of CO_2 in the air to 0.8/1000. With stronger illumination, about 10,000 lux, the optimum concentration would be 1.3/1000.

Naturally, for the same illumination, it is useless to increase still more the proportion of carbon dioxide in the air. But extrapolation from the preceding results shows that illumination of 70,000 to 80,000 lux, which is that of a fine day at noon, would be fully used only if the proportion of CO_2 in the air were 5/1000 to 6/1000; assimilation would then be ten times more rapid than it is in normal air.

At the same laboratory, an experiment was made on a larger scale in daylight with wheat cultivated in a glass chamber in which the atmosphere was enriched in carbon dioxide by the slow circulation of the gas through it. The concentration reached about 1.4/1000—four times higher than the normal.

Compared with the control, the crop grown in the artificial atmosphere produced more straw, more and larger ears, and more seed.

This example shows that in natural conditions the process of photosynthesis, even in sun plants like cereals, is generally limited, not by an insufficiency of light but by other factors, particularly by the poverty of the atmosphere in carbon dioxide.

Incidentally, it may be remarked in passing that, according to some calculations, the total quantity of carbon dioxide absorbed in a year by photosynthesis is $\frac{1}{70}$ of that contained in the atmosphere.

The possibility of increasing the crop by providing plants with a larger quantity of carbon dioxide has practical applications in a glasshouse or in frames. Rotting manure gives off this gas in abundance and its influence can be seen in manure hotbeds. Solid carbon dioxide, or dry ice, can also be supplied; this white solid passes to the gaseous state without passing through the liquid state and sublimates to give off a very pure gas. Naturally, an increase in carbon dioxide can benefit the plant only at times when the illumination is sufficiently strong; otherwise the deficiency of light will limit the photosynthesis.

Temperature can also be a limiting factor; when it is too low, it can arrest photosynthesis, even if carbon dioxide and light are present in abundance.

Such, briefly, are the results of observations on the influence of light, combined with that of the carbon dioxide content of the atmosphere and of temperature.

Other observations show that the process of photosynthesis is subject to multiple and complex influences which may often mask the simple laws just explained.

One curious fact is that in certain plants the process is checked, and may even be stopped completely, when the light is too strong. A desert plant of this kind accomplishes all its photosynthesis in the early hours of the morning.

With *Trichomanes radicans* (a shade fern), Montfort found that photosynthesis steadily increased as the illumination increased from 0 up to $\frac{1}{8}$ of the daily maximum, then steadily diminished and stopped completely at half the maximum.

The cause of this inhibition is not very well understood, but it is clear that in some cases light which is too strong may be more detrimental than useful. In other cases, on the con-

trary, photosynthesis has been known to continue in an illumination forty times more intense than full sunlight.

The Influence of Temperature

The influence of temperature, considered in more detail, seems to be extremely complex. According to the plants used for experiments, there may be an increase of photosynthesis over a certain range of temperature rise; above and below this range, variations of temperature have no effect. If the light is poor, photosynthesis may be more active at low than at high temperatures, but with increased illumination a rise of temperature will greatly favour the assimilation.

Lundegård, followed by other investigators, found, for the potato and the haricot bean for example, several successive peaks in the curve of photosynthesis as a function of temperature. The position of these peaks changes with the illumination; as it becomes weaker they are displaced towards the lower temperatures.

Many other factors also have an influence. Nitrates, phosphates and potassium are necessary and if they are deficient the process is slowed down. This is one reason why mineral fertilizers are useful.

It has recently been shown that minute traces of a number of chemical elements are indispensable; their action does not necessarily bear directly on photosynthesis but on the ultimate chemical elaborations of its immediate products, which are conveyed by the sap away from the leaf where they have been created.

The Photosynthetic Effect of the Different Radiations of the Spectrum

Only visible radiations and radiations of the very near ultra-violet seem to be usable by the plant for photosynthesis. The limit on the side of the long wave-lengths is situated in the neighbourhood of 7,500 Å or 7,600 Å; several observations agree on this point. The limit on the side of the short wave-lengths is not so well known because these ultra-violet

radiations are difficult to produce with great intensity. The mercury line, 3,654 Å, is still active and the extreme limit appears to be near 3,300 Å. These radiations are quite invisible but their activity is small. The most effective wavelengths, situated between 4,000 Å and 7,300 Å, almost coincide with those of the visible region of the spectrum.

Outside this range, the infra-red and ultra-violet radiations, inactive for photosynthesis, would have rather the effect of disturbing and slowing down the action of the visible radiations, but this fact does not seem to be established with certainty.

With equal energy, the monochromatic radiations of the visible spectrum are not all equally effective for photosynthesis. It has been known for some time that the orange yellow and the red have the maximum efficacy. This region of the spectrum, near 6,500 Å, coincides with an absorption band of chlorophyll.

More recent research has revealed a second, but lower, maximum of efficacy in the blue, in the neighbourhood of 4,300 Å or 4,400 Å. In this region there is also an absorption band of chlorophyll. Between these two maxima, the efficacy of the monochromatic radiations is a little less, but it is still considerable.

Among the experiments which have given these results are those made by Hoover and described in the *Smithsonian Annual Report* for 1936, page 364 (see also the *Report* for 1931, page 130). The plant used for the investigation was wheat. The stem emerged from a double-walled glass tube, in which a current of air, of controlled composition, circulated slowly, while the carbon dioxide content of the air which came out of it was continuously measured.

Between the two walls was a solution opaque to the excessive infra-red rays of the lamps and maintained at a constant temperature. The lighting conditions in the tube itself were measured by means of a special thermopile.

To take advantage of the principal maximum in cultivations in artificial light and thus obtain a higher efficiency,

light sources are chosen to give the greater part of their luminous emission in this spectral region. For this reason neon tubes are recommended; the spectrum that they emit includes several intense monochromatic radiations situated between 5,764 Å and 6,402 Å.

The tubes with fluorescent walls which have been put on the market during the last few years are made with various casings enabling the composition of the light emitted to be modified within wide limits. Up to the present, there seems to have been no attempt to do more than compose a light agreeable to the eye, but when these tubes are used for plant illumination the manufacturers will no doubt develop light sources perfectly adapted to make the best possible use of the maxima of efficacy for photosynthesis.

The solar spectrum possesses a maximum of power in the yellow, in the neighbourhood of 5,500 Å, at equal distance from the two maxima of activity for photosynthesis. In view of the shape of the spectral distribution curve of the solar radiations, which is analogous to that of the emission of non-selective incandescent bodies, the adaptation of the curve of efficacy, although it is not as perfect as it could be if its maximum coincided with the solar maximum, is nevertheless excellent; it could even be worse without any disadvantage, for the light is generally superabundant.

It is interesting to combine the solar curve with the curve of efficacy and to obtain from them a third curve showing the participation of each of the solar radiations in photosynthesis. It is obtained from the product, for each wavelength, of the ordinates of the first two curves. This third curve is very similar to the curve of efficacy; the two maxima are situated at the same wave-lengths, but as the smaller is in a region where the solar power is greater, it is increased and becomes about four-fifths of the maximum situated in the red. In the interval between these two maxima, the participation of the green and yellow solar radiations remains more than half of that of the principal maximum (Fig. I, 14).

At the ends of the spectrum, especially towards the violet, the fall of power per unit wave-length in the solar spectrum combines with the decline of efficacy to reduce the participation of these radiations in photosynthesis.

Fig. I, 14. Curves showing the relative efficacy of radiations for photosyntheses as a function of wave-length, according to Hoover, 1937. *Dotted curve*: composition of the solar radiation on the ground

Duration of the Illumination and Interruptions

When a green plant is brought out of the darkness into the light, photosynthesis begins immediately with absorption of carbon dioxide and liberation of oxygen. If the illumination is kept constant from the beginning of the experiment, the speed of photosynthesis does not remain constant but may steadily increase or decrease. By a process of adaptation, it increases if the experimental illumination is lower than that

in which the plant was previously cultivated and to which it has become accustomed and decreases if it is higher.

The stronger the illumination, the more intense is the activity at the beginning; then the plant progressively modifies the efficiency of the operations involved so that the speed tends to be the same value in spite of the change of illumination. The period of adaptation depends on the temperature; it lasts some hours when assimilation is being accelerated in poor light and is much shorter when it is being slowed down in unusually strong light.

In the course of the day, the natural variations of sunlight have very marked effects on some plants. Kostytschew reported examples in which assimilation is balanced, and even more than compensated, by respiration at midday, while it passes through two maxima, one in the middle of the morning and the other in the middle of the afternoon.

If, after an interruption, a plant is again placed under the illumination to which it is accustomed, the rate of assimilation begins by increasing, then returns to normal after a few oscillations. Every sudden variation of illumination immediately provokes a corresponding variation of the rate of photosynthesis, followed by a new adaptation which tends to minimize the influence of the disturbing cause.

It is apparent from these observations that, even for one and the same plant, a given rate of assimilation does not correspond to a given illumination. This rate depends on the time for which the plant is illuminated and especially on its previous history and on the illumination to which it has adapted itself.

Great caution is therefore needed before a quantitative correlation between illumination and photosynthesis can be stated. For example, the point of compensation, i.e., the illumination at which assimilation exactly balances respiration, depends to a large extent on the adaptation to light; when one part of the same plant has been put in the sun and the other in the shade, the first has its point of compensation at 170 lux, the second at 37 lux.

It is remarkable that, according to the experiments made by Li, a sudden change of the colour of the light, without modification of the power of radiation, does not cause any appreciable variation of the rate of photosynthesis. This would seem to indicate that, apart from the variations of efficacy, the plant regards the different active radiations as equivalent.

The processes which come into operation in these various reactions of the plant have not been elucidated; the movements of the chloroplasts are obviously insufficient to explain such large variations in photosynthesis. No doubt other processes are affected in experiments in intermittent light with periodic variations repeated several times per minute or per second.

Efforts have been made to obtain from these investigations information on the nature of the complex chemical reactions which result in photosynthesis.

It is promoted by intermittent lighting. The same quantity of light (which therefore presupposes stronger illumination during the flashes) is better utilized when it is given in small quantities than when it is given continuously. There is a surprising difference in the efficiency; with an interruption every fifteen seconds, it is increased by 10 per cent. Flashes at a frequency of 130 per second stimulate twice as much assimilation as the same quantity of light supplied continuously.

These results were obtained by Warburg with equal periods of light and darkness. Emerson and Arnold experimented with extremely brief flashes, the duration of which did not exceed ten microseconds at a frequency of 50 per second; the efficiency can then be increased fivefold.

The interpretation of these results will be given later. Note simply here that they can very easily be turned to practical advantage in cultivations under artificial light by using alternating current supplied from light sources of low inertia which are extinguished at each alternation of the current. The new fluorescent lamps seem well adapted to this purpose because their light becomes fainter, at the instants

when the current changes direction, than that of incandescent lamps; in the latter, the thermal inertia of the filament reduces the fluctuations. The increase of efficiency, in the conditions in which Warburg experimented, ought to be about doubled.

The advantages of these fluorescent tubes for plant illumination have already been mentioned, first because their radiation is poor in infra-red (infra-red, which is too abundant when incandescent lamps are used, is a serious disadvantage), and then because fluorescent cases can be chosen to emit radiation the composition of which can be regulated, within wide limits, to enable the power to be localized in the most efficacious regions—the blue for the balanced formation of the plant, the blue and the orange for photosynthesis.

To these advantages is added the possibility of choosing fluorescent substances of rapid extinction, which will concentrate the emission of light during the maxima of the alternating current without prolonging it between the alternations.

Not only, therefore, is the efficiency excellent for the conversion of electrical energy into luminous energy, but there is the prospect of a better efficiency than that of daylight for the conversion of luminous energy into plant products. Unfortunately, fluorescent tubes are expensive to instal.

It must be added, however, that, although a rapid alternation of light and darkness is favourable, this does not hold good for alternations of a longer period, one hour to thirty seconds, for example. Alternations of one to five minutes appear to constitute a real poison for the plant, which is incapable of developing in those conditions, whatever care it may receive. This strikingly illustrates to what point light is essential to vegetation and that the way in which it is distributed matters quite as much as the total quantity offered. Other examples of this occur in connection with photoperiodism.

CHAPTER VIII

THEORIES OF ASSIMILATION

Photochemical Character of Assimilation

THE observations mentioned in the last chapter fully confirm a fact that has long been known, namely, that assimilation through chlorophyll has the character of a photochemical reaction. It cannot be accomplished without light and nothing can take the place of light.

Between the molecules of water and of carbon dioxide, and the products of combination elaborated in the green parts of plants, intermediate compounds, which have not yet been identified with certainty, are formed.

Obviously chlorophyll also has a chemical role, but the hypotheses that we shall consider are not fully proved and photosynthesis, in spite of the numerous studies that have been made of it, remains a still mysterious natural phenomenon.

The overall reaction can be written as follows:

The compound CH_2O is formaldehyde or formol.

Klein and Werner (1926) claim to have demonstrated, although the fact is still in dispute, the presence of formol in leaves which assimilate normally. Generally, the two sides of this chemical equation are multiplied by 6; the compound $(\text{CH}_2\text{O})_6$ is a sugar—glucose—or one of its isomers.

But as we do not know whether the immediate product of photosynthesis is this sugar or another polymer molecule, we shall keep to the simplest formula indicated, at the same time stressing that it does not necessarily imply the formation of formol, but perhaps only of a polymer combination of formol, or of a molecule of similar composition.

For the chemist, each term in this equation represents a gram-molecule, i.e., a well-determined mass of matter: 18 grammes of water, 44 grammes of carbon dioxide, 30 grammes of formol, and 32 grammes of oxygen. Thermochemistry would enable us to calculate exactly the quantity of energy necessary to effect the reaction if we knew the substance that was really formed (the substance that we have supposed to be formol). It happens that every reasonable hypothesis on the nature of this substance leads to results very close to 112,000 calories; we can therefore complete our equation, without knowing exactly the product of the reaction, by stating that such is the energy provided by light.

Our intention now is to explain the initial phase of a photochemical reaction. The action of light came to be understood by the physical study of extremely simple cases when our knowledge of the atomic structure of matter, and of the quantic structure of light, permitted the analysis of the elementary phenomena of interaction between matter and radiation.

We must first show how the process of a chemical reaction is generally represented. Take a concrete example—the combination of chlorine and hydrogen, with the formation of hydrogen chloride. The real phenomena are extremely complex, but suppose that influences such as the presence of water vapour, the nature of the walls of the receptacle, etc., do not play any part.

In the dark, the two gases mix and remain in contact without combining. This is a very common case; even very exothermic reactions are not produced when the constituents exist alone, but only when an “excitation factor” or a “catalyst” is added to facilitate the passage from the initial state of the uncombined substances to the more stable final state in which the combination has been accomplished.

Similarly, billiard balls at rest on a table do not fall to the ground, although their fall would correspond to a diminution of their energy and therefore to a more stable final state

from which they would not be able to return to their previous position without receiving a supply of energy from an external source.

Most often, the "excitation" just mentioned is the effect of thermal agitation. This is so with reactions that can be produced in darkness, but in a photochemical reaction the excitation is provided by light.

Finally, a catalyst is a substance which reacts on one of the constituents without excitation, or with very slight excitation, and provides an intermediary product which is capable of reacting, in its turn, with the other constituent to give the expected combination, the catalyst being restored to its initial state.

Excitation, whether it be thermal or photochemical, has the effect of bringing the molecules into a state in which they have more energy, called the "activated" state. This activation may be a change in the electronic configuration of the molecule; the possible configurations form a discontinuous series of quantified states of increasing energy. It may be an ionization, i.e., the separation of an electron torn away from the molecule, or a dissociation, i.e., a splitting of the molecule into two parts, atoms or groups of atoms, or again, more simply, an activation of the internal vibrations and rotations within the molecular structure.

The result is always the creation of a state of greater energy, a state in which the molecule can overcome the resistances which oppose the chemical reaction.

To return to the analogy of the billiard balls, let us imagine that the edges of the table are raised so that the balls cannot fall unless they receive an impulse setting them in motion with sufficient energy to enable them to surmount the obstacle.

Thermal activation differs from photochemical activation. The first is due to thermal agitation. We know that the molecules of a gas are in continual motion. They have kinetic energy and internal energy, and the higher the temperature of the gas the greater is their average total energy. It is almost zero at -273°C , a temperature that is called for this reason

absolute zero; if we reckon temperatures from this zero, which means adding 273 to the Centigrade temperature, we obtain the absolute thermodynamic temperature, which is of great theoretical interest.

The average energy, E , attached to each degree of freedom of a molecule, is proportional to the absolute thermodynamic temperature, T ; the coefficient of proportionality, k , or Boltzmann's constant, is the same for all the molecules, whatever their constitution may be:

$$E = kT$$

where the constant k has the value 1.372×10^{-16} ergs per degree C, so that $E = 4.11 \times 10^{-14}$ ergs (at 300° absolute or 27° C. Trans.).

A gram-molecule, which contains N true molecules ($N = 6.06 \times 10^{23}$), possesses, at ordinary temperature (about 300° absolute) and per degree of freedom, the following thermal energy:

$$\begin{aligned} NkT &= (6.061 \times 10^{23}) \times (1.372 \times 10^{-16}) \times 300 \\ &= 8.3 \times 10^7 \times 300 = 24.9 \times 10^9 \text{ ergs.} \end{aligned}$$

To employ a unit more familiar to chemists, this represents an energy of 600 calories per gram-molecule.

The average thermal energy is therefore kT , but the energy at a given instant may be greater or smaller. In particular, a very small number of molecules acquire, at each instant, an energy which is considerably higher than the average and which may become sufficient to bring them to the "activated" state; the lower the energy of activation and the higher the temperature, the greater is this number. Thus chemical reactions are in general accomplished more rapidly when the combining bodies are heated.

The billiard ball analogy can be followed once more; let us suppose that the table is shaken, the balls will be set in disordered motion and from time to time one of them will be impelled with enough force to clear the edge of the table. A more vigorous agitation corresponds to a rise of temperature and its obvious consequence is that the balls will fall at a

more rapid rate—an analogy with a chemical reaction which is performed with greater speed.

We now pass on to the photochemical action of light. The luminous energy is concentrated in photons or light quanta; each of them carries a quantity proportional to the frequency of the luminous vibration. For green monochromatic light, for example, of which the wave-length is $5,500 \text{ \AA}$ (consequently the frequency $\nu = 0.545 \times 10^{15}$), the energy E of a photon is $E = h\nu$ (where $h = 6.554 \times 10^{-27}$), so that $E = (6.554 \times 10^{-27})(0.545 \times 10^{15}) = 3.58 \times 10^{-12}$ ergs.

This energy is about ninety times greater than the average thermal energy of a molecule at ordinary temperature. If such a molecule receives and absorbs the energy of a photon, it will therefore be brought to a high energy level and strongly activated. It will become capable of chemical reactions which would be impossible by thermal activation alone.

The billiard balls individually receive violent impulses which in all probability will throw them off the table.

Because photochemical activation operates by supplying energy, it can make endothermic reactions possible—reactions which absorb energy instead of liberating it, as we have previously supposed.

The impulse received by a ball throws it up to a higher level, where it will remain if it finds, for instance, a shelf higher than the table; molecules confronting one another combine, giving a compound of which the chemical energy is greater than the energy of the constituents.

This is exactly what happens in photosynthesis by green plants; while in the majority of photochemical reactions light is only a stimulus, in assimilation through chlorophyll the luminous energy is used not only to “activate” the molecules taking part, but also to fix this energy, in the form of chemical energy, in the substances created.

It would seem, according to the process outlined above, that a molecule participating in the reaction corresponds to each photon absorbed.

But complications often arise from simple phenomena.

Thus, the molecules excited by the absorption of a photon, having absorbed its energy, very frequently lose it again by sharing it with the neighbouring molecules in the form of kinetic energy, i.e., of thermal agitation. This is the commonest case, in which the absorption of light produces a heating up of the absorbing substance; the energy of radiation is thus put to the worst use, since it is converted into heat, a degraded form of energy.

Again, the molecules excited by light may return to their normal state by losing, in the form of light, the energy that they have absorbed—this produces fluorescence and phosphorescence—or the energy of excitation may be transferred to a single foreign molecule of another chemical nature by a secondary impulse. This is a method of exciting molecules which are not excited directly by light; they are mixed with other molecules capable of absorbing this light. It is the principle of the sensitization of photographic emulsions containing silver bromide, by colorants, which enables the sensibility to be extended into the red and the near infra-red, while, without colorants, photographic emulsions are sensitive only to the blue, the violet and the ultra-violet.

The molecules, activated by light, may therefore, wholly or in part, lose their excitation in several ways before they have been able to take advantage of their state of activation to react chemically. To a certain number of photons absorbed, there corresponds a smaller number of molecules entering into reaction.

But the opposite also occurs—a photon may bring into play a large number of molecules. The example just quoted, of the action of chlorine on hydrogen, will illustrate this.

According to Nernst's hypothesis (which has since been revised) light dissociates the molecule Cl_2 into two Cl atoms:

Each Cl atom then acts chemically, without the intervention of light, on the molecule of hydrogen:

The liberated atomic hydrogen H acts on a molecule of chlorine:

The atom of chlorine can repeat reaction (2) which liberates H, and so on; we could thus explain, by these chain reactions, the combination of an infinite quantity of gas under the impulse of a single photon.

But each of these partial reactions is exothermic. In photosynthesis by plants, when the reactions form an endothermic process, according to the principle of the conservation of energy, only those quantities of matter will combine which have, through the absorption of light, sufficient energy at their disposal.

Now, a gram-molecule of CO_2 and a molecule of H_2O require, in order to be converted into carbohydrates, an energy estimated at 112,000 calories.

