illustrated, the level of the soil surface, the bottom-water-level, and probably the salt content, are the correlated physical features which determine the distribution of the vegetation. Similar conditions often obtain in fresh-water marshes where the bottom water level is close to the surface.

CHROMATIC ADAPTATION.

FACTS AND THEORIES CONCERNING THE ADAPTATIONS OF PLANTS TO DIFFERENCES OF ILLUMINATION.

BY F. F. BLACKMAN.

A CERTAIN human interest attaches to the different adaptations by which plants attempt to rise superior to unfavourable variations in their environment.

The green land-plant, as a generalised structural type, is an expression of the necessity, under which it always is, of obtaining energy by the absorption of radiation from above. Nearly all the striking variations of this type which the plant-world displays are correlated, however, not with variations in illumination, but with special variations in the water supply of their particular habitat.

The absence of striking adaptations to different intensities of natural illumination ceases to surprise, when one realises the fact that no plant under existing natural conditions can utilise more than a small fraction of the energy of the direct sunshine which may fall upon it. There may be enough chlorophyll in a leaf to absorb 20% to 25% of the sun's radiation¹ in addition to the amount absorbed by the sap, cell-walls and protoplasm, but the actual CO₂-assimilation performed cannot, under natural conditions, represent more than about $\frac{1}{8}$ th of the available energy. The reason for this is that, in nature, assimilation is limited not by light but by the available CO₂-supply, because sufficient CO₂ cannot diffuse into a leaf from an atmosphere containing only three parts of CO₂ in 10,000. The writer has shown that an active leaf exposed both to the bright diffuse light and to the direct sunshine of a brilliant August day can absorb enough energy *in a form available for CO₂-assimilation* to produce a photosynthesis of six litres of CO₂ per square metre of area per hour. Now, from determinations made

¹ Timiriazeff. The Cosmical Function of the Green Plant. Proc. Roy. Soc., Vol. 72, p. 449.

by Horace Brown¹ of the gain in weight² of actively assimilating leaves, it would seem that a leaf in the open air is limited to acquiring about 800cc. of CO₂ per square metre of area per hour.

It is clear then that the energy available for assimilation in sunshine is so much in excess of the supply of raw material available for the leaf to work up, that comparatively feeble light is adequate for all assimilatory possibilities.

We should not expect, then, to find adaptations for making the most of the light that reaches a leaf, except when the natural illumination falls below a certain low level. Confirmed "shade-plants" show a certain amount of structural adaptation in this direction, but the differences between sun-leaves and shade-leaves are also partly correlated with the function of transpiration. The most efficient illumination-adaptations seem to take the form of lens-like arrangements of cell-walls which focus upon the chromatophores such light as is available. It is very striking that, in no case, does a land-plant heighten its assimilating power by developing in its chromatophores a pigment which will absorb some of the rays of light which chlorophyll transmits unutilised.

With plants growing submerged in various depths of water the state of things is quite different. Water is a blue liquid, and the deeper the water the more the rays of the red end of the spectrum are absorbed. Spectroscopic observation has shown that at fourteen metres below the surface of the sea the light that penetrates is mainly composed of green and blue, feeble in yellow, and lacks red entirely.³ These red rays are just those most efficient in CO₂-assimilation and this loss, combined with loss of light of all kinds by reflection from the troubled surface of the sea, and by absorption by fine suspended particles brings the efficiency of the light so low that it falls below the intensity corresponding to the quantity of CO₂ available for assimilation.

An adaptation is then profitable to promote the assimilating activity of sea-weeds at these depths, and we find that this takes the form of a brilliant red colouration, which provides an efficient absorber of the green and blue rays that preponderate in these depths. Between the red deep-water algæ and the superficial algæ which

¹ Horace Brown. Presidential Address, Chemical Section of British Association, 1899.

² Sachs deduced from one of his experiments that 1400 cc. might be absorbed, but there are good reasons for regarding this number as too high.

³ Engelmann. *Couleur et Assimilation*. Arch. Néerlandaises.

