The Effects of Tropical Insolation.

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IN a previous paper¹ an account has been given of the phenomena of assimilatory inhibition by insolation in the temperate regions, in which it was shown that most plants are resistant to ordinary exposure; but that, in the leaves of certain Phanerogams and shade-loving plants, by prolonged exposure to perpendicular illumination, a generally temporary stoppage of CO₂-assimilation, with or without an accompanying more or less complete decolourization of the chlorophyll-corpuscles, might be produced, whilst in certain Algae, *Chara*, &c., relatively short exposure might readily cause a stoppage of assimilation, generally accompanied, however, by a marked decolourization of the chlorophyll-corpuscles, and if at all prolonged being followed first by the death of the chlorophyll-grains of the part exposed, and finally by the death of the part exposed *in toto*².

Advantage was taken of a stay in the tropics at Buitenzorg, Java, to corroborate and extend these observations; whilst, during a short stay in Ceylon, a number of accessory and

¹ Assimilatory Inhibition: Journal of the Linnean Society, 1896.

² Loc. cit. p. 439; and Journal L. S., Vol. XXXI, 1897, p. 573.

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confirmatory observations were made. The methods employed were the same as those already described in previous papers, the evolution or non-evolution of oxygen, as detected by the Bacterium-method, under optimal illumination, being taken as a test for the presence or absence of the power of assimilation.

It might at first sight appear probable that under the intense tropical sunlight all fully exposed green leaves should suffer considerably; but, as a matter of fact, so long as the plant is abundantly supplied with water and is kept cool by transpiration, it suffers no more under such exposure than do plants in temperate regions. It may indeed be concluded, with a fair amount of certainty, that practically in all tropical plants which normally grow in fully exposed situations, provided the leaves are healthy and abundantly supplied with water, no assimilatory inhibition directly due to insolation ever takes place under normal conditions of exposure. Thus the healthy adult leaves of the following plants, after a full day's exposure to perpendicular solar illumination, were green, fresh, and showed an active power of assimilation: *Caryota maxima*, Bl., *Musa Ensete*, *Kentia McArthurii*, *Alocasia indica*, Schott., *Artabotrys Blumei*, *Uncaria sclerophylla*, and *Areca Catechu*, L.; whilst in *Bauhinia*, *Caesalpinia*, *Acacia*, and *Dalbergia lingua*, if the leaves, owing to their paraheliotropic irritability, are allowed to droop or fold together, no appreciable effect is produced; but if they are kept fully exposed to perpendicular illumination they become much paler green in colour, are more or less wilted, and the power of assimilation is weakened, diminished, or inhibited, temporarily or permanently.

There are a variety of ways in which the leaves of exposed tropical plants may be rendered capable of withstanding excessive insolation. Perhaps the commonest, though the least obvious, is by means of some invisible inherent organic change or difference in the chlorophyll-bodies of plants growing in exposed situations, as compared with those frequenting shady habitats. Along with this go changes in the

shape and position of the palisade-parenchyma layers, and in the thickness, shape, and transparency of the epidermis and cuticle, adding to the protection afforded by the apostrophic position assumed by the chlorophyll-grains of the palisade-parenchyma when the illumination is intense.

Another important mode of protection is by the folding or sinking of the leaves or leaflets when exposed to strong illumination, so that their surfaces are parallel to the incident ray. In leaflets which fold together and overlap one another, and perhaps also to a slight extent in leaves or leaflets which simply twist on their axes, as a secondary consequence of the change of position, the amount of transpiration is more or less markedly diminished, and it is quite possible that in certain cases this may be an important function of the paraheliotropic movement.

Finally, the presence of a red pigment in the leaves of many plants must shield them to a certain extent from the effects of too intense and prolonged illumination.

It must be remembered that the photochemical intensity of the tropical sun is by no means so great as might be supposed, and this is especially the case in moist, damp climates, such as those of Buitenzorg (W. Java) and Peradeniya (S. W. Ceylon), in which the moisture causes an absorption more especially of the photochemical rays. In a recent research Wiesner¹ has shown that the greatest chemical light-intensity observed at Vienna was 1.5 units, and at Buitenzorg not more than 1.612 units, whilst the daily total amount in Buitenzorg during November and December is equal to that in August in Vienna, and the total amount daily in January at Buitenzorg is equal to that in June in Vienna, the greater intensity of the tropical light being counterbalanced by the shorter day.