If all the molecules of a gram-molecule absorbed a photon of radiation of wave-length λ , the energy absorbed per gram-molecule would be (in calories so that it may be compared with the chemical energy):

λ (Å)	$Nh \frac{c}{\lambda}$ (calories) Energy per gram-molecule
4,000	71,200
5,000	56,900
6,000	47,400
7,000	40,700
8,000	35,600

In red monochromatic illumination for which $\lambda = 7,500$ Å photosynthesis is accomplished; to obtain the 112,000 calories required, the concentration of the energy of 4 photons on one molecule of CO_2 or of H_2O is necessary; 3 would not be sufficient unless the kinetic energy of thermal agitation were used, as sometimes happens. At the wave-length of 4,000 Å, 2 photons would suffice.

It is rather curious to note that the two maxima of efficacy of photosynthesis as a function of wave-length correspond very closely to the radiations of 4,400 Å and 6,600 Å and that

the corresponding energy per gram-molecule is very near to one half and one third of the energy of the reaction of photosynthesis; at 4,400 Å, 2 photons would be necessary, at 6,600 Å, 3 photons, giving, in both cases, a very slight excess of energy.

Without stressing what is only a coincidence, and approximate at that, we must remember that the participation of several photons is always necessary for the assimilation of a molecule of CO_2 ; that is an inescapable energy requirement, whatever hypothesis may be formulated on the process of assimilation. Now, we shall see how difficult it is to imagine any probable process by which the energy of several photons can be concentrated on a single molecule of CO_2 or of H_2O .

Briefly, the general theoretical considerations that we have outlined enable us to deduce that at least 4 quanta of red light, but perhaps less for light of shorter wave-length, are required to supply the energy necessary for the assimilation of an atom of carbon.

Each active quantum contributes its energy in a particularly effective way, for the molecule which absorbs it instantaneously acquires, for itself alone, the whole of this energy, which has the effect of putting it in an activated state favourable to the chemical reaction.

Such is the true photochemical action. Before or after, the molecule in action, which is probably a molecule of chlorophyll, doubtless unites with other molecules, of carbon dioxide for example, but these are chemical and not photochemical phenomena. These chemical phenomena which precede or follow the photochemical action are designated by the general name of the "dark reaction" (because they are accomplished without the direct intervention of light) or the Blackman reaction. Their speed is dependent on all the factors which control the speed of chemical reactions: temperature, concentration of the bodies which participate in the reaction, etc.

Measurement of the Maximum Real Efficiency

We may define the efficiency as the ratio between the chemical energy of the products obtained and the luminous

energy expended in their formation. But it is necessary also to define the manner of calculating the energy expended. If by that is understood the total energy of the radiation which strikes a plant, the efficiency in good conditions of cultivation is less than 1 per cent.

It is better to consider only the radiation which is really usable, i.e., that which is neither reflected nor transmitted but is absorbed by the plant, and then, of the radiation absorbed, to reckon only that which is absorbed by chlorophyll, and not by the parts devoid of chlorophyll or by the carotenoids. The efficiency calculated in this way is the real efficiency.

An attempt has been made to determine the maximum real efficiency by providing conditions such that no factor other than light intervenes to slow down photosynthesis. The experiments are made in illumination which is low enough to ensure that the factor which limits photosynthesis is the quantity of light available. Thus this quantity of light is used to the best advantage and the real efficiency must be maximum.

The measurements made by Wurmser and Warburg (1923) on chlorella with light of different wave-lengths in the visible region gave the following results showing that the real efficiency may exceed 50 per cent. According to Warburg, this energy efficiency is:

In the red	($\lambda=6,600 \text{ \AA}$)	59%
„ „ yellow	($\lambda=5,780 \text{ \AA}$)	53.5%
„ „ green	($\lambda=5,460 \text{ \AA}$)	44%
„ „ blue	($\lambda=4,360 \text{ \AA}$)	34%

These results have been criticized, but before discussing them and comparing them with others, let us examine their meaning.

For the yellow, for example, the energy efficiency is 53.5 per cent. This means that for the initiation of the reaction of a gram-molecule of CO_2 and the liberation of a gram-molecule of oxygen, with the formation of a molecule of

formol or of its starch equivalent (which in total corresponds to the fixation of 112,000 calories), the chlorophyll had to absorb $112,000 \div 0.535 = 209,000$ calories.

On the other hand, the absorption of a photon per elementary molecule is equivalent to the absorption of 49,200 calories per gram-molecule. As a result, a little more than 4 photons per molecule are necessary to effect the photosynthetic elementary action expressed by the equation

Similarly, it would be possible to calculate, according to Warburg's measurements, the number of quanta absorbed per molecule of oxygen liberated at the other wave-lengths; these are:

Red . . .	4.3 quanta
Yellow . . .	4.3 „
Green . . .	4.8 „
Blue . . .	5.1 „

The measurement of the energy absorbed does not appear to take into account the loss due to absorption by parts of the plant other than those containing chlorophyll; the real efficiency is therefore a little higher, especially in the blue where the carotenoids may have a considerable influence. It has been agreed that the minimum number of quanta necessary for the whole of the visible spectrum is 4.

This simple result, which is attractive because it accords rather well with the idea that has been formed of the process of a photochemical reaction, confirmed by other experiments like those of Schmucker (1930) on other plants (*Cryptocoryne ciliata* and *Cabomba caroliniana*) and those of Rieke (1939), has always had a great influence on the theories of photosynthesis which have been propounded.

Nevertheless, these measurements are very difficult, and considerable uncertainties still exist, so that other investigators, repeating Rieke's experiments, have found that 20 quanta, rather than 4, are necessary to the reaction.

A variation of this kind in such an important result,

obtained from carefully performed experiments, would certainly have stimulated much more research if the war had not diverted scientific investigation into other channels. Let us consider for the moment both the difficulties of principle and the experimental difficulties.

The experiments are made on living material and the choice of the plants, and their preparation, are very delicate operations. We have seen how numerous are the factors, in the actual conditions of the experiment or in the previous history of the plant, which have an influence on its photosynthetic capacity.

To obtain the maximum efficiency, and to ensure that light is not the limiting factor, rather low illuminations are used, e.g., one-thousandth of the solar illumination in Warburg's experiments. Respiration is then much in excess of photosynthesis, so that what is measured is not the liberation of oxygen and the absorption of carbon dioxide, which are the indications of photosynthesis, but the reduction of the rate of the reverse phenomenon—respiration—at the moment when the plant passes from darkness into the light.

It is supposed, without direct proof, that the rhythm of respiration is not altered by illumination and that the only cause of variation in the gaseous exchanges is the operation of photosynthesis. This question would demand a thorough investigation which would not be easy to undertake.

In fact, even if the quantity of light which falls on a surface can be measured, and if the fraction absorbed can also be measured by deducting from the first quantity the part reflected and the part transmitted (although in this case the methods employed have rarely been beyond criticism), it is difficult to know by what constituent of the plant substance this fraction has been absorbed and in what measure chlorophyll has profited from the absorption. This apparently is a problem to which a complete solution has not yet been found.

When we consider the nature and extent of these difficulties, we can easily understand that the most recent estimates of the

optimum efficiency give varying results, one indicating the necessity of 4 quanta, the other of 20 quanta, of visible light for the combination of a molecule of H_2O with a molecule of CO_2 and the liberation of a molecule of O_2 .

To conclude this discussion of the experimental results, we may say provisionally that the elementary action can be accomplished, in the most favourable conditions, by means of a contribution of energy corresponding to the absorption by chlorophyll of 4 photons. It remains to be seen in the future whether the few experiments which contradict this result are confirmed or not.

This being admitted (rather arbitrarily), the most obvious and important consequence is that the photosynthetic capacity may be extraordinarily good; in fact, according to established thermochemical data, the energy absorbed by the photosynthetic reaction corresponds, for the extreme red radiations, to 4 quanta of light. In the other regions of the spectrum, the efficiencies are of the order of 50 per cent.

The above is an assertion which greatly limits the processes imaginable in considering the detailed reactions of assimilation through chlorophyll; in the course of the partial reactions which result finally in a photosynthetic elementary reaction, the utilization of the luminous energy absorbed must be nearly perfect, without any appreciable waste.

The Dark Reaction

We have seen at the beginning of this chapter that light produces an activation of the molecules capable of absorbing it and have explained what this means.

After the activation, the role played by light generally comes to an end; the activated molecules are in a higher energetic state and the course of events no longer depends on the agent by which they have been brought to that state, but only on its nature and on the medium in which the molecules are placed.

The cascade of reactions which follows the absorption of light, like those which have preceded it, therefore constitutes

a process which is not properly speaking photochemical. Because light does not play a direct part in it, it is called the dark reaction (or the Blackman reaction).

The occurrence of the dark reaction is in accordance with the results of the study of the law of the minimum and of the observation of photosynthesis in intermittent light.

By this law, the rate of photosynthesis is linked with the various factors which can influence it and is regulated by the lowest; since all the factors have their part to play, the least effective retards the whole operation. Thus, when the temperature is adequate and the carbon dioxide abundant, but the illumination is poor, variations of the first two factors are unimportant because the rate of assimilation depends only on the illumination. On the other hand, in strong illumination, the rate of photosynthesis depends on the CO_2 content of the air, or on the temperature, or on both, according to which are deficient.

Although the law of the minimum is not universally valid, it best expresses the known facts. It is usually explained as follows: the action of light is independent of any other factor; on the other hand, the dark reaction, like every purely chemical reaction, is accelerated by a rise of temperature and its speed depends on the concentration of the substances taking part in it.

The molecules activated by light can also be classed among these participants and their concentration obviously depends on the illumination. Regarded in this way, the law of the minimum is easily interpreted. Briefly, the "dark reaction" includes the whole of the chemical processes initiated by the presence of molecules activated by light.

Let us turn now to experiments on photosynthesis in intermittent light, or, more precisely, those in which the plants are irradiated by very brief luminous flashes ($\frac{1}{100,000}$ second) separated by dark intervals of variable duration.

Each flash brings a certain quantity of luminous energy, which is always the same. As the experimental conditions remain invariable, we should expect the products of photosynthesis to be formed in a quantity proportional to the

number of flashes, whatever their frequency might be. This is so when the interval between flashes is sufficiently long—more than $\frac{1}{80}$ second in the conditions in which Emerson operated. If the flashes succeed one another more rapidly, the utilization of the light is not so good and the efficiency of each flash diminishes.

It is ordinarily concluded that the dark reaction, stimulated by photochemical excitation, is accomplished during this interval of $\frac{1}{80}$ second. Emerson stated that the minimum duration of this dark interval depended on the temperature and that it was affected by hydrocyanic poisoning. We must suppose, too, that excessive activation by light militates against a high efficiency of photosynthesis. We have already mentioned several manifestations of this—inhibition in excessively strong light arresting photosynthesis and intermittent lighting resulting in an increase of efficiency.

Emerson compared these results with those that would be obtained if the number of chlorophyll cells were limited. When the light has acted on one of them, other reactions, which can be accomplished in darkness, must take place before this cell becomes available for a new action of light. Before these reactions are completed, the light is without action and its energy is wholly unused. In the conditions of the experiment quoted, the duration of the re-entry into a state of receptivity is $\frac{1}{80}$ second.

This process must not be taken literally; it is only an hypothesis or a simple way of describing the principal results observed. Other hypotheses are undoubtedly possible and the real process is still unknown to us.

Emerson's Functional Units

The experiments with intermittent lighting introduce, according to Emerson, a new conception of very great interest—the idea of functional units, which is linked with that of the chlorophyll cells just described. The idea is introduced in this way.

If the illumination in continuous light is progressively

increased, the rate of photosynthesis increases up to a certain point, then remains stationary or even diminishes. The law of the minimum explains this by the deficiency of a factor other than the illumination. We have seen, for instance, that in an atmosphere enriched in CO_2 , the illumination can with advantage be raised to a higher intensity than it can be in a normal atmosphere.

In intermittent light, on the other hand, the dark periods can be adjusted to allow time for the various factors to come into operation. For example, the poverty of the air in carbon dioxide is compensated by a longer period of contact between the activated elements and the atmosphere, and the slowness of the reactions in a moderate temperature is of little importance if they are given sufficient time to be accomplished.

If, therefore, the dark intervals are always long enough, we ought to be able to increase at will the rate of photosynthesis by more and more powerful flashes, each bringing a greater luminous energy. This increase is certainly achieved, but only up to a certain limit at which the plant tissue is, as it were, saturated with light. Emerson, assuming as before that the chlorophyll cells are limited in number, affirms that at this moment they have all received sufficient luminous energy for each to combine a molecule of CO_2 and a molecule of H_2O and give off a part of the oxygen.

These chlorophyll cells, which are assumed to contain active chlorophyll and to be capable, at each flash when the tissue is saturated with light, of attacking a molecule of CO_2 , by a chemical process provoked by light and lasting about $\frac{1}{10}$ second, are called by Emerson "functional units".

The number of these functional units is easily determined, since, at saturation, each of them will reduce a molecule of CO_2 . Thus a measurement of the number of molecules absorbed per flash will give the number of functional units. For the alga, *Chlorella*, for example, there is one unit for about 2,500 molecules of chlorophyll.

Under the microscope, the chlorophyll in each chloroplast is seen to be arranged in minute globules called "grana".

It is possible that each granum represents one of Emerson's functional units, but it is also possible that there is no relation between these two kinds of groups, since one granum may, for example, attack several molecules of CO_2 and constitute several functional units and another granum may be inactive.

An hypothesis has been put forward that the molecules of chlorophyll may be arranged in monomolecular layers oriented at the surface of contact between a lipid phase, towards which the hydrophobe phytol groups would be turned, and a proteinic phase towards which would be directed the tetrapyrrol groups, which are hydrophile.

It is certain, in any case, that chlorophyll manifests its photosynthetic activity only in the particular structure of the chloroplast, without which it is powerless.

The Reducing Reactions of Photosynthesis

It is doubtless premature to try to describe in detail the chemical transformations of which the final result is interpreted simply by the formula:

a formula which expresses a reduction of CO_2 and of H_2O , i.e., an extraction of oxygen.

Nevertheless, several theories have been propounded, although they have not been proved experimentally.

As early as 1918 Willstätter and Stoll advanced the following hypothesis: as carbon dioxide and water are fixed to the atom of magnesium with a molecule of chlorophyll, the luminous energy causes a displacement of the atoms of oxygen and the formation of a structure of peroxide:

The peroxide group easily loses an atom of oxygen.

Wurmser's theory (1930) is based on a photolysis of water, dissociated into 2H_2 and O_2 by light—a dissociation, however, which it is impossible to effect in the laboratory under visible light. The hydrogen thus produced, or the energy of its recombination with oxygen, would be available for the reduction of carbon dioxide.

This theory is much simplified and the combinations concerned, in which the living matter of the leaf takes part, are, on the contrary, extremely complex. Nevertheless, it has just received very clear confirmation through the use of an isotope of oxygen.

Chemical elements are generally mixtures of atoms, the masses of which are very nearly whole numbers. Thus, ordinary chlorine contains atoms of atomic mass 35 and others of atomic mass 37. Both have exactly the same chemical properties and are never separated, except by certain long and delicate physical methods only recently used in laboratories. That is why they are always encountered in the same proportion, which gives the mixture an average atomic mass of 35.5, a value found in chemical textbooks. These two kinds of atoms are called isotopes of chlorine.

Similarly, oxygen possesses two isotopes, one of mass 16, the more abundant, and the other of mass 18, which is much more rare. An important result has recently been obtained through the use of this second variety of oxygen of atomic mass 18. This isotope is always present, mixed with the oxygen of mass 16, but in a smaller quantity. With oxygen enriched in isotopes of mass 18, water and carbon dioxide are prepared, and either the water or the carbon dioxide is offered to illuminated chlorella. Oxygen is given off during photosynthesis and the measurement of the atomic masses (by the mass spectograph) enables one to determine whether this oxygen enriched in isotope 18 is present or not in the gas liberated. The conclusion of these experiments is that it is the oxygen of the water that is given off. The overall reaction often written as

would be better described by two equations, one of which expresses this liberation of oxygen of the water. Wurmser propounded it in 1930 as

This then is a new fact which the theories must take into account. The result should be compared with the photosynthesis effected by purple sulphur bacteria using luminous energy for the synthesis of carbohydrates from CO_2 and H_2S . The latter compound, hydrogen sulphide, is chemically analogous to water, the oxygen being replaced by sulphur, but more easily dissociated.

This photosynthesis may be written in the following form:

Just as the element liberated, sulphur, can come only from hydrogen sulphide, so also, in plant photosynthesis, the oxygen liberated comes, as we have just seen, from water. The overall formula of plant photosynthesis should be written, by analogy:

a formula in which the oxygen of the water initially used is identified by the sign *O*.

Rabinovitch has evolved a theory, although there is still insufficient evidence to support it, of a rather complicated process taking these data into account.

He assumes the existence of two unknown catalysts, A and B, one of which is perhaps chlorophyll. A is capable of removing the hydrogen from water and of giving it up to B. B in its turn is capable of yielding this hydrogen to carbon dioxide. These three phases are written:

The square brackets indicate that $[\text{CO}_2]$ and $[\text{HCO}_2]$ are in combination with other substances.

At the same time as the last reaction, Rabinovitch supposes that the following is accomplished, the simultaneity rendering the whole process easier:

The photosynthetic action is terminated by:

The resultant of these five reactions is simply:

Rabinovitch says, without being able to state precisely which, that one of these partial reactions is caused by light. As the total energy necessary for the whole of these transformations is contributed by light, it would seem that the true photochemical reaction ought to be by far the most endothermic and thus to be clearly distinguished from the others. On this point at least his theory appears therefore rather defective. We can only confess our ignorance, as, of course, he does himself.

The identification of some of the intermediate products would be of the greatest interest. An experimental method is available, since a radioactive isotope of carbon can be separated and is easy to distinguish from ordinary carbon, even when it is present only in minute traces. If a plant is supplied for a short period of time with CO_2 containing some atoms of radioactive carbon, among the multiple organic compounds of the tissue of the leaf those which contain this special carbon can be recognized as the products which have just been created by photosynthesis. This distinction between the compounds just formed and those which were already in existence was scarcely possible before a label could be fixed to atoms of carbon by making them radioactive without modifying their chemical properties.

The use of isotopes opens a new, and certainly promising, line of research, for it has already given results conducive to a better understanding of plant photosynthesis and encouraged scientists to hope to extend their knowledge of one of the most essential processes for life.

Unanswered Questions

Experimental results fully confirm the photochemical character of photosynthesis—activation and accumulation of energy by the action of light, and chemical transformations, capable of being produced in darkness, resulting in the assimilation of carbon from the air. Nevertheless, several very simple but very important problems remain and at present their solution appears to the physicist to be difficult to foresee.

It is assumed, from experiments on the maximum efficiency of photosynthesis, that 4 quanta of light are necessary, and may be sufficient, for the formation of a formal group, combined or not. This statement alone gives rise to several difficulties.

The 4 quanta are absorbed in the tissue, doubtless by molecules of chlorophyll, on a molecular scale and at different points, separated from one another. It must of necessity be assumed that these 4 quanta of energy are capable of moving and of converging towards the exact spot where there is a molecule of CO_2 or of H_2O ; this transmission of energy must be made without loss and without degradation. Now, there is no phenomenon of this kind in any of the conditions physically known in the photochemistry of gases and vapours; resonance radiation is an example of a transfer of energy without degradation, but it occurs at random in any direction and not towards a precise objective.

There must be in the molecular associations of the chloroplasts an organization which is well adapted to this transfer and which does not exist in a gas. The energy is propagated in the form of electrons raised to high energy levels. These energy levels will have to be determined, as well as the laws which govern their occupation and the mobility of the electrons excited. This work has not even been started in the case with which we are concerned.

There is another difficulty related to the preceding one. If the time necessary for 4 quanta to attack the same molecule of chlorophyll is calculated, for an illumination of the order

of magnitude of those used in the experiments on efficiency, i.e., 1,000 times lower than sunlight, it is found to be fifty minutes.

Now, however low the illumination may be, photosynthesis begins immediately. We are forced to admit that the 4 quanta whose combined action on a single molecule of CO_2 is indispensable have not been absorbed by the same molecule of chlorophyll and that their energy has been propagated, directed—how, it is not known—from the point of absorption to the molecule of CO_2 about to be reduced.

These difficulties still remain, even if we assume the formation of intermediate compounds each of which requires for its creation only a part of the total energy supplied. If the first quantum gives a first compound A, the second quantum must then encounter A to form B, and so on. Moreover, from the beginning, an encounter, direct or indirect, is necessary between CO_2 and the activated molecule of chlorophyll, and all these phenomena are unimaginable without the transmission of energy.

Again, it must be remarked that the necessity for a cumulative action of 4 quanta ought, in conformity with what is known in physics of actions of that kind, to result in a very low efficiency at low illuminations and a very rapid increase of efficiency with increasing illumination, according to a 4th power progression. This means that if the illumination were doubled, the rate of photosynthesis ought to be 16 times greater. Nothing of the kind is observed; the variation observed is, within certain limits, a simple proportionality, as would be expected if a single quantum were sufficient to accomplish the reaction.

In fact, the number of centres excited the first time is proportional to the illumination; the number of centres excited the second time is proportional, not only to the exciting illumination, but also to the number of acceptors already excited. It is therefore proportional to the product of these two quantities and so to the square of the illumination. Similarly, the number of acceptors excited three times

will vary as the cube, and the number excited four times as the 4th power, of the illumination. This theory has been confirmed by the study of phenomena of excitation by light in gases.

There is, then, in photosynthesis, owing to a process still unknown, a new condition which this deduction does not take into account. These various problems are of almost insurmountable difficulty if we merely consider chlorophyll as being dispersed in the plant tissue, or even in granules, in a medium which serves only to support it, and we are forcibly reminded that these phenomena take place in living matter.

How are these "grana" which are revealed under the microscope organized? We can only form hypotheses which will need to be checked by experiment. It is an attractive but extremely difficult subject of study. The investigators who attempt it must possess a profound knowledge, not only of the biological phenomena of photosynthesis, and of the organic chemical compounds of the leaf on which there is much research still to be done, but also, and especially, of the interactions between light and matter in solids and particularly in colloids.