⁴ Tome xviii. 1883.

are green, and depend on the same rays as plants in air, there is found an intermediate zone of brown algæ which make up for some deficiency of red light by an added power to absorb, to a certain extent, green and blue rays.

These three coloured algal strata, then, tend to possess complementary colours to the lights in which they are bathed, and thus to arrive at the maximum absorptive efficiency for their respective habitats.

There are yet other types of algæ which are not pure green in colour, the Cyanophyceae or blue-green Algæ. These are all minute forms and show a great range of colouration, being purple, violet, brown, yellow, olive green or blue in different cases, though the most usual colour is blue-green. This group possesses at the present day a much greater mobility of colouration than the other groups.

It is, of course, well known that the red, brown and blue-green algæ all contain chlorophyll in their chromatophores, but that these organs contain, in addition, red, brown or blue pigment which entirely or largely masks the green colour. These adaptational pigments all differ profoundly from chlorophyll in chemical constitution (being usually held to be of a proteid nature) and all are soluble in water and diffuse readily out of the dead cell. These secondary pigments can be readily discharged by dipping a red, brown or blue-green alga in boiling water, after which the chlorophyll green stands revealed.

We now come to the interesting point that as these adaptational pigments are *additional* and not substitutional, it would appear that a red alga should be a more efficient absorber of light than a green one, not only at great depths, but also at the surface. Nevertheless the red algæ have not replaced the green forms at the surface, but are only found there in small numbers. The probable explanation is that assimilation at the surface of the sea is limited by the amount of CO_2 attainable, as it is on land, and that therefore additional power of absorbing light-energy is of no assimilatory advantage. The red algæ have no advantage over the green at the surface, though at a sufficient depth the green alga will be completely out-classed. Here then in the case of marine algæ we have what Engelmann has called "complementary chromatic adaptation" arrived at in the course of evolution.

An extremely interesting case has recently been carefully

investigated by Gaidukov¹ in which "complementary chromatic adaptation" can be brought about in the course of a few weeks, and all the details of the change have been followed by him.

He found that filaments of *Oscillaria* possess the power of changing their colour when grown behind coloured glass or coloured solutions and always in the direction of taking on the complementary colour to the light which they are made to exist in, and so absorbing it more efficiently. According to the views here put forward, this would be a distinct biological gain only if the light were so weakened that it became the limiting factor in assimilation. In this connection it is significant to note that Gaidukov's cultures were grown inside the laboratory, though within a yard of a big south window, and the colour screens used were mostly deeply coloured.

Oscillaria sancta, which is violet in white diffuse daylight, was first investigated, and pure cultures growing on earth or agar in Petri dishes, were kept in the different coloured lights. After one to four weeks they were found to have taken on the complementary colour, being greenish in red light, blue-green in yellow brown light, and yellow-brown in blue light. During this time the cultures had grown rapidly, so that the final colour was due chiefly to newly-formed cells. Another species, *O. caldarium*, which is blue-green in daylight, gave quite similar colour-changes.

When a filament is transferred from one light to another which is spectrally remote from it, as from red to blue, it does not at once begin to assume its correct final reddish colour, but passes in succession through a long series of intermediate stages of colouration, being the colours approximately complementary to the intermediate spectral lights in order. This series of colours is given by Gaidukov as (1) sky-blue, (2) blue-green, (3) verdigris-green, (4) grey-green, (5) whitish-grey, (6) violet to brown-violet, (7) brown (8) orange to reddish. *O. sancta* in ordinary white light happens to have colouration 6. Transferred to red light it passes *up* the series to 1. Placed in blue light it passes through 7 to colour 8. *O. caldarium* happens in white light to have colour 2 and transferred to green light it passes *down* the series to 7 or 8.

As the individual cells are multiplying all the time it may be that each generation only takes a short step in the direction of the

¹ Gaidukov. Über den Einfluss farbigen Lichts auf die Färbung lebender Oscillarien.

(a). Anhang zu Abh. k. Preuss. Akad. Wiss. Berlin, 1902, v.