In several more or less shade-loving tropical plants, however, prolonged exposure to perpendicular illumination² pro-

¹ Wiesner, Untersuchung über das Photochemische Klima von Wien, Buitenzorg, und Kairo: K. Akad. d. Wiss. in Wien, July, 1896.

² The necessary daily periods of uninterrupted sunlight were obtained in Java

duces a distinct effect upon the power of assimilation which may, if the leaf be sensitive and the exposure very severe and prolonged, result in a permanent stoppage of assimilation, followed by the death of the leaf, wholly or in parts only. In all cases, after prolonged exposure, the leaf is paler than normal, and may become browned (*Cocculus Beccari*, &c.), or in some cases almost colourless (greenish or yellowish white, *Pisonia*, *Selaginella*). After being examined, the plants are kept well shaded, and from time to time fresh portions of the still attached leaves are examined, this method being necessarily adopted on account of the difficulty of obtaining perfect recovery in isolated parts.

Cocculus Beccari. Exposed from 6 a.m. to 4 p.m. Many leaves, especially the older ones, more or less yellowish or brownish entirely or in patches. Young adult leaves show weak assimilation, chiefly in spongy mesophyll, older leaves none or very weak. In one day assimilation active in young leaves, in older leaves weak to moderately active, in yet others not perceptible, though leaves have not become perceptibly greener. After full exposure for three to four days, many older leaves are quite yellow, younger leaves green in parts and show none or very weak assimilation. Next day weak to moderately active assimilation in younger leaves, older yellowish leaves none. Of latter many do not recover, although they may remain living for several days, the younger leaves finally become almost without exception quite green and normal again.

Pisonia alba, Sparr. Plant exposed for several days. Leaves from almost quite white to yellow or yellowish green: latter faint to moderately active assimilation. After thirty hours in faint diffused daylight, former leaves faintly green and show weak assimilation. In three to four days leaves all deep green to yellowish green and assimilation active. In the quite white leaves the chlorophyll-grains are almost colourless and difficult to distinguish. Such leaves do not become

towards the close of the dry season of 1896 and during various cloudless days during the wet season of 1896-7, the S. W. monsoon of this period being unusually well favoured in this respect. A few, chiefly physical and biological, observations, were made in Ceylon during the dry period in the spring of 1897 between the two monsoons.

fully green for from seven to ten days. Young but adult leaves exposed for ten hours to perpendicular rays are pale green to yellowish green, assimilation absent or faint in parts. Next day leaves slightly greener, assimilation weak to moderately active. Similar leaves exposed, but layer of cold water interposed, show the same colour as before, assimilation absent, or in parts weak to moderately active; in some leaves weak assimilation in all parts: recovery as before.

Dendrobium crumenatum, Lindl. Plants exposed to perpendicular rays from 6 a.m. to 4 p.m., assimilation weak or absent; leaves slightly paler and yield weaker chlorophyll-extract than equal weight of shaded leaves. If part of one leaf is covered by paper or tinfoil, at end of exposure it is distinctly fresher and greener, and shows moderately active assimilation, rest of leaf weak or none. Next day nearly all leaves are living, normal; assimilation is moderate to quite active. In a few leaves assimilation is weak or in parts absent, these leaves in a few days turn yellow and die.

Selaginella sp.? Exposed for some days, leaves turn quite pale, and become when shaded green again. One day's exposure causes a distinct fading; and many leaves on the exposed side, though green to pale green or yellowish green, show weak or no assimilation in parts or entirely. If the half of the leaf only is used, the corresponding half next morning may show a fairly active power of assimilation.

Drymoglossum piloselloides, Prsl. After ten hours, exposed vegetative leaves slightly paler; chloroplastids normal and with abundance of starch; assimilation weak or absent; in partially exposed leaves with similar abundance of starch, fairly active. Next day assimilation moderate to quite active, but in a few leaves none. The latter may in some cases remain living for several days without regaining the power to assimilate; they slowly turn pale yellow or brownish yellow, and finally die. A weak power of assimilation may return to the preparations previously examined if they are kept in a drop of water in a damp chamber.

Adiantum cuneatum, Lug. and Fisch. and *A. assimile*, Sw. After six hours' exposure, assimilation faint or absent. Leaves paler and some may not recover; the rest in one day show fairly active assimilation.

A. rhodophyllum. Leaves thicker, stouter, and more resistant. After eight hours the leaves are paler than normal, and show weak, or in some cases almost imperceptible assimilation; next day active again. If the leaves are old, assimilation may be absent after eight hours'

exposure and not return. Young leaves are red till half grown, and show normally weak to moderately active assimilation; but after six to eight hours' exposure weak or none, assimilation in some cases not returning, but in others in one day being normal again.