This physical study has scarcely begun even in simple cases. It seems, therefore, that our scientific knowledge is still insufficient to enable such a study to be successfully attempted, but the interest that it presents cannot fail to be a stimulus to the scientific, chemical and physical researches now in progress the results of which will bring new methods of exploring this mysterious and vitally important domain of plant photosynthesis.

CHAPTER IX

PHOTOSYNTHESIS AND PHOTOGRAPHY

Photochemistry in a Solid

ALTHOUGH for the moment we must abandon the attempt to understand in detail the process of plant photosynthesis, physical science has recently enabled us to describe the sequence of elementary actions by which light decomposes silver bromide in a photographic emulsion. A remarkable theory of the formation of the latent image and of the total decomposition of silver bromide under the prolonged action of light was propounded by two English physicists, R. W. Gurney and N. F. Mott, in 1938. On the basis of modern theories of the ionic structure of chloride, bromide or iodide crystals of monovalent metals, and of the experiments of Gudden and Pohl on alkaline salts in this category, they succeeded in giving an almost complete description of the principal photographic phenomena, which then appear as a direct result of the properties of the ionic constituents of silver bromide crystals arranged in a crystal lattice.

It must be stressed that the chemical decomposition

is much simpler than the photosynthetic reaction in which carbon dioxide, water and the photo-catalyst, chlorophyll, take part—a reaction which occurs only in the living plant.

But this photographic theory is one of the first to explain the chemical action of light on solids, which is much more complex than that on gases, for the molecules are no longer isolated from one another, but are well organized with almost perfect regularity in a crystal lattice. The exchanges between molecules are not limited to accidental shocks, but are governed by the structure of the crystal itself.

Thus, in spite of the simplicity of the photographic action compared with the photosynthetic action, new analogies appear and the theory of Gurney and Mott provides a pointer towards the solution of the difficulties mentioned at the end of the last chapter.

What constitutes the photographic action of light on silver bromide? If bromide paper, i.e., paper covered with a layer of gelatine in which a number of grains, or small crystals, of silver bromide are submerged, is exposed to sunlight, it soon turns black. Each grain of bromide is progressively decomposed; the bromine escapes and leaves the silver in the form of colloidal black grains.

If the sensitized paper, instead of being exposed to intense sunlight, is partly exposed to a lower illumination for a few seconds only, no blackening is visible. Nevertheless a modification has taken place; a "latent image" has been formed, for when the paper is plunged into a suitable reducing solution (the developer) the parts which were exposed to the light are seen to darken in a few minutes, while the parts which were protected from the light still remain white. This is called the development of the latent image, which prolongs the invisible action of a short exposure to light. It is agreed today that this latent image is imprinted in the gelatine emulsion in the form of a few atoms of free silver in the grains of bromide on which the light has acted.

One can explain why the developer attacks these grains in preference to others. Thus, whether the light is made to act for a short period to give an invisible latent image which can be brought out in a developer, or for a longer period until blackening is produced, the photochemical effect is manifested by the liberation of metallic silver.

Two observations play an important part in the theory. The first is that a large crystal of silver bromide—an electrical insulator—becomes a conductor while it is receiving the light; the second is the accumulation of silver, in small crystals of irradiated bromide, in grains visible under the microscope. Now, the quanta of light are absorbed in each

crystal at points dispersed at random; the energy of each quantum, necessary for the liberation of an atom of silver, is available and is effectively used at the point where the absorption has taken place, the absorption of light being, by definition, the transformation of luminous energy into a different form of energy. It is therefore at these dispersed points that one would expect to find the atoms of silver, which means that a grain of bromide would become uniformly grey.

By what means of transport, by what directing influence, can this grouping of the atoms of silver in visible grains in the same region of the crystal be explained? The theory of Gurney and Mott makes this clear.

It may be recalled that in photosynthesis the energy of 4 quanta, which were necessarily absorbed at dispersed points, must accumulate for the reduction of a molecule of carbon dioxide, which presupposes a directed transport of the absorbed energy towards a fixed goal. The now familiar phenomena of the photochemistry of gases did not offer any analogous example. The photochemistry of silver bromide shows such a transport and it can be explained. New possibilities are seen to exist in an ordered solid structure, like the regular periodic structure of crystals, that may be considered as a rudimentary outline of the organized structures of living matter.

Growth of the Grains of Silver in Light

Before describing Gurney and Mott's conception of the photographic action, let us consider the internal architecture of a crystal of silver bromide. A crystalline grain contains an equal number of bromine ions and silver ions (not atoms). The first have one electron more than atoms of bromine and the second one electron less than atoms of silver and are thus denoted by the symbols Br^- and Ag^+ . They are arranged like a regular pile of cubes and form a three-dimensional rectangular lattice. On all the lines parallel to the edges of these cubes, the two kinds of ions succeed one another

alternately, so that a bromine ion Br^- is surrounded with 6 silver ions Ag^+ and, reciprocally, an ion Ag^+ is surrounded with 6 ions Br^- .

In a photographic emulsion, these grains have linear dimensions of the order of one micron; like the grana of green plants, they contain a number of ions amounting to hundreds of thousands of millions. In moderate illumination, they each absorb about a hundred photons per second.

We have said that they become conductors of electricity under the influence of light. This is explained by assuming that a bromine ion, having absorbed the energy of a photon, ceases to retain its supplementary electron and becomes a neutral atom, while the electron escapes in the crystal lattice. An electron, in such a lattice, as is shown by calculation, is free to move in almost any direction; it can therefore be instrumental in carrying a current in an electric field. These electrons, having become free and being set in motion by thermal agitation, may obviously finish up by finding again either the atom of bromine that they have left, or another one, recombining with it and restoring the initial state. But, if there is already in the bromide crystal a small aggregate of silver, a consideration of the energy levels in the bromide and in the silver shows that a free electron passing into the vicinity of a grain of silver will be captured by it and will be unable to escape.

If, therefore, grains of silver are present in a bromide crystal, they will accumulate to themselves nearly all the electrons liberated by light until the negative charge of electricity acquired is sufficient to repel the oncoming electrons unless the grains of silver can become discharged by receiving positive charges. This is exactly what happens.

At ordinary temperature, the crystal lattice does not possess the perfect regularity described. As a result of thermal agitation, a small number of Ag^+ ions, positive ions, are not in their place, but have become intercalated in the lattice; for example, in the cubes whose outsides have ions of the normal structure there are "voids" at the centres. These ions are able

to move and, attracted by the negative charge of the grain of silver, attach themselves to it and there neutralize an electron by becoming atoms. This explains both the discharge of the grain of silver, which will be able to collect new electrons, and its increase.

To sum up, in a grain of bromide, already containing some grouped atoms of free silver, the electrons snatched from the bromine ions by light are captured by the silver, and this negative charge assures the increase of the grain of silver by attraction of the Ag^+ ions wandering in the crystal.

Such, in outline, is the process of the decomposition of silver bromide under the action of light. It still does not show how the grain of silver comes to be formed, but only how it grows. It grows because it is a trap for electrons; by assuming that such traps, of another nature, are present at the surface of the grains of bromide, we can understand that a grain of silver will be formed there during irradiation.

Sheppard had already shown, before this theory was formulated, that photographic sensitivity seemed to be localized at certain points of the grains of bromide at which small spots of silver sulphide had formed; it was known, in fact, that silver salts easily become sulphurated when the atmosphere contains traces of hydrogen sulphide. These traces of silver sulphide must act as traps for electrons at the surface of the grains of bromide, but only on condition that the energy levels for the electrons are lower there than in the bromide, which is very probable.

It therefore appears easy to explain the origin of the grains of silver at certain superficial points, and then their growth, by processes of the same nature.

The Influence of Temperature

The authors of this theory also explain why, in strong illuminations, the sensitivity of photographic plates diminishes when they are cooled (Webb's experiments on this subject extend over the temperature range $+50^\circ$ to -75°C), while, on

the contrary, it increases in very low illuminations given for a proportionately longer exposure time.

In other words, if the same quantity of light is sent several times on to different parts of the same sensitive plate, first by strong illumination of short duration, then by lower and lower illuminations of longer and longer duration, the darkening of the plate will become fainter and fainter, at a temperature maintained at $+50^{\circ}\text{C}$, and, in contrast, stronger and stronger at a temperature of -75°C .

These observations may be compared with those relating to photosynthesis. The latter, although more complex, may be summarized, as regards the essential facts, as follows: at ordinary temperature, strong illuminations of short duration are more effective than continuous illumination of the same average value. The influence of variations of temperature, within the limited range in which the plant can still live normally, is difficult to determine and depends on other conditions. To consider only this factor, as in photography, it assists or checks the action of light according to the level of illumination.

It is therefore interesting to have, for the simple case of photographic blackening, the explanation given by Gurney and Mott of phenomena analogous to those of photosynthesis.

In strong illumination, free electrons are abundantly produced in the silver bromide; in its formation the grain of silver collects a larger number, and its increase in size depends only on the speed at which the Ag^{+} ions detached from the lattice by thermal agitation can reach it. The higher the temperature, the more numerous the ions are and the more freely they move. At a low temperature they do not arrive in sufficient quantity to neutralize the electrons being liberated by the light and the formation of the grain of silver is checked.

At very low illuminations, the stray Ag^{+} ions are numerous enough not to hamper the increase of the grain of silver, but the photo-electrons are rare. Gurney and Mott explain that the grain of silver in formation captures them

easily at a low temperature, but at a higher temperature the electrons tend, at the same time, to escape from the metal. This is the classic thermionic effect—a sort of evaporation of electrons. The grain of silver remains negatively charged only if it is surrounded with an “atmosphere of electrons” the pressure of which is sufficient to prevent this evaporation.

Therefore, in a poor light and at a high temperature, the light is badly used; the electrons that it liberates in the bromide do not succeed in fixing themselves on the grain of silver, which does not increase in size in default of a negative charge capable of attracting to it the available stray silver ions.

The different properties of silver bromide emulsions according to temperature and intensity of illumination are thus explained.

Put in this way, the theory offers an analogy with the “law of the minimum” often referred to in photosynthesis; the least active of the factors which take part in the accomplishment of a photochemical transformation slows down all the operations and determines the speed of the reaction.

The merit of the theory of photographic blackening is that it gives in detail a description of the phenomena within the framework of the conceptions of atomic physics and enables us to understand in a more concrete fashion how analogous processes may be performed in the photosynthetic organ of the plant.

The Action of Sensitizers

Gurney and Mott also explain the action of sensitizers. The first photographic emulsions were sensitive only to the blue, the violet and the ultra-violet, but not to the green, the yellow, or the red. The incorporation of certain colorants in the emulsion enabled the sensitivity to be extended to the whole of the visible spectrum and even to the near infra-red.

These colorants are adsorbed at the surface of the grains of bromide. They, and not the bromine ions of the crystal lattice, absorb the light and provide the free electrons.

Analogies with Photosynthesis

The essential processes in this theory of the photochemical reduction of silver bromide may be divided into three successive phases:

(1) The absorption of light, either by the bromine ions or by molecules of the adsorbed colorant, each photon yielding its energy to detach an electron which becomes capable of moving some distance from the ion or from the molecule from which it was extracted;

(2) The grouping of these electrons in a few places where they are more or less immobilized in a relatively stable energy state—on a small grain of silver or of sulphide present at the surface of the grain of bromide;

(3) An attraction, starting from the electrified centre thus constituted, of the stray Ag^+ ions which collect there, each taking an electron, becoming neutral atoms and progressively forming a colloidal grain of silver.

It is probable that three analogous functions exist also in photosynthesis and that this theory will be useful to those investigating it.

As we have said before, the chemical constitution of silver bromide is much simpler than that of chlorophyll. The theory of Gurney and Mott takes into account the irregularities of crystalline structure caused by thermal agitation, and the Ag^+ ions which have left their normal place play an important part in it. Superficial spots of sulphide or silver where the free electrons are captured have also had to be considered. In modern orthochromatic emulsions, it is not generally the bromine which absorbs the luminous energy, but added colorants. Thus, even without mentioning crystalline defects, edges, cracks, and other factors which have been passed over for simplification, we are far from the ideal periodic and monotonous structure of an edifice of Br^- and Ag^+ ions alternating in the meshes of a cubic lattice; the lattice is rather a sort of support in which impurities and irregularities play active parts. Even the gelatine in which the grains of bromide are embedded is important in Gurney and Mott's theory.

In the molecule of chlorophyll, associated with other molecules of the living plant in which photosynthesis is effected, nature has doubtless created an organization in which these active roles have devolved upon groups of atoms which are constituent parts of the molecules and not upon impurities or accidents of structure.

It seems certain that the group of atoms where the luminous energy is absorbed is situated in the chlorophyll because the radiations absorbable by chlorophyll and the radiations capable of producing photosynthesis are identical. It is in this group of atoms of the chlorophyll that an electron is displaced by the energy of the photon absorbed.

What happens afterwards? Since isolated pure chlorophyll is inactive, what are the molecules of the living plant which must be associated with it to produce photosynthesis?

The recent success of the photographic theory holds out I hope that these questions will be answered.

CHAPTER X

PHOTOTROPISM

Principal Facts

EVERYONE has noticed that an indoor plant placed near a window grows towards the light and that it has to be turned every day to keep the growth symmetrical. A simple experiment can be made with oats sown in a box receiving the daylight laterally. The seedlings shoot easily and instead of growing vertically are all inclined towards the direction from which the light comes. Light therefore has a considerable influence on the growth of plant cells.

These facts may be compared with the great difference in appearance between potato shoots kept in the light and those kept in the dark. In the light, they remain short, squat and coloured; in the dark, they stretch out into thin stems and have the characteristics known as etiolation, although there is no lack of nutritive substance because the tuber is full of it. But among the many phenomena distinguishable in etiolation we are concerned here only with the rapid growth in darkness.

When a plant is illuminated on one side only, this side grows less quickly than the other which is in the shade, hence a curvature is produced which directs the tip of the stem towards the light. This influence of light on the inclination of the tip of the stem is called phototropism.

Owing to phototropism, plant stems are directed from regions with less illumination towards those with more. Thus, parts of the same plant, like the branches of a tree, or different plants in a group, like the blades in a field of unripe corn, do not bunch themselves together in the same place, but, on the

contrary, space themselves out with a certain regularity to make the best use of the light. Phototropism is therefore a very important factor in agriculture, as it is in forestry, although its action is imperceptible.

Effective Radiations

White daylight is a mixture of radiations of different wavelengths. Have all these monochromatic radiations the same influence on growth? Johnston's experiments in 1934 showed that the blue and the violet of the spectrum are the only radiations really effective for phototropism.

He illuminated a young oat plant on one side with green spectral light and on the other with blue spectral light. If the plant inclined towards the source of blue light, he concluded that the blue has a greater retardative influence than the green.

In order to measure this retardative influence, the more active blue illumination was reduced, or the green illumination increased; then a new oat stem was placed between the two sources of light and the experiment continued until a vertical growth was obtained, the unilateral action of each of the two radiations then being balanced. At this moment the energy of the two radiations was measured.

After a series of measurements of this kind, a curve can be drawn giving the sensitivity of the oat stem for radiations of the same energy as a function of the wave-length. The curve, reproduced in Fig. I, 15, shows that the retardative activity of light is due almost solely to radiations between 0.4 and 0.5 μ , i.e., those situated in a spectral region to which the human eye is only very slightly sensitive. It would be possible to produce the growth curvature of a stem with practically invisible light by using the wave-length 0.4 μ . By way of comparison, the dotted curve indicates the curve of average luminosity of the different radiations of the spectrum to the human eye. It may be recalled that the blue rays prevent etiolation and are necessary to the balanced development of the higher plants.

What is the process of this particular action of blue light? Light can only cause the activation of certain chemical molecules which absorb a light quantum. These activated molecules then become capable of entering into reactions which

Fig. I, 15. Curves of relative efficacy of radiations for phototropism as a function of wave-length, according to Johnston, 1934. *Dotted curve:* curve of visibility to the human eye. *Broken curve:* curve of efficacy for photosynthesis

otherwise would be impossible for them, so that light may have the effect, either of starting a chain of new chemical transformations, or of transforming the sequence of reactions at one of its stages and modifying the result.

Auxins

An action similar to that of phototropism is produced by a substance, or a class of substances, called auxin, which behaves like a growth hormone. It is present in the coleoptiles of young oats, principally at the tip. If the tip is cut off and placed on a piece of gelatine, the gelatine collects a small quantity of auxin, as is shown by the following experiment.

The piece of gelatine is placed on the side of an oat stem from which the upper part of the coleoptile has been removed. The growth of the stem then becomes asymmetrical; it grows more on the side which has received the gelatine and bends. With this substance, therefore, the reverse effect of the retardative action of light is obtained. Apparently, light checks either the production, or the transport, or the activity, of auxin.

This description is merely a summary and greatly simplifies the complex phenomena which are really observed. Thus, a certain quantity of light, given for a short time to a plant kept temporarily in the dark, may produce, either a reduction of the rate of growth, for a duration of the order of an hour, or, on the contrary, sometimes an increase, manifested by an effect which is the reverse of phototropism in these particular conditions. Much research therefore remains to be done to elucidate this phenomenon of phototropism.

As in all investigations on the action of light, the experimental conditions can be specified only by giving the energy curve of the radiation used; the illumination in lux signifies very little, since this photometric unit has been created to characterize the luminous effect of the radiation on the eye and the sensibility of the human eye to different radiations is very different from that of the plant.

CHAPTER XI

PHOTOPERIODISM

Definition of Photoperiodism

LIGHT, the principal nourishment of green plants, must be given to them in sufficient quantity and not in excess. It must be of suitable composition, without injurious ultra-violet and without too much infra-red; natural daylight is in general well adapted to them. There remains a third factor which is extremely important—the length of the day and night.

The same quantity of light may be offered each day in a number of different ways, either by strong illuminations for a few hours followed by a long night, or by lower illuminations spread over a longer “period” and followed by a short night. The development of the same plant under these varying conditions may be profoundly different. With a certain period of daylight, a plant may be incapable of producing either buds, or flowers or fruit; one species of onion will not form a bulb; another tuberous plant will remain without a tuber; a tree may remain in leaf until the winter and be killed by the frost, while the same plants, supplied with the same quantity of light, on the same ground and at the same temperature, but with suitable periods of daylight and darkness, will flower, produce seeds, bulbs and tubers and resist the winter frost.

These curious consequences of daylength, which were called “photoperiodism” by the two Americans, Garner and Allard, who drew attention to them in 1920, are therefore of considerable economic importance. For example, a species adapted to the long summer days of northern climates may be incapable of developing at a lower latitude, even if the temperature is the same, because the summer days are shorter.

Chrysanthemums may be made to flower earlier or later, by artificially lengthening the day with electric light, or by shortening it with opaque material covering the plants.

A thorough knowledge of these phenomena would be of great advantage in obtaining a better yield of crops. This investigation is in progress, but will inevitably take a long time for several reasons.

Photoperiodism is still rather mysterious. It is strange, for example, that a very low illumination, of 5 to 10 lux—10,000 times lower than the maximum illumination from the sun—given at nightfall for a few hours to lengthen the day, is sufficient to produce a fundamental change in the development of a plant. It cannot be said that chemical substances elaborated by the plant, necessitating a luminous activation for their synthesis, will be produced in sufficient quantity only after a rather long period of daylight, for then the quantity of light would be important and not its duration.

Perhaps certain slow syntheses are possible only when the action of the light is sufficiently prolonged, perhaps others go beyond the stage of their accomplishment to give other combinations if darkness comes later. Such stringent demands can be imposed only for the synthesis of compounds of a complex structure, produced in very small quantities, as is shown by the action of very low illuminations, and acting as catalysts or organizers, rather like the genes which transmit all the hereditary characteristics in the single cell of the egg.

The observations themselves, and their diversity and complexity, make this necessary study difficult. Experiments can give useful results only under two conditions:

- (1) The species and variety under investigation must be specified, for the behaviour of similar varieties may be very different;

- (2) As always, not only the duration, the intensity and the composition of the illumination must be stated, but other circumstances as well, and particularly the temperature, which plays an essential part in the photoperiodic action of daylength.

Obviously such a study is lengthy, but clear and definite results have already been obtained. Here we give a few characteristic examples in which the influence of the day-length is manifested by particular aspects.

Short-day Plants

Two pots of chrysanthemums, A and B, are cultivated when the natural day is short and the night long. They are tended in exactly the same way, except that at night A is illuminated with an electric lamp, while B remains in darkness. During the day, both are illuminated normally in natural daylight.

Pot A receives a nocturnal illumination of about 50 lux—1,000 times lower than the natural light on a rather bright day. This supplementary light, too weak to modify the nutrition of the chrysanthemum through photosynthesis, reacts profoundly on its development, and no flower buds appear.

On the other hand, pot B, which is not illuminated during the night, flowers normally. Flowering has been prevented in pot A by a very small quantity of supplementary light given throughout the night.

If the same experiment is repeated with a stronger lamp for only half an hour in the course of the night, flowering is still suppressed. In order to flower, the chrysanthemum requires long *uninterrupted* nights of from twelve to sixteen hours, according to the variety.

The flowering of the chrysanthemum can be retarded at will by night illumination before the formation of the buds, that is, from 15th August. According to some American experiments, an illumination of 100 lux is perfectly suitable and can be interrupted every other minute, giving the same result more economically than by continuous lighting.

Conversely, if the length of the day is shortened in the summer, flowering will be produced earlier, and this process is already being used to advance flowering by one to two weeks. At five or six o'clock in the evening, black cloth, which may be rubberized or not, is stretched on frames surrounding the

plants and removed at seven o'clock in the morning. The "black-out" must be done with great care; the screens should be well arranged and opaque enough to reduce the illumination on all parts of the plant to $\frac{1}{10,000}$ of the normal illumination.