(b). Ber. deut. bot. Gesell., Bd. xxi., Oct., 1903.

(c). " " " " Nov., 1903.

final colour, and so the culture goes on gradually improving its biological position.

It is interesting to note that if the cultures were brought back to white diffuse light they retained for months the colour that they had acquired behind the coloured screen, and even the new cells formed thus under natural illumination exhibited the acquired colour. The ultimate fate of these nascent new "forms" has not yet been announced.

As has been pointed out, white daylight probably supplies sufficient of all the spectral radiations to allow *any* of the *Oscillaria*-colours to assimilate abundantly, so that there would be no *assimilatory* gain in the new forms reverting to their ancestral colour.

Gaidukov's first paper gives very excellent full details of the colour-changes and is illustrated with coloured figures of the filaments themselves, of the colour-screens and of the absorption spectra of the different coloured pigments. Also there are given detailed measurements of the change of absorption for different rays as one pigment passes into another. The author draws attention to the fact that each stage of colour-progression passes by imperceptible gradations into the next and that here, as elsewhere, *Natura non facit saltum*.

The different shades of colour are due to modifications, not of the chlorophyll in the chromatophore, but of the water-soluble proteid pigment which is here called the adaptational pigment. If abundant this completely masks the green colour.

It has generally been held that the blue water-soluble pigment of the Cyanophyceae belongs to the same class as the red and brown pigments of the Rhodophyceae and Phaeophyceae but it would appear now that when the blue-green *Oscillaria* becomes red under the influence of green light it develops a pigment identical with that of the Rhodophyceae.

The characteristic secondary proteid pigments of these three groups of algæ can be crystallised from their watery solutions so that in time we may hope to know their chemical relation. The watery solutions are slowly decomposed by light but show no indication of complementary colour change outside the living cell.

It is interesting to note that the pure green algæ and the higher plants which have evolved from them, appear to have no water-soluble proteid pigment in their chromatophore though to the best of the writer's knowledge such a pigment has never been carefully looked for. If so, they would seem to be devoid of, or to have lost, the material basis for carrying out complementary

chromatic adaptation, for chlorophyll itself is apparently essentially the same substance throughout the whole range of CO₂-assimilating plants.

This experimental production of complementary chromatic adaptation takes rank as a quite new phenomenon, both from a physical and from a biological point of view. The production of the converse phenomenon, "*sympathetic* chromatic adaptation" is however known physically in a few cases and has often been observed biologically in such cases as the "protective colouration" of insects.

In the latter we find the insect developing a pigment of the same colour as the light which is shining on it from its environment, while of the former we have a very good example when a surface of mixed chlorides of silver and other metals, illuminated by a spectrum, gives an image of the spectrum in approximately the true colours in all its parts. This phenomenon, extraordinary as it appears at first sight, has been satisfactorily explained by Wiener.¹ It is due to the salts being sensitive to all wave-lengths of light and giving with white light an appearance of darkening due to a mixture of all possible coloured particles. When now the red of the spectrum shines on this it slowly decomposes all the particles that absorb the red rays. The only particles of the mixture that will not absorb red light are of course the red particles and these alone remain and give a red patch of pigment. So in the blue part of the spectrum all the particles except the blue are decomposed and a blue patch results: similarly with intermediate parts of the spectrum.

The colouration changes studied by Keeble and Gamble² in *Hippolyte varians* seem to be quite different and much more complex.

These reactions of chlorides may throw light on sympathetic chromatic adaptation but it is not clear how they help the case of complementary chromatic adaptation. This latter is not a *direct* complementary reaction of the coloured cell to the new coloured light as is indicated by the long series of colour stages that must be gone through before the final complementary colour is arrived at.

It is to be hoped that investigation may soon bring us a fuller comprehension of this new and important chromatic adaptation.

¹ Wiener. Farbenphotographie, Annalen d. Physik. u. Chemie, Bd. 55, 1895.

² Keeble & Gamble. Quart. Journ. Mic. Sci., Vol. 43; also Phil. Trans., Royal Society, Vol. 196, B.

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