The experiments with *Dendrobium* show that localized exposure produces a purely localized effect. With the stoppage of assimilation a change of colouration is generally associated, but is not an essential accompaniment thereto, for the power of assimilation commonly returns before any perceptible regeneration of the original intensity or shade of colouration takes place. The results obtained with *Pisonia alba* indicate that the effect produced is a photo-chemical one, and is not primarily due to, though it may undoubtedly be aided by, the heating effect of the sun's rays, the latter being the case whenever the leaf becomes at all wilted. It very commonly happens that when a leaf is exposed, the shaded side may retain, especially if the leaf is a thick one, a distinct power of assimilation, even though the palisade-layers composing the upper exposed surface are almost fatally affected. If a bifacial leaf is exposed, under surface upwards, it is much more likely to be fatally affected than when in the normal position.

Thick fleshy leaves do not wilt when exposed for prolonged periods; but, owing to the relatively slight amount of transpiration of which they are capable, they are very liable to be overheated by the absorption of the solar heat-rays. Thus in *Hoya fraterna* the insolation-temperature of the leaf is about 45° C., occasionally rising to over 50° C. The temperature was measured by suddenly bending the leaf around and pressing it against a delicate thermometer which was originally a little below the expected temperature. Since the general optimum temperature for assimilation probably lies between 25° C. and 35° C., steadily diminishing from 40° C. onwards, until at 50° C. or thereabouts the maximal temperature is reached¹, it follows

¹ See Assimilatory Inhibition: Journal of Linnean Society, 1896, pp. 385 and 386.

that the leaves of such plants as *Hoya*, though probably their resistant powers in this respect are above the normal, have, when fully insolated, their assimilatory powers largely diminished by the high temperature which they attain, and may, when subjected to prolonged exposure, have their power of assimilation temporarily or permanently affected, partially or mainly from this cause alone. This is the case in the following experiments.

Vanilla aromatica. After ten hours' exposure, leaves paler green; yield weaker extract of chlorophyll than normal; assimilation weak or absent in palisade-parenchyma, weak to nearly normal in spongy mesophyll. Next day assimilation active, except in few parts where faint or absent, the latter finally dying. Preparation difficult owing to presence of mucilage and raphides. Full insolation-temperature is about 40°C. , occasionally rising to 45°C.

Hoya fraterna. Similar results to those with *Vanilla*, but the inhibition is more complete; the leaf is pale green to pale yellowish or brownish green, and in latter cases none or only a partial recovery takes place. Insolation-temperature 45°C. occasionally rising to 50°C. Leaves in exposed situations soon become yellowish, and assimilation is weak or absent. If kept in weak diffuse daylight, provided the change of colouration was not too pronounced, they become green again in one to two weeks, but show active assimilation long before this.

A cut stem of *Vanilla*, 4 ft. long, left entirely without water, remained living for a long period of time, the power of assimilation in the leaves being after one week fairly active, after two faint, and after three absent. But in the last case, on placing such a leaf with the cut surface in water, after two days a weak power of assimilation was shown. The stem and leaves began to wilt basally upwards after six weeks; after the seventh week a small leaf and root produced at the apex after separation from the parent plant ceased to grow; the leaves were thin and shrunken, the cells in the basal leaves dead and unplasmolysable, though the colour was but little altered. After ten weeks all the leaves are dead. *Vanilla* is therefore

very resistant to drought, and any effects produced by insolation are not due to any excessive loss of water, but to the heating and photo-chemical effect of the sun's rays.

In the young green leaves of *Hoya fraterna*, when $\frac{1}{2}$ to $\frac{1}{3}$ full size, minute starch-grains are present in the chlorophyll-corpuscles, and later, several larger ones are present in each; but it is only after the leaf is adult, and has been actively assimilating for some time, that the characteristic large oil-drops (soluble in ether and turning brown with osmic acid) appear in the assimilating cells. If such leaves are kept in darkness, in five days the oil-drops disappear in almost all the cells, but the starch is not perceptibly, or only very slightly, diminished in amount, whilst in ten to fifteen days almost every trace of starch has also disappeared. The protoplasm hence first absorbs and uses up the stored oil, and later the chlorophyll-grains yield up to it their stored carbohydrate. The slower disappearance of the starch is not due to the chlorophyll-grains being sick, for on examination after fifteen days in darkness a fairly active power of assimilation is shown. In *Dicranum scoparium*, *Musa*, *Vaucheria*, &c, the assimilatory products are at once converted into oil, starch-grains appearing in the chloroplastids only when a superabundance of assimilated material is formed. In *Hoya*, on the other hand, oil is formed only when an excess of assimilated material is present; it is the last to appear and the first to disappear. This peculiarity enables an interesting corroboration to be made of the results already obtained with *Hoya*. Thus in leaves, in which, without any fatal injury being inflicted, the power of assimilation is inhibited or reduced to a minimum by continued over-exposure, the oil originally present may entirely or almost entirely disappear.