Other plants which require long, uninterrupted nights to make them flower are begonia, cosmos and *Poinsettia pulcherrima* (the night temperature must be maintained between 14° and 10° C.).

There is also the economically important Mammoth tobacco of Maryland, which does not flower or produce seeds in the summer in the State of Maryland (latitude 39° N.) because the days are too long, but does so when it is cultivated in a glasshouse in the winter with long nights. In the south of Florida (latitude 26° N.) it also flowers in the winter. There, again, low supplementary illumination at night is sufficient to prevent the flowering entirely.

In our latitudes, plants which form buds and flowers when they are subjected to long nights find these conditions naturally at the end of autumn, in the winter and at the beginning of spring. In the summer, it is necessary to lengthen the night artificially to make them flower.

Long-day Plants

Some plants, on the contrary, require long days and short nights and begin to flower naturally only in summer.

Nasturtium (*Tropaeolum majus*), cultivated at a temperature of 17° to 18° C., does not flower if the days are short.

China-aster (*Callistephus chinensis*) flowers at a temperature lower than 24° C. only with short nights. When the temperature is above 24° C., the length of the day makes no difference.

Centaurea cyanus, *imperialis* and *suaveoleus* flower only during the long days. Supplementary lighting from October to March hastens the flowering and makes it more abundant.

Other plants like lupin, Buddleia and *Browallia* are indifferent to the length of the day and night.

General Characteristics of Photoperiodism

This division into three categories—long-day plants, short-day plants, and those indifferent to daylength—has the advantage of simplicity and is useful for classifying plants raised within a specified range of temperature.

Some interesting facts relating to photoperiodism have been learnt from the recent work of Professor P. Chouard and others in France and from that of investigators in America and Russia. The experiments were made on plants cultivated under normal conditions, i.e., in rich soil and receiving, at least for the greater part of the day, the illumination without which plant life is impossible.

The necessity of long nights for the flowering of the chrysanthemum is most probably due to the slowness of the nocturnal chemical reactions which are indispensable for the transformation of the terminal buds into flower buds. These reactions obviously start with the substances elaborated through photosynthesis, from which most of the organic compounds constituting nearly the whole of the plant are derived. They are completed only if their chain remains unbroken by light. It is not surprising that they, too, like all chemical reactions, are dependent on temperature; if the temperature is too high (38°C.) or too low (10°C.), they do not achieve the expected result with long nights and the buds are not formed.

On the other hand, the action of light in preventing flowering remains effective whatever the temperature may be, which seems to indicate that light acts directly on one of the substances whose chain of transformations ends in the production of buds.

These substances have not yet been isolated and their nature and composition is still uncertain. They can, however, be made to pass from one plant to another, which shows that they are similar in character in spite of the difference in the behaviour of species.

If a short-day plant, A, is cultivated in the summer, it does not flower because the nights are short, but when it is

grafted on a long-day species, B, which produces in the summer the substances for flowering, they spread to A and cause it to flower. The experiment has been successful with Jerusalem artichoke as the short-day plant A, grafted on a sunflower as the long-day plant B. It was found necessary to strip plant A of its leaves, which shows that the principal action of light in preventing the flowering of short-day plants is on the leaves and not on the buds where the transformation is most apparent.

More direct experiments have proved that the action of light on flowering is effected through the leaves, and through adult leaves, not through those which are too young. We have seen that the chrysanthemum can be brought into flower before the normal date if it is withdrawn from the light in the evening and in the morning to lengthen the night artificially but allowed full daylight in the middle of the day to ensure its normal nutrition. But if the whole plant is not withdrawn and a black cloth is wrapped round the lower part to cover only the adult leaves, which are then subjected to long nights, flowering is stimulated just as effectively although the terminal buds, where the flower buds appear, are still subjected to short nights. Conversely, if only the terminal buds are covered, flowering is not produced. It is therefore the length of the day on the adult leaves which is important and it is in them that the chemical reactions necessary for the production of flowers, and then of seeds, take place.

Other experiments in which buds have been made to appear on the lower part of the chrysanthemum stem by partial covering of the plant show that, if the adult leaves only are given a long night, flowering is produced as effectively above them as below them. The substances which cause flowering are therefore transported just as well downwards as upwards.

These substances circulate through the bark and can be arrested by incisions.

The influence of the composition of the radiation has scarcely been investigated. Are incandescent lamps the most

suitable for supplementary lighting? On the gillyflower, a long-day plant, flowering is stimulated by the orange red, the red and the extreme red. The green, blue and violet rays, of shorter wave-length, and the infra-red, have no effect. On a short-day plant, *Salvia*, which normally flowers in the autumn, artificial lengthening of the day prevents flowering; there again, it is only the red light which is effective in suppressing the formation of buds when supplementary lighting is given at night. If these observations prove to be of general application, incandescent lamps, rich in red radiations, will be satisfactory. Neon tubes would be even better.

Treatment by light can give more complex results connected with flowering. For instance, deformed buds will appear on chrysanthemums if the plants are kept in darkness for ten days in July and then left in the light for the natural length of the day.

If the period of darkness is prolonged until the buds appear, their development is no longer subject to the same conditions and they will still be formed. This does not mean that the light has no effect; if the days are lengthened, the capitula will be fuller and the ligules narrower and tubulous; if the days are short, the flowers will be deeper-set and the ligules flatter and more unfolded.

But the length of the day affects many other processes besides flowering, and there are many different actions which are still grouped under the name of photoperiodism.

A late variety of potato, McCormick, cultivated in summer at a rather high average temperature, remained without a tuber when supplementary lighting was given from nightfall to midnight; a subterranean eye, which would normally have formed a tuber, lengthened into a new stem. From other experiments with various daylengths, the conclusions were that the best useful crop resulted from a day-length of thirteen hours; nevertheless, longer daylengths give larger plants and a greater total weight—stems, leaves and tubers included.

These conclusions obviously relate only to this particular

variety; other varieties may react differently. When potato seeds are selected, the daylength should be considered with the planting date and the latitude of the district in which the crop will be cultivated.

The form of dahlia roots, tuberous or fibrous, also depends on the length of the day; the tubers containing stored food appear only when the day becomes short. The *Silverskin* species of onion, if it is kept with a rather short daylength of ten hours, remains more than twelve months without forming either bulb or flower. On the other hand, if the day lengthens, as it does naturally in the summer in our latitudes, the bulb forms and grows and flowers are produced, the plant then becoming dormant and resuming later, during the short days of autumn, a new activity of growth.

As a general rule, the formation of tubers is checked when the days are too long and the formation of bulbs when the days are too short. But here again, different species and varieties behave in a different way.

The distinction between annuals, biennials and perennials is generally a consequence of the seasonal variation of the daylength. This would be shown by the difference in vegetation in different latitudes if the temperature and humidity conditions were the same, and is shown by experiments in the daylength modified artificially.

The light conditions which promote flowering accelerate the life-cycle of annual plants and cause them to die earlier. But if they are brought into conditions of daylength which prevent flowering, they resume the course of their growth. Thus, with the soya bean, two cycles of development and growth can be made to alternate in four months.

Ligneous plants, like trees, are greatly influenced by the length of the day. *Salix lanata*, for example, which thrives at high latitudes, with very long summer days, does not grow well at Leningrad, where the days are shorter, until the beginning of the winter.

On the other hand, *Robinia pseudoacacia*, originating from lower latitudes, with shorter summer days, is overtaken by

the winter and destroyed by frost before it enters into its dormant period. Dormancy can even be retarded, with the same results, by supplementary lighting at the top of the tree.

The Economic Importance of Photoperiodism

The influence of the daylength, natural or artificially modified, therefore has considerable practical importance. Since the daylength and its seasonal variations depend on latitude, the selection of crops ought to take into account the effects of photoperiodism scientifically studied and combined with other effects which vary with the geographical situation, such as temperature, rainfall, humidity of the atmosphere and nebulosity.

One example is wheat. Australian varieties are early and do not do well in England; English varieties are late and give poor results in Australia. These different varieties have been tried with different daylengths, modified artificially, and it has been shown that the length of the summer day, which is shorter in Australia (latitude 38° at Melbourne) than in England (latitude 52°), is at least one of the causes of these failures.

CONCLUSIONS

WE have tried, in the preceding pages, to give the reader an idea of what is known, and also of what is not known, of this vast and varied subject of the relationship between light and vegetation. As our knowledge advances, new problems arise, as well as new methods of approaching them. The means at the disposal of research today appear enormous; in fact, methods of measuring radiations, formerly neglected, are extending rapidly and will soon be in the hands of biologists; organic chemistry is advancing and radioactive indicators provide a new and very promising tool for biological chemistry.

Beside the recent methods available to laboratories, the knowledge already acquired has practical applications of not inconsiderable economic importance. Certainly, the cost of electricity is too high to make one despise natural daylight, but plants can be cultivated successfully in entirely artificial light. G. Truffaut was one of the first to do this from 1929–1933 by illuminating oats with overrun incandescent lamps. Generally speaking, the use of artificial light to extend the natural day has the best chance of being economic, either for bringing on early vegetables or for obtaining a photoperiodic effect. Large lamp-manufacturing companies have studied various special lamps for these purposes and have taken an interest in the subject for many years.

The action of natural light can also be modified by powders or sprays, which appreciably change the optical properties of leaves. This has been confirmed at the Institute of Optics, and it is certain that agricultural washes do not have only a chemical effect.

Such applications will be further developed as science enables us to acquire a better understanding of plant life—a life in which the importance of light becomes more and more evident.

PART II

CHLOROPHYLL AND ENERGY

Jules Carles

INTRODUCTION

So eager are we for energy that anything we think capable of supplying it will capture our interest. The atom has just made a triumphant entry into our schedule of resources because we see the possibility of using the energy that lies hidden within it.

The general infatuation for these new sources must not make us forget or underestimate our most solid capital, on which we have lived up to the present, which feeds us, clothes us and warms us—the energy stored and put at our disposal by chlorophyll.

Is it possible to overestimate the importance of chlorophyll? We can do without atomic energy and until today humanity lived without having discovered it, but, without chlorophyll, no man and no animal could survive a day on earth. Millions of centuries before the first man saw the light, the humble and discreet chlorophyll in the remote past prepared for his coming.

In making known the work of this most indispensable servant of life, we shall recall first how its role and its importance were discovered and show that we have recently been able to form an idea, although still very imperfect, of the nature of its activity.

We shall introduce, then, chlorophyll, that substance—or rather those chemical substances—located in the chloroplasts of green leaves, study its general properties and see how it appears, works and disappears.

Although we do not know exactly what happens inside the leaf, the progress of biochemistry, of which this is perhaps the greatest achievement in the last ten years, has enabled us to acquire some understanding of the chemical processes of photosynthesis or assimilation. Later we shall examine the

result of photosynthesis, showing how it is measured and the various factors which influence it.

We shall then be able, in a final and less technical chapter, to consider the place of chlorophyll in the world and its role in relation to ourselves. We shall see how much we depend on it, since the energy which it collects, and by which we benefit, enables us to occupy, close to it, our place in the sun.

CHAPTER I

HISTORICAL

THAT admirable naturalist, Aristotle, knew the physiology of animals very well and it was through them that he tried to understand plants and their life. The latter draw from the soil their nutrition, which is so well dissolved and digested in the water that it has no more modification to undergo. The vegetable organism may therefore be extremely simple, or may indulge in the luxury of green leaves, the sole purpose of which is to protect the fruits against the burning sun.

In the seventeenth century, a Dutchman, Van Helmont, convinced that the plant was nourished not with soil, but with water, made the following experiment. After filling a large pot with 200 lb. of well-dried earth, he planted in it a willow branch weighing 5 lb., watered it regularly with rain-water and placed a cover over the surface of the soil to prevent dust being added to it. At the end of five years, the willow had grown and weighed 169 lb. The earth was dried again and weighed; only 2 ounces had been lost. His conclusion was that "it is not with soil that plants are nourished but with rain-water, from which they elaborate all their substance."

Towards the end of the eighteenth century, the Italian, Malpighi, discovered the importance of the leaves. He had observed that a young plant will not germinate if its cotyledons are suppressed. After giving much thought to this experiment, he concluded that the capital transformation—the assimilation or, more precisely, the digestion of the substances absorbed by the roots—is made in the cotyledons or leaves to which the plant transports these substances through the vessels and where, with the help of the sun, the raw material is transformed into living matter.

Some precise ideas began to be formed, and Malpighi already suspected the importance of the air for respiration, but it did not occur to anyone that any substance whatever could penetrate into the plant otherwise than through the roots.

Gaseous Exchanges

Nevertheless, at this period research started on an entirely new line. In 1769, Bonnet, a Swiss, plunged a twig of vine in water, in full sunlight, and saw that bubbles escaped from the leaves. Did they come from the leaves or from the water? Bonnet boiled the water, then plunged the leaves in again; no more bubbles appeared and he concluded that they had come from the water and not from the leaves. Moreover, even dry leaves produced bubbles in well-aerated water.

Such experiments would have been only an obstacle to progress if Priestley, an Englishman, had not become interested in these bubbles and observed that they consisted of very pure air, perfectly suitable for the respiration of animals. From this he concluded that the respiration of a plant was diametrically different from that of an animal, the one using what the other rejected. Vitiating air that an animal could no longer breathe was purified by the presence of a plant. And did not Priestley hint at all future discoveries on this subject when he said, in terms that had not then been explained by Lavoisier, that the plant dephlogisticates the air?¹ "It follows that the phlogiston of the air is retained in the interior of the plant and is there used for the work of nutrition."

A Dutchman, Ingen-Houss, affirmed that this purification of the air was accomplished only in sunlight and by the green parts of the plant and that it consisted in a fixation of the carbon of carbon dioxide. In darkness, particularly during the

¹As phlogiston was the principle of inflammability, dephlogisticated air became incapable of burning. (Today we say that a substance which has been burnt is saturated with oxygen and has not suffered any loss.) These old investigators thought that the plant built itself up by taking phlogiston from the air and accumulating it.

night, plants did not purify the air but vitiated it, as did the breath of animals.

Senebier, a Swiss, resumed the experiment that Bonnet had so misinterpreted and showed that, if green leaves plunged in water released bubbles, they could do so only in the presence of carbon dioxide that sunlight enabled them to decompose.

At the beginning of the nineteenth century, the great Swiss physiologist, Théodore de Saussure, assembled all these ideas, extracted what was valuable from them and demonstrated the action of the plants by well-arranged experiments. Thanks to him, the problem was clearly posed, and he established a schedule exact enough to show that the increase in substance exceeded the weight of carbon retained: carbon combined with the elements of water in the plant to form plant material.

It was difficult at that time to say more, and A. de Candolle wrote, in 1835, with a charming naïveté, that there did not seem to be many more discoveries to be made in this field.

“As a result of the work, in particular, of Senebier and of Théodore de Saussure, the circumstances and consequences of plant respiration are today very well known.

“The only organs showing this phenomenon are the parts coloured green, principally the leaves. The green colour is not the cause of the chemical action; it is, on the contrary, the effect of it. It would be more exact to say that plants and organs which give off oxygen are coloured green or that they become so; but as it is easier to judge of the colour than of the chemical action, we use rather the reverse expression and say that oxygen is given off by the green parts. The colour is an indication and a criterion.”¹

It was not until the German, Sachs, linked assimilation with chlorophyll and the chloroplasts that justice was done to the green parts. “Carbon is fixed by the leaves in the form of starch from which all the organic products are elaborated.”

Thus was defined the role of photosynthesis that the French physiologists, Garreau, Boussingault and Claude Bernard, had just clearly distinguished from respiration.

¹*Introduction à l'étude de la botanique*, I, page 264.

By the use of anaesthetics, Claude Bernard suspended the assimilating capacity of plants which still continued to breathe, both in the light and in the dark. In this way an idea could be formed of the effects of photosynthesis, for experiments comparing plants kept in the dark with controls showed that respiration was not modified by the anaesthetic.

Garreau ingeniously dissociated the two phenomena on a normal branch. Two identical branches were placed in two sealed tubes exposed to the light. In one of the tubes he placed baryta, which became turbid, because, Garreau concluded, "the plant breathes and produces carbon dioxide, which is fixed immediately by the baryta." In the other, without baryta, the exposure to the light was the same, but the baryta was not there to compete for the carbon dioxide, which was used entirely and so effectively for assimilation that at the end of the experiment the confined air in this second tube did not make the baryta water turbid. The two phenomena were thus demonstrated, but, for the sake of accuracy, it must be added that turbidity would not have been produced in the first tube if green leaves only had been placed in it, for, in full sunlight, the chloroplasts use the carbon dioxide from respiration even before it has been given off from the leaf; in this experiment, carbon dioxide from the non-green parts passed into the atmosphere where the baryta and the leaves shared it.

Another method of approaching the problem is to consider the quantities of gas absorbed or given off. Bonnier and Mangin showed that the value of the exchanges due to chlorophyll could thus be determined independently from the respiratory exchanges which take place at the same time. There is a respiratory quotient, which is the ratio of the carbon dioxide given off to the oxygen taken in, CO_2/O_2 , and a photosynthetic quotient, which is the ratio of the oxygen given off to the carbon dioxide absorbed, O_2/CO_2 . It may be said, as a first approximation, that carbon dioxide will be more abundant in the final atmosphere if respiration is

predominant, while, if photosynthesis predominates, the result will be the reverse.

Many physiologists vied with one another in determining these quotients, for, although it is possible to suppress assimilation by keeping the plants in darkness, it is impossible to suppress respiration. Also, the respiratory quotient varies, being sometimes higher, and sometimes lower, than unity.

After very detailed analyses and calculations, first Maquenne and Demoussy, and then Willstätter and Stoll, concluded that the photosynthetic quotient was constant, whatever the external conditions might be, and that it was always equal to unity, the oxygen given off corresponding exactly to the carbon dioxide absorbed.

Thus the balance of the gaseous exchanges between the plant and the surrounding air can be fairly accurately determined. Some of the experiments showed great ingenuity; for example, the younger Schloesing succeeded in making a stem of meadow soft grass accomplish all its life cycle in a confined atmosphere, perfectly conditioned and frequently analysed.

After noting the quantity of carbon dioxide introduced, estimating what was given off from the soil and calculating what remained in the air at the end of the experiment, he concluded that the plant had absorbed 1,527 cubic centimetres of carbon dioxide; then, making the same calculations for the oxygen, he found that 1,734 cubic centimetres came from the plant. The total assimilation or photosynthetic quotient O_2/CO_2 was therefore greater than unity, namely, 1.12. The additional oxygen was provided by the degradation of oxidized substances of the soil, such as nitrates, which are used by the plant.

First Hypotheses on the Chemistry of Photosynthesis

During the last ten years great progress has been made in the investigation of the chemical processes which take place in the interior of the cell. One of the first problems was to find how carbon dioxide was transformed into glucosides.

Boussingault and Bayer expressed the view that glucosides resulted from the union of carbon with the elements of water, hence their first name of carbohydrates. Most of the formulae representing glucosides can, in fact, be written as if they were the result of the polymerization of this fundamental molecule CH_2O , for example, glucose, $\text{C}_6\text{H}_{12}\text{O}_6$ or $(\text{CH}_2\text{O})_6$.

It was not difficult to find this molecule from which all the glucosides would be derived since the carbon dioxide had only to replace its 2 atoms of oxygen with a molecule of water according to the equation

Such a reaction, simple as it may be on paper, immediately seemed to be improbable, and a double decomposition of carbon dioxide and water was suggested, showing carbon monoxide combining with hydrogen:

If this were so, photosynthesis ought to be facilitated when carbon monoxide is given to the plant, but this gas is quite unsuitable for the purpose.

Another suggestion was that carbonic acid, which is normally formed by the contact of carbon dioxide and water, might have some part in the reaction; it would need only to lose 2 atoms of oxygen

Nobody succeeded in explaining how such a reduction could be accomplished in the plant, but, since photosynthesis certainly existed, it had to be admitted that the reduction did actually take place.

The first result then of photosynthesis is formaldehyde, HCHO . From this Fischer was able to effect the synthesis of glucosides, which contributed in no small measure to the success of the theory.

Nevertheless, formaldehyde is a poisonous substance to the plant, even in small quantities, and its presence in the plant

is not easy to demonstrate. If it is formed, it must be very fleeting and must polymerize instantaneously before it has had time to exert its toxic effect.

This hypothesis of the synthesis of glucosides by way of formaldehyde was retained for some time, although it was far from satisfactory and had scarcely anything in its favour but its disarming simplicity.

In 1924, Maquenne elaborated the theory in which formaldehyde had no part. He suggested that carbonic acid combined with the magnesium of the chlorophyll, then isomerized to pass to the peroxide form. This unstable form released 2 atoms of oxygen liberating two valencies of the carbon. The same reaction was produced on all the molecules of chlorophyll, and the proximity of these molecules enabled the carbon chain to be elaborated as soon as the oxygen liberated the valencies. The polymerization was therefore very premature and the first substances formed were glucosides.

This theory was, in many respects, attractive and had many supporters. But is it true that chlorophyll combines with carbon dioxide?

On closer consideration, the weakness of these theories becomes apparent. They claim to solve the problem as simply as possible, but this simplicity, striking enough when the formulae are set out on paper, ignores life and the nature of living things. It has, in fact, not been possible to discover in the living organism any of the intermediate substances through which carbon passes as it is being transformed into glucosides and which, in the theories, are assumed to be necessary.

New Techniques

In the last twenty years the situation has changed. Through the study of the phenomena of fermentation and of respiration, we have begun to understand the working of the living organism; instead of effecting violent reactions, it degrades energy progressively through all the intermediate stages of oxidation-reduction.

The use of radioactive isotopes has revealed some of the intermediate reactions. This technique is described in Chapter VIII of Part I (*Light and Vegetation*).

The technique of chromatography has also been used to separate the chemical substances in solution. As it spreads out on a filter-paper, a solvent carries the different substances dissolved in it to a certain distance. Under the same conditions, a given substance is carried to a given distance and is separated in this way from the others by the use of an appropriate solvent. To effect a better separation, two solvents are used successively on the same paper and are made to spread out at right angles, e.g., one from the bottom and the other from the right-hand side. If the two solvents were identical and the starting point placed at the bottom on the right, the substances would be distributed on a diagonal from their starting point; but as the solvents are different and do not carry the dissolved substances to the same distance, the latter are distributed over the whole surface at different and precise

points. It is easy to see, with the Geiger counter, how the radioactive carbon is distributed. The property of radioactive substances of producing an image on a photographic plate can be used to obtain a radio-autograph from the sheet of filter-paper. There the size and distribution of the spots indicate the substances which contain radioactive carbon and the proportion contained.

These new techniques have enabled new theories to be formulated from concrete data.

CHAPTER II

CHLOROPHYLL

IF green leaves are pounded in alcohol, the liquid soon turns green, while the leaves become discoloured. This solution of chlorophyll contains a mixture of a number of substances, including all the secondary pigments.

Various methods may be used to separate the pigments from one another, but the simplest is that of chromatography. There is a red pigment (carotene) and several yellow pigments (xanthophylls) beside the green pigment, chlorophyll proper. The last is divided into two pigments, *a* and *b*. They have very similar properties but can be easily separated, not only by chromatography, but particularly by petroleum ether, in which chlorophyll-*b* is insoluble.

A kilogramme of fresh leaves contains on an average 2 grammes of chlorophyll-*a*, 0.75 of chlorophyll-*b* and 0.5 of carotenoids—xanthophylls and carotene.

Chemical Properties

The chemical formula for chlorophyll was gradually defined through the work of Willstätter and of H. Fischer. It was not difficult to find the overall formula, $C_{55}H_{72}N_4O_5Mg$, but the nature and place of all the elements of this molecule were determined by long and patient research and the structural formula can now be written fairly certainly as opposite.

We notice immediately the tetrapyrrol central nucleus centred on an atom of magnesium and bearing on two carboxyls and two alcohols—phytol ($C_{20}H_{39}OH$) and methyl alcohol.

As a result of the presence of magnesium, burnt chlorophyll leaves a residue composed uniquely of magnesia and repre-

Structural formula for chlorophyll-a

senting 2·7 per cent of the total weight. When treated with a weak acid such as oxalic acid, chlorophyll loses its magnesium and turns brown; if it is treated with a strong acid it loses the phytol as well.

Treated with a diastase, chlorophyllase, it loses the phytol but retains the magnesium. Another alcohol then generally replaces the phytol, for example in the course of extraction by alcohol, for this diastase acts rapidly in case of injury.

When acted on by alkalis, chlorophyll loses its methyl alcohol, and, if it is heated while the reaction takes place, it loses one of its acid radicals at 140° C. and the second at 200° C.

The essential nucleus of the formula is the tetrapyrrol square at the centre of which the magnesium is fixed. It is the same as the nucleus surrounding the iron in the molecule of haemoglobin—a remarkable identity in the fundamental part of these two pigments which are so important in the life of the plant and of the animal; all life revolves round this nucleus without which the plant could not assimilate nor the animal breathe. The essential difference between the animal and the plant resides there, for the animal destroys by respiration the reserves accumulated by the assimilation of the plant; he is heterotrophic, feeding himself at the expense of others, while the plant is autotrophic, depending only on itself, and this difference seems connected with the replacement of magnesium by iron!

This identity does not arise from a mere coincidence; it is an effect of this dependence of animals, which do not seem to be able to synthesize such a nucleus, but use for their essential pigment that derived from chlorophyll, whether they feed on green leaves or on other animals which eat chlorophyll.

Beside this chlorophyll-*a*, there are three others—chlorophyll-*b*, chlorophyll-*c* and chlorophyll-*d*. They have a very similar composition and the same chemical properties as chlorophyll-*a*. Chlorophyll-*b* is distinguished by the fact that an atom of oxygen replaces 2 atoms of hydrogen in the group $-\text{CH}_3$ on the third atom of carbon, in the upper part of the

formula. The formulae of chlorophyll-*c* and chlorophyll-*d* are not defined.

The quantity of these secondary chlorophylls found in the plant is generally a little less than one-third of the quantity of chlorophyll-*a*. An equilibrium seems to have been established between them and the passage from one to another seems to present no difficulty.

In the higher plants, the secondary chlorophyll is always chlorophyll-*b*. In the lower plants, it is replaced by chlorophyll-*c*, in brown algae, and by chlorophyll-*d*, in red algae.

Beside the chlorophylls, carotenoids are always present—carotene, at least. The formula for this substance is very simple, for it contains only carbon and hydrogen, $C_{40}H_{56}$. The formula for xanthophyll is the same with the difference that at two points the group CH_2 is replaced by $CHOH$; two alcohol radicals appear causing 2 atoms of oxygen in the formula, $C_{40}H_{56}O_2$.

Carotenoids are often present in organs in which chlorophyll is absent; for example, in the carrot root they persist in the autumn after the chlorophyll has disappeared. Carotene is very important in animal nutrition because its formula may change to that of vitamin A; this change can be effected by the animal organism and that is why carotene is called a precursor of vitamin A.

The Chloroplasts

In the palisade tissue in the interior of the cytoplasm of green leaves are small, strongly-coloured green plastids called chloroplasts. They are so abundant that they constitute a quarter or even a third of the dry weight; there are from twenty to a hundred in each of the cells of the palisade tissue. With care, they can be extracted intact. See Fig. II, 1.

Fig. II, 1. Cross-section of a leaf. 1, Upper epidermis; 2, Palisade tissue; 3, Chloroplasts; 4, Lacunose tissue; 5, Lower epidermis; 6, Stroma

In the higher plants, they are in the form of a disc of 3 to 10 μ in diameter and 1 to 2 μ thick. They are bounded by a semi-permeable membrane.

The microscope resolves the chloroplast into a certain number of small discs—from ten to a hundred—that are called grains of chlorophyll. The diameter of these grains varies from 0.2 to 2 μ ; for example, for spinach they are 0.6 μ in diameter and 0.1 μ thick. All the chlorophyll is located in these grains the framework of which is formed by a support—a colourless stroma.

Carotene

Vitamin A

Xanthophyll

The electron microscope reveals in the grain a pile of lamellae 0.01 to 0.02 μ thick; there would therefore be about ten in each grain.

Chlorophyll constitutes a relatively small part of the chloroplast—only 8 per cent of its weight, in spinach for example; the quantity of xanthophyll and carotene is about one-fifth of this and constitutes a little less than 2 per cent.

The presence of these chloroplasts is directly connected with that of anterior chloroplasts.

In the lower plants the existing chloroplasts give birth to new ones which enter into the daughter cell.

In the higher plants, the chloroplasts develop from mitochondria which are pre-chloroplasts. These pre-chloroplasts are not made by the cell but originate from parent cells and are brought by the cytoplasm of the pollen and especially of the oosphere. If the flower develops on a branch without chlorophyll, it will not be able to transmit chlorophyll and the daughter plant will be devoid of it. The presence and quantity of chlorophyll are influenced by a number of genes of which not less than fifty have been counted in maize. In this species, the pre-chloroplasts increase in size from less than 1 μ to 3 or 4 μ before beginning to be covered with pigment. Chlorophyll does not normally appear until half the final size has been attained.

The Synthesis and Disappearance of Chlorophyll

There is little information on the way in which the synthesis of chlorophyll is accomplished. Genetics are introduced in the last stages, for a mutated green alga, chlorella, accumulates protoporphyrin, i.e., chlorophyll in which the magnesium, the two alcohols and the closing of the tetracarbonate external cycle are lacking. One gene prevents the synthesis from reaching its conclusion. Another arrests the evolution a little later, after the fixation of magnesium, when the tetracarbonate cycle is still lacking. It may therefore be supposed that two of the last stages of the synthesis of

chlorophyll involve the fixation of the magnesium and the formation of this cycle.

Up to this point the process can be accomplished without light, but at the last stage light is necessary, at least for the higher plants, although certain algae and even certain conifer seeds can pass through it in the dark.

This last stage seems to consist in a reduction—in the acquisition of 2 atoms of hydrogen by a group $-\text{CH}=\text{CH}_2$, which is situated in position 4, at the top right-hand side of the formula, and which becomes $-\text{CH}_2-\text{CH}_3$. Protochlorophyll has accumulated in the dark and as soon as light appears the transformation is accomplished; in less than two minutes chlorophyll is formed.

As one would expect, the different wave-lengths of light do not all have the same influence and the most effective are those which chlorophyll absorbs best. Nevertheless, a small difference may be noticed; the longest wave-lengths seem to be relatively more efficacious. Simónis made a comparative study of the formation of the chloroplasts in red light and in

blue light. Red plants have more chlorophyll than blue, but less carotenoids—their photosynthetic capacity for the same luminous energy is greater. Moreover, the radiations which promote the synthesis of chlorophyll are almost identical with those which promote the growth of the whole plant; it is therefore difficult to dissociate the two processes.

Temperature also has an influence. Here chlorophyll is more narrowly limited than growth and is not produced when the temperature is too low or too high, although growth is not suppressed. The cold causes certain leaves to develop without chlorophyll and sometimes they lose permanently the capacity to form it. Every species has its critical maximum and minimum temperature and its optimum for the formation of chlorophyll; the two extremes seem to be $+4^{\circ}$ and $+40^{\circ}$ C.

A rather large number of chemical elements is necessary for the formation of chlorophyll. If etiolated leaves are kept for two days in distilled water in the dark, they consume all their glucosides. If they are then exposed to the light, some in distilled water and others in a solution of glucosides, only the latter form chlorophyll. Glucosides are therefore necessary, but they must not be too abundant. If they are, the plant will not produce chlorophyll because the need for it does not exist in the presence of an excess of precisely those products which chlorophyll provides; in other words, the superabundance of glucosides mobilizes the albumins and makes them unavailable for the formation of chlorophyll.

Nitrogen is necessary, and it is well known that nitrogenous fertilizers produce remarkably green leaves, while a deficiency of nitrogen makes them yellow because there is not sufficient chlorophyll to mask the carotenoids. Nitrogen is one of the constituent elements of chlorophyll and, according to Roux and Husson, it enters into the synthesis of the pyrrolic nuclei in the form of glutamic acid.

Magnesium is also a constituent element and its deficiency is manifested first on the old leaves by almost the same symptoms as the lack of nitrogen.

It has been known for a long time that iron is necessary

and this first led to the belief that it was present in the molecule of chlorophyll. It would seem to take part in a synthetic process involving albumins, for the etiolation caused by its absence is accompanied by an accumulation of them.

Although we do not know precisely what part they take in it, manganese, copper, zinc, potassium and sulphur are also necessary for the synthesis of chlorophyll.

Chlorophyll is not a stable substance which, once formed, persists throughout the life of the leaf; its quantity depends on the equilibrium established between its rate of formation and its rate of disappearance. During the growing period the rate of formation is much greater, but the reverse normally occurs in the autumn, or when a necessary substance such as carbon dioxide, nitrogen or iron is lacking, or again when the illumination is very strong; the plant then changes from green to a more or less distinct shade of yellow because chlorophyll no longer masks the carotenoids whose rate of renewal is more rapid than its own.

Chlorophyll disappears under the influence of light and of oxygen; the products into which it is transformed are very probably products of oxidation, although they have not yet been isolated.

In the absence of oxygen it seems to be stable, but, on the other hand, it soon disappears when oxygen is plentiful or when carbon dioxide is lacking. When a plant is subjected to much more intense illumination than it ordinarily receives, instead of a release of oxygen there is a fixation of oxygen several times greater than that of respiration; the oxidation seems first to affect the neighbouring oxidizable material but soon attacks the chlorophyll, which rapidly disappears.

Light acts on chlorophyll through the wave-lengths that the latter absorbs. Dangeard demonstrated this very clearly; he illuminated chlorophyll by a spectrum which was active only in the absorption bands and also by rays which had already traversed a green leaf and were shown to be totally inactive. See Fig. II, 2.

It is difficult to calculate the average life of chlorophyll,

Fig. II, 2. Absorption spectrum of the chlorophyll pigments.
 1, Whole chlorophyll; 2, Chlorophyll-*a*; 3, Chlorophyll-*b*;
 4, Carotene; 5, Xanthophyll

especially in natural conditions. The active period, at least, seems to be extremely short, since the average life of excited chlorophyll has been estimated at 8×10^{-8} to 8×10^{-11} second.

The Action of Chlorophyll

Chlorophyll seems to be the only pigment which enters into photosynthesis, for it is the only one in which fluorescence

is excited. As it has the lowest level of excitation, the other pigments transmit to it the energy absorbed. A single exception occurs with chlorophyll-*d* of red algae, which does not transmit the energy received although it is incapable of using it for photosynthesis.

Chlorophyll-*a*, with which we are exclusively concerned, plays the role of a photo-catalyst; it is capable of taking hydrogen from a donor at low potential, such as water, and fixing it on a substance at high potential, such as carbon dioxide or an organic acid. It is reversibly oxidized and reduced.

Emerson's experiments on photosynthesis in intermittent light are described in Chapter VIII of Part I (*Light and Vegetation*).

As we have said, one of the physical properties of chlorophyll is fluorescence. The molecule absorbs light of short wave-length and great energy, is excited by it and rids itself of the energy by re-emitting it, but in the form of a photon which is less charged with energy—ultra-violet, or blue, incident light is transformed into red light. This reddish glimmer can easily be seen by looking sideways at a solution of illuminated chlorophyll. If a substance capable of receiving the energy absorbed by the chlorophyll is placed in the solution, the fluorescence disappears.

Kautsky observed this fluorescence in the course of photosynthesis. At first it is weak because at the beginning the greater part of the energy absorbed by the chloroplasts is used for photosynthesis. As the illumination continues, the fluorescence rapidly increases, for the chlorophyll needs a certain time to use this energy and energy arriving during that time is unused and dispersed in fluorescence. But a régime of continuous utilization is soon established, when this maximum fluorescence decreases and a level similar to the first is stabilized.

CHAPTER III

THE CHEMISTRY OF PHOTOSYNTHESIS

PHOTOSYNTHESIS produces glucosides from carbon dioxide, while respiration, in destroying them to extract chemical energy, produces carbon dioxide.

Respiration

The work of Warburg and particularly of Wieland has considerably increased our knowledge and understanding of the process of respiration.

From the chemical point of view, the passage from glucose to carbon dioxide is made in two main stages, the first from glucose to pyruvic acid and the second from pyruvic acid to carbon dioxide.

Pyruvic acid is the pivot of all these transformations. The main biochemical routes of degradation of glucosides regularly reach it, e.g., fermentations, but from there the absence of oxygen diverts the reactions away from respiration and carbon dioxide and in the direction of alcohol.

The first stage begins by the fixation of a molecule of phosphoric acid on the 6th atom of carbon of the glucose, which thus becomes glucose-6-phosphate. This acid is fixed by means of a diastase, hexokinase, and is provided by adenosine triphosphate (commonly known by its initials ATP). which becomes adenosine diphosphate, ADP.

The glucose-6-phosphate isomerizes, i.e., transforms its molecule, without any addition or loss, into fructose-6-phosphate by means of another diastase, an isomerase.

The hexokinase, which had fixed a molecule of phosphoric acid on the 6th atom of carbon, intervenes again and another

molecule of this acid is fixed at the other end of the chain on the first atom of carbon to give fructose-1-6-diphosphate.

Rendered fragile by these two phosphoric appendices, the chain of glucosides breaks in the middle, through a diastase, aldolase, and we have a mixture of phosphoric dihydroxyacetone and glyceraldehyde-3-phosphate. In this last substance, the aldehyde is transformed into alcohol, the phosphoric acid passes from the 3rd atom of carbon on the 2nd and is finally liberated, giving rise to pyruvic acid.

No molecule of carbon dioxide has yet been given off and the degradation of the glucose has consisted of scarcely more than splitting its carbon chain in two, but this degradation has provided much more energy than it has required.

The second stage takes place entirely in the citric acid cycle, a gigantic millstone to pound the molecules to extract carbon dioxide from them.

Pyruvic acid enables this to be done. With its 3 atoms of carbon, and by means of a diastase, aconitase, it combines with oxaloacetate which has 4; the first molecule of carbon dioxide is given off, and we have a substance with 6 atoms of carbon or, rather, several substances. An equilibrium is, in fact, established, in which citrate (80 per cent) is predominant, with a little aconitate (4 per cent), but more particularly isocitrate (16 per cent). The last-named enters into the cycle in losing 2 atoms of hydrogen, then, successively, 2 molecules of carbon dioxide, the second and third, and we arrive at succinate which has no more than 4 atoms of carbon. It loses hydrogen, fixes a molecule of water, loses hydrogen again and brings us back to oxaloacetate. The cycle can begin again and, by a single turn of it, the 3 atoms of carbon brought by a new molecule of pyruvic acid will be oxidized and transformed into carbon dioxide. From these oxidations comes the energy which life needs for its functions.

Respiration could be represented as a thermal power station in which the combustion of glucose by its progressive transformations into pyruvic acid and carbon dioxide turns a dynamo—the citric acid cycle—generating a current of energy

which will be transported by the molecules of phosphoric acid. See Fig. II, 3.

Oxidation is effected progressively to a remarkable degree. Carbon possesses four valencies of which only one in the

Fig. II, 3. Citric acid cycle

glucose is saturated by the oxygen of the alcohol radical. The first step is the transformation of alcohol into aldehydes or ketones; two valencies of carbon are saturated by the same atom of oxygen.

1. Citric acid

2. Cis-aconitic acid

3. Isocitric acid

Formulae of acids taking part in the citric acid cycle

A third valency is seized by a new atom of oxygen and we have a carboxyl, an organic acid $-\text{COOH}$. The end of the evolution is reached when the fourth valency is also saturated by the oxygen and we have carbon dioxide, CO_2 .

One can expect that reduction will proceed in the opposite direction to oxidation; the carbon dioxide will liberate its first valency from oxygen in becoming organic acid, and so on. The research is thus set on a definite course.

Oxidation-reduction

Oxidation has, of course, its necessary counterpart, reduction, for, if any substance is oxidized, the oxygen that it acquires must come from another substance or at least from

an environment which is consequently deprived of it or, in correct terms, is reduced. We should not, therefore, speak of oxidation pure and simple, but of oxidation-reduction. If we speak of oxidation, we are considering an isolated substance and all the rest will be the environment in which the complementary reduction is effected and with which we are not directly concerned. But obviously a reaction cannot be understood and reproduced unless it is seen in its entirety and all the terms in question and all the exchanges involved are included in the equation.

There are two sorts of valencies that may be called positive and negative. Electronegative atoms lack a few electrons with respect to the complete external layer which characterizes the rare gases. Oxygen is the classic type of these electronegative atoms; it lacks 2 electrons and when it finds a substance capable of supplying them it fixes on and oxidizes it. Electropositive atoms possess surplus electrons and are capable of giving them up to electronegative atoms. Hydrogen is the classic type of these substances.

Oxidation corresponds to a liberation of electrons, while reduction corresponds to a capture of electrons. The more the environment is reduced, the greater the number of electrons in it; the more it is oxidized, the smaller the number of electrons. The arrival of electrons in an environment will therefore be a reduction and, conversely, we should say that iron is oxidized when its third valency is saturated, even if oxygen does not intervene.

Since electrons have a negative charge of electricity, their presence will necessarily modify the electric potential of the environment and make it negative, while a greatly oxidized environment will be strongly positive.

Thus there appears the potential of oxidation-reduction which is evaluated in maintaining the *pH* at 7. A strongly oxidized environment will have a potential of about +0.8 volt, while glucose-6-phosphate will have one of -0.4 volt.

The work of photosynthesis consists in maintaining this void which oxygen tends to fill with all the force given to it

by this potential difference of 1.2 volt. The energy used by life proceeds from this difference in the level of potential—from this provision of electrons.

The Stages of Photosynthesis

A reduction is a much more complex operation than an oxidation because an oxidation produces energy and consequently can be effected entirely without demanding anything from the environment. But a reduction needs energy and can develop only if this is supplied; it therefore involves two stages—the first to capture the necessary energy and the second to utilize it in the reaction.

These two stages are found in photosynthesis. The first, the luminous phase, which the Americans call the *Hill reaction*, captures solar energy; the second, the dark phase, which is sometimes called the *Blackman reaction*, uses this energy in chemical syntheses.

The existence of these two phases has been shown by a number of observations. In 1932, Emerson and Arnold studied the speed of photosynthesis, using as the luminous source very brief flashes of a hundred thousandth of a second. The efficiency is higher if the flashes are spaced to give the dark phase time to be completed. At a temperature of 25° C., the maximum efficiency is attained with an interval of four hundredths of a second, while at 1° C. the same efficiency is attained, but only when the interval between flashes is ten times longer. Since the efficiency is not altered by it, the temperature does not affect the capture of energy but only the chemical reactions which take place during the dark phase and are slowed down by cold.

The influence is of the same order if a small quantity of hydrocyanic acid or heavy water is used—the chemical reactions are effected more slowly. If the interval between the flashes is lengthened, the reactions will have time to be completed and the process will continue unchecked. A low temperature, heavy water or hydrocyanic acid hinders only the dark phase.

On the other hand, if the quantity of chlorophyll is reduced, the fixation of energy will be affected and it will be useless to lengthen the intervals between the flashes because the efficiency will not be increased. A decrease in the quantity of carbon dioxide, or the presence of a narcotic, has a similar effect on the luminous phase and on that only.

The Luminous Phase

In 1901, Friedel observed that pulverized green leaves give off a little oxygen when they are illuminated. Hill discovered in 1937 that this liberation of oxygen is prolonged if ferric salts, which become ferrous, are added to this green powder; while the oxygen is being given off, a reduction is accomplished by light through the agency of chlorophyll.

This experiment is made by extracting the chloroplasts and suspending them in an artificial medium. Not all leaves can be used satisfactorily; those from trees are rather disappointing, but lettuce or spinach provides excellent material. The pulverization must not be carried too far, for if the grains of chlorophyll are split up and reduced to too small a size their activity soon declines.

Although the chloroplasts are slightly modified by being outside the cell, investigations have shown that this reaction obeys the same laws as photosynthesis and is modified similarly by the same circumstances. The Hill reaction therefore fairly accurately represents the luminous phase of photosynthesis, which can now be studied *in vitro*.

The energy fixed by chlorophyll can be estimated only to the extent that it is seen to be used. Since photosynthesis uses it to liberate electrons, i.e., to reduce, a substance capable of reduction is associated with the chloroplasts.

Hill used ferric oxalate which is transformed into ferrous oxalate by means of the electrons liberated by the release of oxygen. To enable this reaction to continue, he added ferricyanide which reoxidizes the ferrous oxalate, and the reduction recommenced. In view of the potential difference (1.2 to 1.3 volt) separating carbon dioxide from the

glucosides, it is evident that only the half-way stage has been reached.

Attempts have been made to go a little further by varying the oxidants. The ideal would be to use carbon dioxide itself, but it has not yet been possible to achieve this directly. It has, however, been possible to fix it on pyruvic acid by using a mixture of pyruvate, with carbonate as the source of carbon dioxide, triphosphopyridine nucleotide (TPN) as the source of energy, salts of manganese as catalysts and malic diastase. This diastase normally transforms malic acid into pyruvic acid by a decarboxylation, i.e., by liberating in the form of carbon dioxide the atom of carbon which forms the acid radical —COOH , so that we pass from a tetracarbonate molecule to a tricarbon molecule. This decarboxylation produces energy, for it oxidizes the fourth valency of an atom of carbon. The Hill reaction accomplishes the reverse; one atom of carbon, the four valencies of which are saturated with oxygen, liberates one of them to fix on the pyruvic acid which becomes malic acid.

Wood and Werkman showed that plants, and even animals, are capable of fixing carbon dioxide on pyruvic acid. This is therefore not a specific reaction of photosynthesis, but is accomplished by borrowing the necessary energy, not from an internal oxidation, but from light. Is there also a reaction peculiar to photosynthesis, characterized by the utilization of light only?

In any case, the speed of liberation of oxygen in this reaction is rather interesting since, under the best conditions, one molecule of oxygen per molecule of chlorophyll is released every thirty or forty seconds; in the cell, this speed may increase to one molecule every fifteen or twenty seconds.

Since all the valencies of carbon in the carbon dioxide are saturated with oxygen and the fixation cannot take place without liberating at least one valency, it seems obvious that the liberated oxygen comes from the carbon dioxide fixed. To check this point, Holt and French, in 1948, used radioactive oxygen and found that the liberated oxygen came, not from

the carbon dioxide, but from the water. The 2 atoms of oxygen of the carbon dioxide enter into the first substances synthesized and we are forced to the conclusion that the first reaction of photosynthesis consists in capturing the hydrogen of the water to use it for different reductions, particularly for the reduction of the carbon dioxide the valencies of which are progressively freed of oxygen during its progress towards glucosides.

A first step is therefore accomplished; we have succeeded experimentally in making chlorophyll capture luminous energy and use it to decompose water and fix carbon dioxide.

The Dark Phase

This phase brings us up against the chemical problem of photosynthesis, which can be considered in three aspects, namely, the necessary energy which accumulates through phosphoric acid, the diastases which catalyse the reaction, and the course followed by carbon in its transformation from carbon dioxide to glucosides.

THE ROLE OF PHOSPHORIC ACID

When Lundegaard observed the progressive disappearance of certain phosphorated compounds in the course of muscular activity, new horizons opened up to the biochemists and, through the work of Lippmann in particular, an increasingly important role in the functioning of life was attributed to phosphoric acid.

Phosphoric acid combines with other substances through a bond capable of liberating a quantity of energy by hydrolysis. When it is fixed on an alcohol radical (ester bond), as it is in fructose-phosphate, this bond contains 2,000 to 3,000 calories and nearly double—4,800 calories—in glucose-1-phosphate, perhaps because the carbon, on which it is fixed, has two valencies saturated with oxygen. When it is fixed on an organic acid (carboxyl-phosphate) and consequently linked with an atom of carbon three bonds of which are oxidized,

the bond energy rises to 16,000 calories. When it is fixed on one atom of nitrogen, for example in arginine-phosphate, or on another phosphoric acid (pyrophosphate) the energy capable of being liberated is between 10,000 and 12,000 calories.

There are therefore two main types of phosphoric bonds—the first of low energy, less than 5,000 calories, the second exceeding 10,000 calories.

Here, one of the essential substances of both the animal and vegetable organism—adenylic acid—intervenes. It is one of the constituents of nucleic acid and does not exist only in the voluminous molecule of this fundamental part of the cell nucleus, but is also found more or less isolated, and we are beginning to perceive the large and important part that it plays.

Ribose, a glucoside with 5 atoms of carbon, is attached at one end of its carbon chain to an organic base, adenine, and thus become adenosine. At the other end of the carbon chain, phosphoric acid is fixed and we have adenylic acid, which is also called adenosine-monophosphate and commonly designated by the initials AMP.

This bond between phosphoric acid and ribose through the intermediary of an alcohol radical is low in energy. But on this phosphoric acid another phosphoric acid is fixed and sometimes even a third. These two new bonds, between phosphoric acids, are pyrophosphate bonds and consequently of high energy, and we have adenosine diphosphate (ADP) and adenosine triphosphate (ATP).

In the living cell ATP seems to be the pivot of the exchanges of energy. It is, in fact, capable, when necessary, of liberating a rather large quantity of energy by abandoning one or even two phosphoric acids and being transformed into ADP or AMP. On the other hand, it is capable of storing a large quantity of energy by the formation of ATP. This possibility of acting in the two directions according to circumstances gives adenosine triphosphate primordial importance in all the intermediate metabolism.

It enables the oxidations of the organism to be effected by degrees. The total oxidation of a molecule of glucose is capable of liberating 680,000 calories; more than half of this energy can be used for the formation of phosphoric bonds of high energy. In this way reserves are built up to be used by future reactions, but it is not impossible that this provision is made at the expense of other sources of energy—luminous energy, for example.

Adenylic acid intervenes in a slightly more complex form. It unites through its phosphoric acid with phosphoric acid of which the composition of the molecule is of exactly the same type—with ribose and phosphoric acid—but in which the organic base is not adenine but nicotinamide. This substance is called diphosphopyridine nucleotide and is designated by the letters DPN.

A third phosphoric acid may be attached to the adenylic ribose and we have triphosphopyridine nucleotide or TPN.

Triphosphopyridine nucleotide (TPN)

DPN specializes in the transport of hydrogen even more than in the transport of energy and it can, according to circumstances, be reduced and become DPNH₂, or be oxidized and become again DPN.

We can see the significance, in the processes of photosynthesis, of everything which bears on the accumulation and transport either of hydrogen or of energy and if, as we might be tempted to think, the luminous phase results in the accumulation of hydrogen and energy, the role of adenylic acid is of primary importance in its two forms of ATP and DPN.

DIASTASES

Diastases take part in every chemical activity of the living organism. Their action is catalytic and they are necessary auxiliaries which are theoretically unchanged at the end of the reaction.

They consist of a proteic support, the apodiastase, which is relatively voluminous and on which depends the adaptation to a particular function. Fixed to this support, the active parts, the codiastases, will act only if they are placed on site by their support. ATP and DPN seem to be among the principal codiastases.

The first reaction of photosynthesis, the fixation of carbon dioxide in the form of carboxyl, is effected, as we have seen, either by the animal or vegetable organism in the Wood and Werkmann reaction, or by chlorophyll in the Hill reaction. Carbon of one valency is freed of its oxygen and fixed on a dicarbonate or tricarbonic substance, for example, on pyruvic acid, which becomes malic acid:

The change from malic acid to pyruvic acid, because it oxidizes carbon of one valency, produces energy and is accomplished theoretically without difficulty; the opposite process needs energy. The presence of an appropriate diastase enables the reaction to take place; it can be effected in one direction or the other according to the conditions of the environment.

Evans discovered in pigeon liver this diastase, the malic diastase, which, through its apodiastase, is specially adapted to malic acid. Its active part, its codiastase, is triphosphopyridine nucleotide, sometimes oxidized (TPN) and sometimes reduced (TPNH₂).

This malic diastase is added to a medium composed of pyruvate, carbon dioxide, salts of manganese and TPN. Hydrogen is provided by the addition of glucose-6-phosphate and a special diastase, dehydrogenase, which will decompose it, liberating hydrogen at the same time as the energy necessary for the reaction. By means of the malic diastase, this liberated hydrogen will be fixed with the carbon dioxide on the pyruvate to give rise to malate.

Such a reaction can be accomplished in the animal organism but it can also be accomplished, as we have seen, through chlorophyll, which will provide the necessary energy, not only for the fixation of carbon dioxide, but also for the liberation of hydrogen from water. In the presence of carbon dioxide, TPN, salts of manganese and malic diastase, pyruvate is transformed into malate with the release of oxygen.

We are not far from the actual conditions in which the first reaction of photosynthesis is effected. All the substances taking part in this experimental reaction have been found in the tissues of the higher plants.

Many other reactions whose place can be predicted in the processes of photosynthesis have been reproduced in the laboratory, particularly by S. Ochoa. The following is another.

The object is to transform phosphoglycerate into fructose-1-6-phosphate and to couple 2 tricarboxonate molecules to give rise to a molecule containing 6 atoms of carbon. It is possible to effect this synthesis by means of chloroplasts illuminated in

the presence of ATP, by manganese salts and a number of diastases—transphosphorylase, dehydrogenase, isomerase and aldolase. The transphosphorylase causes a molecule of phosphoric acid of the TPN to pass on to the phosphoglycerate:

The luminous energy having reduced the DPN to DPNH_2 , the dehydrogenase makes this hydrogen pass on to the diphosphoglycerate, which loses a molecule of phosphoric acid and becomes phosphoglyceraldehyde.

The isomerase transforms a part of this substance into dihydroxyacetone phosphate which, by means of another diastase, aldolase, combines molecule to molecule with the phosphoglyceraldehyde to give rise to a molecule of fructose diphosphate.

Two of the most delicate parts of this complex process of photosynthesis have thus been carried out in the laboratory by means of the diastases which are seen to play an essential part in plant physiology and particularly in photosynthesis. They facilitate the passage of hydrogen, or of electrons, from one substance to another and enable the available energy to be completely utilized.

THE PATH TAKEN BY THE CARBON

It was thought that carbon dioxide entered living material only by means of photosynthesis and that animals, since they lacked chlorophyll, were incapable of fixing it.

But, in 1942, Wood and Werkmann discovered that micro-organisms are capable of lengthening the carbon chain of certain acids by fixing on it a molecule of carbon dioxide according to the reaction:

Thus, tetracarbonate succinic acid changes into pentacarbonate ketoglutaric acid, tricarbonic pyruvic acid becomes tetracarbonate oxalo-acetic acid, etc.

It caused great surprise to find this reaction in many plants and even in animals—in the muscles, the hepatic tissue, etc. Moreover, physiologists have given it an important place in the chemistry of the cell, having observed, on the second atom of carbon in most of the chemical substances found at the great cross-roads of metabolism, this ketone radical which confers on their molecule a special reactivity.

Pyruvic acid, oxalo-acetic acid and ketoglutaric acid all have in their formula this group $-\text{CO}-\text{COOH}$, and that alone would be sufficient to indicate the importance of the Wood and Werkmann reaction. It must therefore be concluded that the fixation of carbon dioxide by the living organism is not peculiar to photosynthesis.

This discovery, and the fact that luminous energy liberates, in the first place, the oxygen from water and not the oxygen from carbon dioxide, disturbed all the classic conceptions of the chemistry of photosynthesis.

It is curious to observe that all these theories attempted to show how the construction of glucosides could be effected from carbon dioxide, first reduced and then progressively polymerized to glucose and starch, as though this synthesis was made in isolation and without the intervention of surrounding substances. The use of radioactive carbon proved finally that the old theories must be abandoned.

If the plant is provided with carbon dioxide, all the molecules of which have their atom of carbon "labelled", these atoms will be very quickly fixed by the plant and distributed in a large number of compounds.

Suppose the time of illumination is shortened to five seconds, for example, and the plant is immediately plunged in boiling alcohol so that the fixed carbon has no time to spread to many secondary compounds.

If the classic conceptions were correct, we ought to find in the plant, carrier of C^{14} , many substances with a single atom of carbon like formaldehyde HCHO —which would not have had time to polymerize—some dicarbonate substances like oxalic acid $\text{COOH}-\text{COOH}$, and fewer tricarbonate

substances. Actually we find nothing of the sort; all the substances which are carriers of C^{14} are at least tricarboxylic, and never, during these brief exposures, are dicarboxylic or monocarboxylic substances found "labelled." Substances are "labelled" by their carboxyl, and this shows that oxygen has liberated only one of the valencies of carbon which has been fixed on a dicarboxylic or tricarboxylic substance; here we find a reaction similar to that of Wood and Werkmann.

After five seconds of exposure to light, 97 per cent of the fixed carbon is found in the carboxyl of two tricarboxylic substances, phosphoglyceric acid and phosphopyruvic acid. The fixation has been effected on a dicarboxylic substance which has not yet been identified; we can only conjecture its anterior state, as the fixation of carbon dioxide may have been accompanied by various modifications.

This substance would doubtless be produced by a special cycle put in operation by photosynthesis. It would be a cycle which is much more rapid than the citric acid cycle and of which the intermediaries are still unknown, for life is much more complex and agile than we can imagine.

Suppose that green algae, provided with carbon dioxide each molecule of which has its atom of carbon radioactive, are illuminated with 100,000 lux and that at the end of five seconds they are plunged in boiling alcohol which kills all the diastases and arrests all the biochemical transformations. If the substances present in the algae are then extracted and analysed by chromatography and radio-autograph, 87 per cent of the radioactive carbon fixed is found in phosphoglyceric acid,

with sometimes a trace in glyceric acid,

10 per cent in phosphopyruvic acid,

and 3 per cent in malic acid,

If the exposure is longer, the number of substances which are carriers of C^{14} rapidly increases and saccharose appears. At first the fructose possesses twice as many carriers as the glucose. At the end of five minutes, in barley leaves, 95 per cent of the carbon fixed has already reached the stage of saccharose and other osides, while in green algae half has been distributed in glucosides and half in albumins. The end product of photosynthesis, glucosides, is reached and all the intermediate stages are passed with disconcerting rapidity.

If the luminous intensity is lowered, this speed greatly diminishes and 4,000 lux for thirty seconds causes only tri-carbonate substances to appear—phosphopyruvic acid and especially phosphoglyceric acid. At low temperatures, the result will be particularly phospho-2-glycerate (phosphoric acid fixed on the central atom of carbon), which is less stable at ordinary temperature and more slowly formed than phospho-3-glycerate. If the luminous intensity is reduced still more and falls to 500 or 600 lux, malic acid becomes abundant.

These experiments throw a new light on the path followed by photosynthesis. It must not be thought, however, that all the intermediate products are known or even that the first have been identified with certainty. It may be that phosphoglycerate is the first compound formed by the carbon dioxide fixed, but there is still some doubt, for the chemical cycles in biology are so rapid that if one stage is passed slightly more slowly than the others it will very probably eclipse them and make them imperceptible. Moreover, a substance may seem to be abundant because in the cycle it appears in a "side-track" or as a storage product which is more or less stable.

It is therefore possible that substances other than those found "labelled" are produced in the course of photosynthesis and that some of those "labelled" do not enter into it directly.

It cannot be doubted, however, that the first three substances found are important and occupy among the intermediate substances a central place from which the diversion is made towards the principal syntheses, while sooner or later phosphoric acid is detached from their molecules.

Phosphoglycerate by reducing its carboxyl easily changes to a triose (tricarboxylate glucoside) which, by uniting two of its molecules, forms a hexose (hexacarboxylate glucoside), such as fructose or glucose, which can unite to form saccharose or be polymerized to inulin, starch or cellulose:

Phosphoglycerate → triose → hexose → saccharose, etc.

Phosphopyruvate directs us towards lipides through the intermediary of fatty acids, or towards albumins if the phosphoric acid is replaced by an amine radical which thus forms alanine:

Lipides ← fatty acids ← *phosphopyruvate* →
amino-acids → albumins

Malic acid, which is one of the essential elements of the citric acid cycle, can serve as a pivot towards the albumins by way of aspartic acid, or, by reduction and fission of its molecule, towards the dicarbonate substance on which carbon dioxide is first fixed, if indeed it is always fixed on the same substance:

Dicarbonate substances ← *malic acid* →
aspartic acid → albumins

The radioactive carbon can provide some further information. When the assimilation has lasted only a short time, this carbon is not equally distributed among the six links of the glucose; more than half of it is found in the third and fourth in the centre. Fixing on the dicarbonate molecules, the radioactive carbon dioxide forms glycerate the carboxyl of which is "labelled." To form glucose, the two tricarboxylate molecules unite by their carboxyl and that is why the third and fourth atoms are "labelled" first. But how can the other atoms of carbon be "labelled"?

It is obvious that here various cycles must intervene through which glucose can be degraded to provide finally these dicarbonate molecules on which the carbon dioxide will be fixed.

The malic acid "labelled" after a very brief exposure contains radioactive carbon only in one of its carboxyls; this shows that carbon dioxide is not fixed only on the dicarbonate

molecules, but also on tricarbonate molecules, with a strong preference for the latter when the light diminishes. It is true that in these conditions the relatively stronger respiration provides a large quantity of pyruvic acid. Nevertheless, malic acid is not a necessary intermediary in photosynthesis, for if it is prevented from forming, glucosides are still synthesized; it is a means of storage.

This leaves unidentified the dicarbonate substance which is found on the normal path of photosynthesis, or at least on that of the rapid cycle which furnishes by the scission of a tetracarbonate or hexacarbonate molecule dicarbonate molecules already "labelled" by C^{14} . Ochoa suggests that it could well be glycolic acid, $CH_2OH \cdot COOH$. Whatever it may be, this scission must give symmetrical elements, since the second and fifth atoms of carbon of the glucose are ordinarily of the same activity as the first and sixth. A cycle which would fulfil these conditions is given on page 192.

It is therefore possible, at least provisionally, to form a fairly accurate, if not complete, idea of the cycle followed by the carbon in the course of photosynthesis. In the presence of hydrogen from the water decomposed by solar energy, carbon dioxide is fixed on a dicarbonate molecule to give, with phosphoric acid, phosphopyruvic acid, unless, the solar energy being lower and the respiration stronger, pyruvic acid is predominant and directs the synthesis towards malic acid as a result of the abundance of tricarbonate molecules.

Phosphoglyceric acid and phosphopyruvic acid, which can easily be changed into each other, constitute the pivot of photosynthesis. Three directions are possible: one towards fatty acids and lipides from phosphopyruvic acid; the second, through the intervention of nitrogen, towards amino-acids and albumins from phosphopyruvic acid or malic acid; finally, the third towards the oses—trioses and hexoses such as fructose and glucose from phosphoglyceric acid. And the cycle is closed by the formation of dicarbonate molecules from malic acid or hexoses.

Thus the essential lines of photosynthesis become per-

ceptible. But it is still not possible to give a definite answer to the question, "What is the first glucoside formed?"

In 1944, J. H. Smith studied the forms in which the fixed carbon is found in the sunflower, and this was the result of his analyses:

Time of exposure in minutes	27	58	101	146
mg. of carbon absorbed	4.11	7.77	15.41	23.14
mg. found in the glucosides	3.96	6.75	13.80	21.05
" " " " oses	0.18	0.77	2.5	5.15
" " " " saccharose	2.28	4	7.05	9.25
" " " " starch	1.5	1.98	4.25	6.65

These analyses seem to suggest that saccharose is the first glucoside formed. First, it represents more than half of the carbon fixed; its proportion only decreases in relation to the whole, in the first place because it is not a form of storage, but also because an equilibrium is doubtless established with the oses which are perhaps the product of its disintegration. It might be, not the first glucoside formed, but the first glucoside free of phosphoric acid; the formation of saccharose might perhaps be a means or an opportunity for glucose-phosphate and fructose-phosphate to abandon their phosphoric acid and leave the cycle which formed them.

CHAPTER IV

ASSIMILATION

PHOTOSYNTHESIS can very easily be demonstrated. If, for example, an aquatic plant, elodea, is placed in the sun with a little carbon dioxide dissolved in the water, bubbles are almost immediately formed among the leaves—bubbles which grow, detach themselves from the branch and burst on reaching the surface, discharging their content of oxygen. During this time, glucosides are synthesized in the leaf and the grains of starch which have been formed can easily be coloured blue with a drop of iodine solution.

To show that this starch is the direct result of photosynthesis, the plant is left for a certain time in darkness until it has used up all its stock; after ten minutes in sunlight the leaves have obtained a new supply.

Although it is easy to see, photosynthesis is difficult to measure. There are three possible methods: to measure the carbon dioxide absorbed, the oxygen given off, or the glucosides accumulated.

The greatest obstacle to precision is respiration, which releases carbon dioxide, absorbs oxygen and destroys glucosides. If these disturbing effects could be measured once and for all, it would be sufficient to take them into account in the calculation of the results. In absolute darkness photosynthesis does not take place, and only respiration is concerned in the gaseous exchanges of the plant, but respiration is not a constant phenomenon and temperature changes cause it to vary; the quantity of glucosides also influences it, as do many other factors which are often difficult to estimate at their just value. When the plant is assimilating to the maximum in full sunshine, can it be assumed that respiration

is no more rapid than in the middle of the night? Photosynthesis is then much more predominant than respiration, but it does not give off more than ten times the quantity of oxygen absorbed by respiration.

The true photosynthesis is measured if everything which does not proceed from it is eliminated, while taking only the final result gives the apparent photosynthesis, whatever the factors may be that have entered into it.

All the methods used measure the apparent photosynthesis, either by the increase of dry weight, by the oxygen given off or the carbon dioxide absorbed.

Measurement of the Dry Weight

Sachs inaugurated the technique of measuring dry weight. To find out what a leaf can absorb in a day, he weighed it in the morning and in the evening, or, more exactly, he dried and weighed half of a leaf in the morning. The other similar half passed the day in the sun and in the evening was dried and weighed. The difference in weight enabled the balance of assimilation and the quantity of glucosides synthesized per unit area to be determined.

The method has been modified by various investigators who have used fragments of a leaf, but a simpler and more reliable method consists in making the measurements on a tree with pinnate leaves like the ash; one foliole is taken in the morning and the opposite one in the evening.

The principal defect of this method is that it fails to take into account the transport of the glucosides which continues throughout the day with a speed and rhythm which are almost unknown. Moreover, it is still difficult to estimate on the whole of the leaf the repercussions of this traumatism which probably modifies the respiration and even the assimilation.

These objections are less important when the plant is not dissected and a long-term measurement is made by estimating the result of photosynthesis according to the total dry weight. But who knows what the plant has expended and what dry weight would truly represent all that it has assimilated? The

result is like a balance-sheet in which all the detailed entries have been omitted and only the remainder appears.

Measurement of the Oxygen Given Off

This is very simple. A branch of elodea, in water charged with carbon dioxide, is exposed to the light and the bubbles of oxygen are counted as they appear. The rate of assimilation, and the influence of different factors such as the temperature or luminous intensity on it, can thus be estimated.

The method, of course, has defects, the most serious of which arises from the fact that all the oxygen is not necessarily formed into bubbles; there may be a considerable difference, depending on the temperature or other conditions of the environment, between the oxygen really released and the number of bubbles. Various suggestions have been made, by Warburg in particular, to obviate this disadvantage.

Measurement of the Carbon Dioxide Absorbed

A leaf is wrapped in cellophane to shut out the external air without preventing the penetration of light. The confined air is renewed by suction and the air, after its contact with the leaf, passes on to an alkaline solution which fixes the carbon dioxide remaining in it. If the quantity of air passed is known, the quantity of carbon dioxide which has come in contact with the leaf is also known, and the measurement gives the quantity of carbon dioxide which remains.

Although this method is simple in principle, it is difficult to apply to the study of a leaf like that of apple or beech in its natural environment. With algae or aquatic plants it is much easier because it consists merely in measuring the carbon dioxide which has disappeared from the water or the variations of the pH of the water.

By the application of one or other of these principles or several at the same time, many methods of measuring the rate of assimilation have been developed and have led to the discovery of the different factors which affect and modify it.

Factors Influencing Assimilation

Assimilation depends on a number of different and interdependent factors. For each of these factors there is an optimum value; for instance, photosynthesis is best effected when there are no glucosides in the leaf and it is checked when they are too abundant. Heat, on the contrary, is indispensable, but it can be restrictive in excess; there is an optimum for it, as well as a maximum when it becomes inhibitory or fatal, and a minimum when it becomes limiting. Also the optimum value of a factor may vary and have its limits displaced according to the quantity of some other factor, since these factors are not independent of one another.

The measurement of their influence will therefore be rather delicate, not only because they are interdependent, but also because, during the time of the measurement, the plant is actively developing. It is useless to keep the external conditions constant if the internal conditions are changing and being modified; glucosides, for example, may accumulate and their accumulation will change the optimum value of another factor.

Moreover, how is the influence of these factors to be measured if not by making several measurements of photosynthesis before, during and after the variations introduced? Optimum conditions as estimated by the maximum of carbon dioxide assimilated, for example, may be measured. But here a new difficulty arises. This factor greatly promotes photosynthesis in the first instants, but, too near its maximum, its restraining or even injurious effect is soon manifest and the rate of assimilation diminishes more or less rapidly until sometimes it becomes very low indeed.

If the measurement is made only for the first few moments, the result will seem amazingly good, while it may prove disastrous if the experiment is continued for several hours. So many precautions have to be taken that it is not surprising to find very different figures given by different investigators for the same factor.

Liebig, one of the first physiologists to approach these

problems of nutrition from the chemical aspect, discovered the *law of the minimum*; when several substances are indispensable to growth, it will be checked as soon as one of them is lacking and will be resumed, in proportion as the missing substance is supplied—so long as it remains below its optimum. As the optimum is approached, the increase of growth will no longer be proportional to the increase of the substance the influence of which will tend to be nullified. Only so long as its quantity is insufficient for the needs of the plant will the substance be limiting by its deficiency. Blackman very fittingly applied these laws to the factors influencing photosynthesis, but the interference of the factors must never be forgotten and it is impossible to trace precisely the curve of influence of any one of them, for this curve will be different if some other factor varies. More intense illumination, for example, will increase the utilization of carbon dioxide and consequently the former requirement, or even the former optimum value, will very probably be insufficient.

In brief, photosynthesis, like other vital functions, allows a certain margin of variation of the necessary factors. Inside this margin none of them has any influence, but they become limiting as soon as they pass beyond it, either by excess or by deficiency, unless the variation of some other factor causes a modification or displacement of the margin proper to each. The further a factor moves from its optimum, the more limiting it becomes.

Since photosynthesis is a utilization of carbon dioxide by chlorophyll under the influence of light, the abundance of chlorophyll, of light and of carbon dioxide will obviously influence it, as well as heat and water and the accumulation of glucosides synthesized.

The Influence of Chlorophyll

Contrary to what might be expected, the quantity of chlorophyll has relatively little influence on the rate of assimilation. A study of leaves belonging to different species discloses no relationship between this rate and the amount of chloro-

phyll; the internal environment, the arrangement or distribution of the chloroplasts and perhaps the quantity of diastases—in brief, the whole specific physiology—seem to assume an unsuspected importance which makes comparison impossible. Investigation therefore has to be confined to leaves of the same species.

The result of comparing the rate of assimilation of very green leaves and of more or less etiolated leaves on the same plant is rather surprising and would seem to indicate that here again the quantity of chlorophyll is unimportant. Willstätter and Stoll studied the rate of assimilation of normal and etiolated elm leaves. For the same fresh weight the first contained fourteen times more chlorophyll, but assimilated only 1.2 times more, so that per unit area, the etiolated leaves, weighing less, were a little more productive, but, more particularly, their chlorophyll was, at equal weight, nearly twelve times more active. The conclusion must be, not that chlorophyll is useless, but that it is normally superabundant in the cells and that the leaf possesses much more than is necessary.

If its production is checked by making iron a limiting factor, chlorophyll is no longer superabundant and its influence on the rate of assimilation becomes evident—the rate increases in proportion to the quantity of chlorophyll. The same result is obtained if the limiting factor is nitrogen, but not if it is magnesium; this element does not seem to have the unique function of forming part of the molecule of chlorophyll.

The diastases collaborate with chlorophyll in assimilation and its rate will be retarded by anything which hinders them in their action. Their influence is still not very exactly known, but it may be perceived fairly clearly in connection with light and particularly heat.

The Influence of Light

The light intensity received by a leaf depends on its position on the tree and on the angle that its surface makes with the sun's rays falling on it. The leaves at the top, except at dawn and dusk, probably have enough light, but many

others, especially when the weather is cloudy, may find light a limiting factor for their rate of assimilation.

The rate of assimilation is difficult to measure when the oxygen given off is less than the oxygen absorbed by respiration. The condition when the two rates are equal is called the *point of compensation* and then the plant is breaking down by respiration as much as it is assimilating. Every morning as day breaks all plants pass the point of compensation, but not all at the same time; shade plants pass it much earlier without waiting for the light intensity needed by sun plants. They also suffer more than the others from an excess of light, for too much of it disturbs the plant; the optimum for assimilation, even for sun plants, is below full sunlight.

In very strong light, assimilation diminishes and the leaf suffers from insolation. Insolation occurs more quickly if carbon dioxide is lacking but more slowly if glucosides are abundant. A high temperature also promotes it and the effects seem to be cumulative, for it is much more rapid following great heat.

Insolation appears to have several effects and, when it has been intense, the plant takes several days to recover. Sometimes it causes a diminution of the chlorophyll and the leaves that have just been exposed to very strong light are a little less green than the others; considerable oxidation of the tissues, apparently auto-oxidation, accompanies this excess of light.

Another effect observed is the orientation of the chloroplasts inside the cells and the manner in which they protect themselves from excessively strong light by sheltering in the shade of one another. This would also explain the diminution of the green colour.

But the most important effect, and the one which would seem best to account for all these symptoms, is the inactivation of the diastases which are sensitive to excesses of heat or light.

It may therefore be concluded that light, which is essential to photosynthesis, can be a very variable limiting factor for

different plants and that, even for sun plants, it often has an inhibitory effect. See Fig. II, 4.

As might be deduced from the absorption spectrum of chlorophyll, it is not only the quantity of light which is important, but also its quality or wave-length. Experiments have shown that the maximum of efficacy for photosynthesis is found in the red band. Although the secondary maximum in the blue has been challenged, Engelmann demonstrated the existence of the two maxima by a spectacular experiment using

Fig. II, 4. Proportion of the absorption, in the different regions of the spectrum, of chlorophyll-*a* (—) and chlorophyll-*b* (---), according to Zscheile

motile bacteria with green algae which liberate oxygen in proportion to their photosynthetic activity. He illuminated a filament of the algae by a spectrum in the presence of bacteria which were very avid of oxygen. The bacteria grouped themselves along the filament, principally round the spot illuminated by the red light. In the region of the blue the grouping was smaller but it still exceeded the average density on the rest of the algae. See Fig. II, 5.

The Influence of Carbon Dioxide

One cubic metre of air contains 589 mg. of carbon dioxide, which, if it were all transformed into glucosides, could give

682 mg. of glucose, 648 mg. of saccharose or 613 mg. of starch. The plant never succeeds in using more than 77 per cent of this quantity and seems powerless to fix it when its proportion in the atmosphere falls below 0.01 per cent.

Lack of carbon dioxide seems often to be a limiting factor, especially in calm weather when the assimilation is rapid. The leaf soon deprives the surrounding air of the greater part of its carbon dioxide so that the wind or the absence of wind

Fig. II, 5. Engelmann's experiment. *Above*: the absorption spectrum of chlorophyll. *Below*: filament of green algae surrounded by bacteria avid of oxygen and grouped in the regions where most is liberated

is seen to have an influence. The leaf takes carbon dioxide much more easily from the air when its content is in the neighbourhood of 0.03 per cent and this content scarcely varies when the air is frequently renewed.

If the carbon dioxide content of the air is increased, the rate of assimilation increases proportionately until it becomes ten times greater, but this content cannot be increased indefinitely. The optimum, although it varies with the species of plant, is nevertheless rather high—on an average between

5 per cent and 10 per cent, which is two hundred times greater than the normal. When it rises above 10 per cent, assimilation decreases; the carbon dioxide becomes toxic and the stomata close. If by the use of ammonia they are forced to remain open, the assimilation decreases less.

The Influence of Temperature

If the plant is not affected by frost, photosynthesis can be observed at rather low temperatures; the common juniper, for example, is capable of assimilating at $-40^{\circ}\text{C}.$, the spruce at $-35^{\circ}\text{C}.$

As the temperature rises, the rate of assimilation progressively increases according to van't Hoff's law and is nearly double for an increase of $10^{\circ}\text{C}.$ This increase continues up to $35^{\circ}\text{C}.$ or $37^{\circ}\text{C}.$, then the rate rapidly diminishes towards $43^{\circ}\text{C}.$ to $45^{\circ}\text{C}.$ —a mortal temperature for the plant.

But here the time must be taken into account. The figures just quoted are based on a brief study of the phenomenon at each of the temperatures given. At $35^{\circ}\text{C}.$, for example, there is no doubt that the rate of assimilation is about twice as high as it is at $25^{\circ}\text{C}.$, but this temperature is unhealthy for the plant and if the experiment is continued the rate decreases and falls below that at $25^{\circ}\text{C}.$, while the latter is maintained indefinitely. The best continuous temperature for photosynthesis is therefore in the neighbourhood of $25^{\circ}\text{C}.$

Another difficulty of measurement arises from respiration. Absent at low temperatures, it becomes established and increases at higher temperatures, but follows a rather different curve from that of photosynthesis. It is therefore difficult to estimate the quantity of oxygen that must be added or of carbon dioxide that must be subtracted from the results obtained.

The temperature of the leaves is also rather variable. It is maintained by transpiration, but it may be up to $10^{\circ}\text{C}.$ above the ambient temperature. If, on a fine summer day, a cloud passes in front of the sun, there may be sudden variations of more than $10^{\circ}\text{C}.$ in the temperature of the leaf. The

temperature of orange leaves can fall 18° C. in four minutes and, when the sun reappears, rise 15° C. in two minutes. These variations in the temperature of the leaf are the only variations of temperature which need be taken into account.

Other Influences

Some investigators have held the opinion that *water* has an influence on photosynthesis. Undoubtedly it is indispensable, but it is indispensable to so many other processes in plant life that its exact influence on the rate of assimilation is difficult to discern. Some lower plants succeed in living, although with reduced vitality, after they have lost most of their water. If the water content of their tissues increases, assimilation increases up to a certain optimum point, too much water being injurious to the plant and to assimilation. Such a curve is easy to trace, but how can the optimum for healthy growth be distinguished from the optimum for assimilation?

Normally, however, a deficiency of water checks assimilation. If the tissues lack their usual turgescence, the stomata close and the penetration of carbon dioxide is reduced; in addition, the glucosides accumulate as there is not sufficient water to carry them into the tissues which would use them.

Glucosides are the products of photosynthesis and it is a general law that a reaction is accomplished more slowly as its products accumulate. This effect can easily be demonstrated by making an incision to prevent the leaf from exporting the synthesized glucosides; the rate of photosynthesis, while continuing to vary normally, is maintained well below that of the ordinary leaf. Conversely, photosynthesis is more rapid after a period of darkness which has given the leaves time to rid themselves of glucosides, or after the application of nitrates which favour their utilization, or in fruit trees whose leaves increase in dry weight in the course of the day more than the leaves of trees which have no outlet for their glucosides.

Another product of photosynthesis is *oxygen*, but it has

not been possible to show any retarding effect resulting from its accumulation. Although an excess does not appear to be an impediment, a minute quantity, on the contrary, seems to be necessary at the beginning. This necessity has, however, been denied and Gaffron was able to start photosynthesis in an alga in the absence of any trace of oxygen. To ensure that the plant is deprived of oxygen, it has to be kept for a certain time in the shade without this element. Very probably life without oxygen, and consequently without respiration, is unhealthy for the plant and certain internal reductions may be performed in an endeavour to supply the deficiency; a reoxidation would be necessary before activity could be resumed. Reversible oxidations of chlorophyll have been observed and this necessary oxygen might be used for that purpose.

Among the mineral elements, all those which take part in the synthesis of chlorophyll have a proportional importance for photosynthesis, but this influence is indirect. Certain observations, however, have shown that the presence of potassium considerably increases the rate of assimilation. This effect, which is not explained, might proceed from a better exportation of the glucosides.

Efficiency

It is difficult to calculate precisely the efficiency of photosynthesis. The highest figures obtained from the method previously explained of weighing half a leaf in the morning and the other half in the afternoon are in the neighbourhood of 1 gramme of dry matter per square metre of leaves in one hour.

This weight of dry matter mostly represents glucosides; it is easy to conclude that 1.54 grammes of carbon dioxide have been fixed and transformed into glucosides in each square metre per hour.

Much higher figures were published by Willstätter and Stoll, who, for a sunflower leaf subjected to an illumination of 48,000 lux, at a temperature of 25° C., observed an increase,

not of 1 gramme, but of 8 grammes of dry weight per square metre per hour. The plant, however, had been kept in an artificially enriched atmosphere with a carbon dioxide content of 5 per cent. The experiments reproduced in natural conditions have rarely given as much as one third of this result.

The measurement of the carbon dioxide absorbed by apple leaves gives, per square metre and per hour, a maximum of 2 to 3 grammes of gas absorbed, which represents in glucosides 1.36 to 2.05 grammes.

The increase of weight proceeding from photosynthesis

Fig. II, 6. The distribution of the light as a percentage of the incident light falling on a leaf

is therefore capable of reaching 2 grammes per square metre in an hour, but this figure represents a maximum which is rarely exceeded.

In 1905, Brown and Escombe made their well-known experiments on the utilization of light by plants. They found that, on an average, 30 per cent of the light falling on a leaf is transmitted or reflected, 20 per cent is transformed into heat and sent back by thermal radiation, 49 per cent is used in evaporation and only 1 per cent (between 0.4 per cent and 1.7 per cent) for photosynthesis. See Fig. II, 6.

The energy used for photosynthesis can also be calculated

from the quantity of material synthesized. In an hour of full sunlight, 1 square metre of leaf receives 720,000 calories. If 2 grammes of glucose are synthesized, this area has accumulated 6,500 calories, which represents 0.905 per cent of the incident energy and nearly reaches the average of 1 per cent.

In considering the luminous energy normally received on the ground and calculated by the meteorological observatories, it may be observed that leaves have, in fact, a larger useful area than the ground for receiving the light; they partly cover one another and are more or less inclined to the rays of the sun. A small quantity of light passes through the highest and a small quantity is sent back on the others; in addition, the maximum for assimilation is ordinarily below the maximum of the light received from the sun. Thus, leaves receiving oblique light may assimilate to the maximum, and that is why in a plant or stem of maize slightly higher yields may be found than the maximum calculated for an isolated leaf.

Maize is one of the plants which seems to make the best and most rapid use of the sun's energy. Transeau took as a basis for his calculations a good field of maize yielding a crop of two tons of grain per acre. The growing period is about a hundred days and the dry matter formed reaches five and a half tons, which corresponds to six and a half tons of glucosides assimilated. A certain quantity of glucosides, which may be estimated at nearly two tons, has been expended in respiration; this brings the quantity of glucosides elaborated by photosynthesis to eight and a half tons.

Each pound of glucosides represents 1,710 kilo-calories. The acre of maize has therefore stored 32,000,000 kilo-calories, i.e., 1.6 per cent of the calories received from the sun during the hundred days of growth. At best, the figure scarcely exceeds the average given by Brown and Escombe.

Studying the plankton of Lake Erie, Verduin nevertheless found that the yield could be as much as three times higher, but he took as his term of reference not the area but the volume, and it is very probable that, for photosynthesis, these small algae use their volume better than maize leaves.

From some points of view these results are a little disappointing; if, however, instead of calculating the quantity of calories stored, we consider the manner in which they are stored and their quality, we cannot but admire the performance of photosynthesis in transforming into food a quarter of the energy stored, which is a two-hundredth part of the energy received from the sun.

CHAPTER V

CHLOROPHYLL AND OURSELVES

EVERYBODY today has heard of chlorophyll. Forced on the attention of the general public, it has become the fashion and has just made a sensational entry into commerce, being widely advertised as a constituent of a number of products.

The Utilization of Chlorophyll

Two of its derivatives are used more than chlorophyll itself. Among the characteristic constituents of its molecule are the atom of magnesium and two acid radicals esterified by two alcohols—phytol and methyl alcohol. If the magnesium is replaced by copper, a much greener product than chlorophyll is obtained, and if the two alcohols are replaced by an alkali metal the product becomes soluble in water; these substances are cuprichlorophyll and cuprichlorophylline of sodium or potassium, which take the place of authentic chlorophyll whose colour is too dull and unstable.

Soluble in oil, cuprichlorophyll is used to colour soaps a uniform and attractive green which is relatively stable in the light; its advantage is that it does not stain fabrics.

Cuprichlorophylline of sodium is much more widely used. Its most distinctive property is its excellent healing power. Our ancestors used leaves as plasters to cover wounds. In 1916, the Swiss doctor, Burgi, struck by the identity of the tetrapyrrolic nucleus of chlorophyll with that of haemoglobin, demonstrated its therapeutic value in certain cases of anaemia but more especially its healing action. This action, which seems to stimulate metabolism, is unsurpassed by any of the remedies hitherto employed in the treatment of wounds.

Chlorophyll has been found to have an excellent action

on the heart in increasing the amplitude of the contractions, so that its use is recommended in cases of arteriosclerosis. It is sometimes also advocated to arrest the development of cancer.

Finally, chlorophyll is bacteriostatic; without directly killing the microbes, it prevents their multiplication. Some suppurating and evil-smelling sores begin to heal and lose their unpleasant smell when it is applied to them. Similarly, the nauseating odour produced by perspiration when it is decomposed by bacteria seems to be mitigated by chlorophyll. No more was required to provide a basis for organized publicity well adapted to the countries in which it was launched.

Chlorophyll is, more than almost any other, a natural product, and everyone remembers from his school days that it renders vitiated air respirable. Can as much be said for cuprichlorophylline of sodium? As a matter of fact, it is seldom mentioned: only chlorophyll is spoken of.

The deodorizing power, which no one ventures to put on a medical or pharmaceutical foundation, would be of a physical or chemical order, and one may wonder whether it is not often a psychological matter. The new chlorophyll cigarettes, while retaining their full flavour for the smoker, cause no discomfort to others who may dislike smoke. As a general rule, chlorophyll destroys bad odours, but not good ones. There are dog foods, much in vogue in America, which suppress the smell of these animals. Chlorophyll underwear is making its appearance, and chlorophyll toothpaste "keeps your mouth fresh for the whole day. . . ."

A host of chlorophyll products has invaded the market in the United States and is turning towards Europe. Large industrial companies have been formed; twenty-seven tons of the product were manufactured in 1951. This figure was more than doubled in 1952 and several factories were under construction. The chlorophyll is extracted from lucerne with a yield of 0.2 per cent and its cost is around £35 per pound.

Fortunately, cuprichlorophylline is a powerful colorant and the colour of the product is often sufficient to sell it.

On the other hand, no advertisement is needed for the authentic chlorophyll, since no one has ever thought of doing without it.

The Benefits of Chlorophyll

Among the very diverse material needs of humanity there are three of primary importance: we must nourish the body with food; we must protect it by wearing clothes and, in an unfavourable climate, by creating a more comfortable atmosphere indoors; finally, we must increase the power available to us for work. We need nutrition, protection and energy.

For nutrition, we use vegetable or animal products which are all derived from chlorophyll, since the animals feed either on vegetation or on other animals which feed on it. Our food therefore depends more or less directly on chlorophyll; it enables carbon to enter into the life cycle and puts at our disposal material charged by it with a chemical potential which can be liberated through the various paths of oxidation-reduction.

For our protection, we wear clothes made from material produced directly by chlorophyll, like cotton, or indirectly like wool, leather or fur. Our houses also depend on chlorophyll, to the extent to which wood is used in their construction.

To provide energy, we use petrol or coal, and nearly all the transport on the road and even on the railway is effected by means of those valuable deposits left by chlorophyll, which worked for us in the distant geological ages. The same energy warms us still and enables us to prepare our meals. Although it is now supplemented by hydro-electricity, we are still far from being able to dispense with it.

Thus on all sides we find this indispensable chlorophyll on which life is so dependent that the problem of its origin is practically identical with that of the origin of chlorophyll. When chlorophyll appeared, life became self-sufficient and, sure of its future, the immense animal and vegetable pyramid could rise, while chlorophyll indefatigably provided its means

of subsistence. Before chlorophyll, life may have appeared on the earth, but it would have been dependent on too many fortuitous circumstances to become firmly established. With the arrival of chlorophyll, it attained its majority; it became independent and could spring into action.

The Importance of Energy from Chlorophyll

When we consider the different types of energy which are, or will be, available to us, they all centre round the atom.

The most common and the best known is chemical energy typified by that accumulated by chlorophyll in starch or wood. These molecules, of which carbon forms the woof, can be broken down or oxidized. All their potential of oxidation-reduction is realized, either in a single operation by burning or by their use as fuel in internal combustion engines, or else by a graduated series of intermediate reactions, as in our own organism.

The atom properly speaking represents two types of energy, one relating to the nucleus and the other to the electrons.

Some of the electrons which revolve round the nucleus may be separated from a group of atoms, thus giving rise to a centre of attraction of electrons and an electric current which, at enormous speed, tends to fill the void which has been created. By means of conducting wires, the potential acquired at any place can be very rapidly transported a long distance; electricity enables energy from the Rhône to be used in Paris, but it must be used immediately. In a certain sense, electrical energy has no more existence than the energy of a belt which transmits the motive power from one pulley to another. It is much spoken of because, in our industrialized world, most of the transport of energy is effected by it and because, for example, a waterfall as well as a stock of coal can be measured by the number of kilowatt-hours that it is capable of supplying; electrical energy is an accepted standard of energy.

Although electrical energy is only transitory, because the

atom quickly recovers the lost electrons, the conditions are different if the nucleus is affected, for, at that level, the losses or gains are definitive. The energy released by the destruction of heavy nuclei such as those of uranium or plutonium, or by the agglomeration of light nuclei such as those of hydrogen, deuterium or tritium, is irretrievably lost to the atom, for the nuclei formed are much more stable than those from which they come. This needs no proof when one considers the enormous quantities of energy liberated by these transformations.

A part of the initial mass is transformed into energy and disappears; this has given physicists the hope that one day they will be able to release, not a thousandth of the mass, but the entire mass of the atom. Such a liberation seems possible, but is still uncertain.

From the point of view of their utilization, all these forms of energy can be evaluated in electrical units. The conversion from one form to another is easy, as is abundantly proved by the generation of electricity from sources as different as coal, waterfalls and the wind, and its utilization for lighting or heating or for driving machines.

There is, however, one form of energy which can be evaluated in terms of electricity but which could not be produced from electricity—the energy of oxidation-reduction that the living organism claims unconditionally. It could be called a noble, irreplaceable energy. Here the quality matters much more than the quantity, for, considered from that point of view, the balance would not be strikingly in favour of the products derived from chlorophyll: 1 gramme of glucose is capable of liberating in the organism or in the calorimeter 4,000 calories, 1 gramme of uranium can produce 20,000,000,000 calories and 1 gramme of matter represents 21,000,000,000,000 calories.

We have become accustomed to drawing up a balance sheet of our resources of energy and are beginning to know what may be of value to us.

The energy of matter represents a capital that can be

considered as infinite, but we are not ready to use it. Atomic energy represents a capital that we have scarcely used up to the present except for destruction, but atomic piles will soon be capable of producing electricity and we can hope to draw plentifully from this fund which appears to be nearly inexhaustible.

Cosmic energy, from which the tides and the geothermal energy of our planet proceed, is a capital which is still almost intact and even in using the tides we are not breaking into it, since this energy is lost every day as it aimlessly combs our shores.

Solar energy is practically the only form that has been employed up to the present. We have not yet used the thermal energy of the earth's surface or of the sea, but we have captured the energy of water torrents. The energy from the sun transforms the water into vapour which, losing some of its energy, falls as snow or rain on the mountains whence it descends to the plains, using its kinetic energy to erode the slopes and carry away the soil. The energy of this descending water is captured and, by means of turbines, is used to provide electricity in the place of the formerly useless or destructive erosion.

More effective than turbines, chlorophyll transforms the energy of the sun into living matter, if one can describe as such the material which enters into the life cycle and without which life would not exist. In the depths of the geological strata the products of its work, ages ago, have accumulated, constituting valuable reserves although they are devitalized and unusable for the internal needs of the living organism. The modern age exploits coal and petroleum with a thoughtlessness that will soon be qualified as criminal, for is it not, to say the least, absurd to use for heating material which, owing to the enormous progress of organic chemistry, is capable—uniquely capable—of so many other uses? Irreplaceable capital is thus being squandered every day!

We come then to the essential energy, on which alone devolves the task of maintaining life, on which the whole of

the immense and swarming biosphere depends. This vast pyramid of living things rests entirely on the energy produced through chlorophyll, which enables life to spring into being and sustains its impetus day by day. How subordinate seem all those other forms of energy that industry values so highly!

The Real Problem

If we draw up a balance sheet of our actual and potential resources and consider the future, we see that there is an increasingly large margin of energy as we descend the scale of importance and that the margin becomes proportionately smaller as we approach the energy produced through chlorophyll. Here the possibilities of increase seem so precarious that a limiting factor—"a constricting bottle-neck"—suddenly rises before us. The future of humanity inescapably depends on this energy.

The first man who seemed to realize this was an English clergyman, Thomas R. Malthus. In a book which caused a sensation, he showed that the number of human beings tends to increase much more rapidly than their means of subsistence. It is possible for each couple to have an average of four or five children; the human population would then be doubled in each generation, while if the farmer succeeds in producing from his field twice the crop that his father did, his son, in turn, will have difficulty in doubling that again and for his grandson the difficulty will be even greater. At the end of a hundred years, a field, however well it is cultivated, cannot produce sixteen times more food, while it is quite possible for the population to be sixteen times larger. For farming, the progression can, at the most, be arithmetic, but not geometric like that of the population. "Nature," he concluded, "has spread the germ of life with a liberal hand, but she has been sparing of space and elements."

Original, and on the whole just, Malthus's views have dominated the nineteenth and twentieth centuries and the Anglo-Saxon countries particularly seem to have been impressed by them. Neo-Malthusian propaganda is very active and we owe to it

the wide-spread use of contraceptives and a spate of pessimistic literature which it is difficult to ignore.

Nevertheless, Malthus's prophecies have not been fulfilled, although the world has since trebled its population and that of Europe has increased nearly four times—from an average of 31 to 118 inhabitants per square mile.

The problem is really very complex. In former times, the peasant, firmly guiding his swing-plough drawn by a robust pair of oxen, laboriously traced a furrow at the rate of $1\frac{1}{4}$ miles per hour. He works ten or twenty times faster on his tractor, but the tractor represents a certain number of man-hours in the mine, the foundry and the factory, without counting the work of the engineers and the preliminary technical studies. Farmers now work better and more quickly, but their number is declining in every country. The United States employ only one-fifth of their population in agriculture. In 1870, half the population of France was engaged in farming, compared with only one-third today, and we must expect to see this proportion become smaller still.

The economic pyramid is gradually rising and seems to be dangerously multiplying its superstructures, while it rests on a vertex which becomes relatively smaller every day. The quantity of arable land is not inexhaustible and the most probable estimates arrive at a total for the whole world of some 6,000,000 square miles, i.e., 11 per cent of the land area. Since there are 2,300,000,000 inhabitants, $1\frac{2}{3}$ acres of cultivated land falls to each one and three men must live on 5 acres. Atmospheric agents covetously degrade these limited fields and every year erosion carries away to the sea a mass of soil rendered still more vulnerable by cultivation, while the land, becoming exhausted as the years pass, demands more work for a diminishing return. "How," exclaim innumerable Anglo-Saxon writers, "can one avoid being alarmed to see the number of human beings increasing and competing ever more strenuously for the produce of these fields which are going to ruin?"

Although these views are shared by a growing section of

the community, they become less convincing when the facts are considered more closely.

It cannot be denied that atmospheric conditions are an agent of destruction of the soil, but they are also, as pedology shows, an agent of construction. If they had had no action, we should find nearly everywhere the matrix intact, without the slightest trace of cultivable soil. Atmospheric agents have made all our soils and are still doing so. We are therefore obliged to conclude, since soil exists, that the rate of destruction is lower than the rate of construction. We alone are to blame for this destruction that the neo-Malthusians adduce to support their argument; we have ill-treated the soil, and this leads us to examine one of the great errors of the economists.

The less work we had to do in cultivating the soil, the greater would be its productivity. The ideal, which could hardly be carried further, would be the practice of the Canadian large farmer who goes out in the spring to plough and sow immense fields of wheat to which he will not return until harvest time. He reaps and threshes the wheat with a combine harvester, taking away only the grain. In the following spring he will return to repeat the process. This extensive cultivation produces 4 to 5 cwt. per acre.

At the opposite extreme is intensive cultivation, which produces ten times more. For example, taking the yield of a Dutch field as a basis, in 1939 only 11 per cent of that yield was obtained in the United States, 30 per cent in France and 52 per cent in Germany.

The soil represents a mass of elements of which only a very small part can serve for the nutrition of the plant; a relatively large accumulation will occur in the stem and especially in the seed. At harvest time the field will lose some of its wealth removed in the grain. In extensive cultivation this is not replaced and the field becomes the poorer. Inevitably, the yield progressively diminishes.

In intensive cultivation, on the other hand, fertilizers are used as well as farmyard manure, which is so important for

the renewal of humus.¹ The soil, far from becoming impoverished, improves from year to year and the yields steadily increase. Obviously this increase is not unlimited and the time comes when fertilizers, used even with the best technique of soil science, cannot give better results or, more precisely, do not pay, because their cost is no longer reimbursed by a higher yield. Are there any fields where this point has really been reached? Probably not, and the apparent exceptions merely show evidence of a bad use of fertilizers.

From the point of view of the land, there is no doubt that intensive cultivation is much more advantageous than extensive cultivation, particularly because it guarantees the future instead of compromising it. But would the farmer give the same reply?

Surprising as it may seem at first sight, he does. With approximately the same work, a Dutch agricultural family obtains from its smaller acreage the same return as an American family. In comparison, the French family hardly obtains 57 per cent and the German 72 per cent; nevertheless the French and German family have more land at their disposal than the Dutch. This reminds us of what the old agricultural economists used to say—that it was more profitable to double the depth of one's field than to double its area.

On 1,000 acres ten workers are employed in the United States and ninety in Holland, but the Dutch worker gains as much by cultivating his 11 acres as the American with his 100 acres. This indicates that the problem is not so much one of over-population in the world as of bad distribution.

We arrive at the conclusion that the cultivated land is giving much less than its potential yield and that it would be capable of nourishing far more people. Its area could also be extended without much difficulty, perhaps doubled or even trebled. In some depopulated districts, many fields remain unploughed for so long that they can no longer be distinguished

¹The humus soon diminishes in the soil when it is not supplied with manure. The general introduction of tractors causes an unforeseen disequilibrium the importance of which should not be underestimated.

from the neighbouring heath! An inventory of the soil and its possibilities in most countries would reveal more wealth than we might suppose.

Beside this abandoned land, there is other land which could easily be gained for agriculture, like that to be irrigated by the great dams being constructed in Algeria and many other parts of the world and the fields of rice or grain which since the war have encroached on the desert of the Crau. The Dutch farmers, in their successful struggle against the sea, have provided the most striking example of these extensions of cultivation, *a priori* discouraged by all the economists, by constructing and maintaining enormous dikes, pumping out the water and removing the salt from the land. And this enterprise has proved profitable in spite of real dangers.

Such considerations seem so completely alien to the neo-Malthusians that it is permissible to wonder whether, instead of examining the facts impartially, they do not merely select from them examples to support a theory the validity of which they never question.

The Future of Energy Obtained Through Chlorophyll

As soon as a product becomes scarce on the market, its price rises in proportion as the demand exceeds the supply. If, on the other hand, the supply is greater than the demand, the price soon falls—we have heard of coffee in Brazil being used for fuel, and of wheat in France before the war being rendered unfit for human consumption so that it could be used only as cattle food. The object in both cases was to “produce a healthy market”.¹

Today, on a free market, prices are not far from their normal level. Compare the prices of energy produced through chlorophyll with those of electrical energy, converting all the energy theoretically into kilowatt-hours.² 1 kWh. of electricity

¹In certain districts of France, at the end of the last war, a pound of hay cost up to three times more than a pound of bread as the price of bread, kept artificially low, did not represent its real value.

²A kilowatt-hour corresponds to 860,000 calories.

costs $1\frac{1}{3}$ d., the equivalent in coal $\frac{1}{6}$ d., in petrol 1d., in sugar 4d., and in butter 1s. Only human labour is rather highly valued, since the equivalent of a kilowatt-hour costs more than 30s.¹

Energy obtained through chlorophyll is therefore far from being appreciated at its just value or, more exactly, electrical energy is still so scarce that it is glaringly over-estimated in comparison. Yet in assessing the real advantages of converting the kinetic energy of flowing water into electricity, it is necessary to consider whether any better use could be made of the water.

The rate of solar radiation at the outside of the earth's atmosphere is 2 calories per minute per square centimetre. Under the best conditions, the soil receives only about half of it. Taking into account the length of the day and the time of insolation, we can estimate the number of calories received annually per square metre as between 1.2×10^9 and 1.5×10^9 calories. Now, a man's normal requirements, about 3,000,000 calories² per day, are below this total. If all the calories coming from the sun were transformed into food through the agency of chlorophyll, a man could live on 1 square metre.

In the best conditions, a leaf fixes, in dry weight, more than a hundredth of the calories received, but a good field of maize transforms into grain only a two-hundredth part of these calories. It therefore seems impossible to nourish a man on less than one twentieth of an acre. We are still far from doing that.

There is no doubt that an effort can and must be made to banish the bugbear of over-population that the neo-Malthusians raise with such persistence. Of particular importance are the quantity and quality of our essential

¹*Translator's Note*—The figures in this paragraph have been converted into the average values prevailing in Great Britain in 1955.

²Here, as elsewhere when we speak of calories without qualification, we mean small calories. Biochemists, in discussing human needs, for example, always quote them in kilo-calories without adding the qualification which appears to them useless. We prefer to sacrifice custom to clarity.

wealth—the products of chlorophyll. The quantity is important because we must promote vegetation, and the problem which poses itself is whether we shall have turbines or chlorophyll. As for the quality, we must make the best use of the energy obtained through chlorophyll, and this poses problems of vegetable and even animal selection.

Turbine or Chlorophyll?

A quantity of water can be used either for its substance, if it is made to penetrate into the life cycle of a plant or animal, or for its mass, if it is used to drive a turbine. When a dam is constructed to use the water which flows aimlessly to the sea, should it serve to generate electricity, or to irrigate the land?¹

One of the most essential needs of the plant is water that it absorbs by its roots and gives off to the atmosphere by transpiration. For the sap to rise and for the necessary substances to reach the leaves, the plant needs to transpire and the process is so critical that there is a fairly constant ratio for each species between the weight of dry matter formed and the quantity of water transpired; this is called the coefficient of transpiration.

A stem of maize builds up $\frac{1}{80}$ lb. of dry matter per day, but it transpires during that time some 10 lb. of water, that is, 300 lb. of water transpired for each lb. of dry substance elaborated. These figures attain an average of 500 lb. for barley, 550 lb. for wheat and 850 lb. for lucerne. The highest figure is 1,000 lb. and the lowest 225 lb. It can therefore be assumed that the average for crops is 500 lb. of water per lb. of dry matter elaborated.

If the plant had plenty of water, irrigation would be unnecessary, but this is rarely the case. Too often, water is so scarce that it becomes a limiting factor in growth. Under

¹The problem is quite topical, for France, for example, is short of electricity. Hydro-electrical engineers calculate that, by making the best use of rivers, a total of 8×10^{10} kWh. could be reached, as compared with 3×10^{10} kWh. today.

these conditions, even if nothing is added, the increase of growth and yield will be proportional to the quantity of water supplied. The circumstances are such that the yield obtained from water alone is maximum.

When a good field of maize is in full growth, it evaporates in a day 24 tons of water per acre. If the soil can provide it with only 16, the growth will be proportionately limited and instead of 198 lb. of dry matter, only 132 lb. will be elaborated; the deficit of 8 tons of water will be shown by a deficit of 66 lb. of dry matter, which represents in chemical energy 120,000,000 calories.

Suppose that the dam is situated in an excellent position for the generation of electricity, with a possible fall of 100 metres. Each litre of water represents a potential of 100 kilogrammetres, i.e., 234 calories; the 8 tons in question therefore represent 1,872,000 calories. The transformation into electricity will not be made without losses, but nevertheless it is reasonable to expect in kilowatt-hours the equivalent of 1,200,000 calories.

It is obvious that in the service of chlorophyll water can give a return in energy a hundred times greater than that of turbines, only ten times if the possible fall is 1,000 metres, but such falls will never be very numerous. On this basis, irrigation is therefore fifty to one hundred times more economic than the generation of electricity.

The results of irrigation are obviously more uncertain than those of hydro-electric generation, but they become less so when irrigation is not indiscriminate but is directed only to the points which lack water. All crops are not as productive as maize, but the coefficient of transpiration never falls below a quarter of the value for maize and an adequate and indisputable margin still remains in favour of irrigation, even if the possible fall were 1,000 metres.

Again, the water used by the plant is immediately returned to the air in the form of water vapour. This water vapour transforms the climate of the region; the atmosphere is more humid and more quickly saturated by passing clouds which

will easily cause rain. Without vegetation, the air is very dry and the whole climate tends towards the creation of a desert.

Much more even than these considerations of energy and climate, arguments of a biological, economic or human kind are strongly in favour of irrigation—a soil under cultivation instead of becoming rapidly denuded, a prosperous and inhabited countryside instead of the mass departure of peasants discouraged by their meagre crops in a country daily becoming more impoverished.

Turbines, which are so important for the development and enrichment of a country, may become a source of ruin if they monopolize water which could otherwise be used for irrigation.

Towards a Better Yield

In the world of the future, the products obtained through chlorophyll will be reserved for uses worthy of them, and other sources of energy will be able to replace them whenever possible—atomic energy may eventually supply these subordinate needs.

The substances produced through chlorophyll are not all of equal benefit to man and most of them gain by being transformed or improved. Progress will undoubtedly be made in this direction, but certain natural processes will probably never be surpassed; there is unlikely to be any better means than bees for making honey, than pigs for producing fat or than cows for giving milk.

The task of the stock-rearer will be to find a breed of pigs to produce 2 lb. of fat from 7 or 8 lb. of meal or breeds of cows which will produce more butter or milk from the same quantity of grass—a task that will become more and more essential, for these “synthetic factories” are unrivalled.

The most important work devolves upon the agriculturists and the botanists; they must ensure that the surface of the ground is always used to the best advantage by chlorophyll and must find the best crops to cultivate in a given environment and climate—those that will store the most solar energy in the most useful form.

Botanical geographers could make an inventory of our resources in vegetation and of their distribution over the earth's surface. It may be possible to increase and exploit some neglected species, or to spread others that have been confined to only a small area.

Plant biology has achieved magnificent results. All the resources of genetics have been brought into use; different varieties have been crossed to concentrate in one single variety the greatest possible number of qualities, to eliminate some hereditary characteristic which, in a given environment makes a particular variety delicate and fragile. A certain peculiarity, favourable in one place, may be a disadvantage elsewhere; it is necessary to experiment at length and select unremittingly.

By this patient work, lands formerly barren are becoming fertile and cultivation steadily advances towards the poles or the tropics. To give only one example, wheat is now cultivated in every continent and in nearly all latitudes, so that there is not a month in the year when, in one country or another, harvesting is not in progress. By the skill of agricultural botanists in selection, ever more varied plants multiply, develop and adapt themselves to our needs.

Soil-less culture, too, opens up new horizons; for example, plants cultivated in nutrient solutions enabled American troops to be supplied with fresh vegetables on desert islands where almost everything was lacking, except sunshine. Better still, lakes and seas are engaging the attention of botanists, who are already thinking of promoting the development of algae to feed certain species of fish. They are beginning to be interested in a green alga, the unicellular *chlorella*, which multiplies so rapidly that it would be possible, by cropping it every day, to obtain an abundant supply of substances rich in albumins and even in lipides that the food industry could use.

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