In a previous paper¹ it has been shown that any agency which, when applied in intense or concentrated form, directly inhibits or prevents assimilation from taking place, may, when the application thereof is much weaker but prolonged, gradually

¹ Loc. cit., Journal of Linnean Society, 1896, pp. 364, 461.

induce in the chloroplastid a condition characterized by a temporary inability to assimilate. Thus when chloroplastids are subjected for prolonged periods to illumination by sunlight of natural intensity, though at first they continue to assimilate normally, their power of performing CO_2 -assimilation is finally more or less markedly inhibited. Pringsheim¹ has shown that chloroplastids when exposed to intense and concentrated sunlight are killed and bleached only when oxygen is present. When subjected to such exposure in an atmosphere formed by an assimilatory mixture of hydrogen and CO_2 the chloroplastids remain green. It follows, therefore, that when exposed to concentrated sunlight, no assimilation of CO_2 or evolution of oxygen takes place. Hence there appears to be a maximal intensity of illumination at which the synthetic assimilatory processes are inhibited and cease, being finally replaced if a supply of oxygen be present by katabolic oxydatory changes. This appears to be in analogy with the general law, exemplified more especially in the effects of temperature upon the combustion of gases, that combinations between substances taking place at a relatively low temperature tend to be less and less complete as the temperature increases, and finally may be replaced by dissociatory changes taking place in the reverse direction.

PROTECTIVE MOVEMENTS BY THE LEAVES OR LEAFLETS.

Of the various modes by means of which tropical plants protect themselves against the injurious effects of over-exposure to sunlight, perhaps the most interesting and commonest is by means of active or passive movements of the leaves. It may be stated as a general rule, to which apparently there are no exceptions, that no tropical plant places or allows its leaves to be in such a position that the upper surfaces are at right angles to the sun's incident rays when at the zenith. In most exposed tropical plants, in which the leaves or leaf-stalks are not stiff and rigid, the leaves at

¹ Pringsh. Jahrb., Bd. xii, 1882, pp. 326, 344.

midday assume a more or less drooping position when exposed to full insolation, this being due in the majority of cases not to any active movement of the leaf or leaf-stalk, but to a general diminution of turgidity, the somewhat flaccid leaf-stalk or leaf-base allowing the leaf in virtue of its own weight to assume a more or less pendent position. In a large number of cases, especially in the Leguminosae, the movements are not passive, but are active, the leaves or leaflets being paraheliotropic; i.e. when exposed to intense illumination place themselves parallel to the incident ray.

This phenomenon has already been described by a number of observers, but many details are still unsolved. Thus the relative irritability of the different parts, the intensity of light forming a minimal and an optimal stimulus for movement, the relative efficiency of light of different colours, whether the position assumed bears any relation to the direction of the incident ray, and whether it is the leaf which perceives the stimulus and transmits it to the motile pulvinus, or whether the latter only is sensitive, being both the motile and the percipient organ, are all points requiring an experimental answer.

Mimosa pudica perhaps affords the most favourable subject for the experimental study of these questions, owing to its marked irritability and sensitiveness, and to its being one of the commonest weeds in both Buitenzorg and Peradeniya. A curious and interesting fact at once brought to light is that the pulvini of the primary and secondary leaves are affected differently to the pulvini of the leaflets. Thus the leaf of *M. pudica* reacts as a whole to the directive influence of sunlight, the movements of the pulvini being such as to place the leaf as nearly as possible at right-angles to the incident rays, if the illumination is sufficiently strong. In diffuse daylight the entire leaf-system is horizontally expanded, but in the morning and late afternoon, when exposed to obliquely falling sunlight, the leaf-system sets itself as far as possible at right-angles to it, the main petioles and secondary axes twisting or bending so that their upper surfaces face the sun. The leaves

pointing towards the sun remain nearly horizontal or bend slightly downwards; those pointing away from the sun rise upwards, and may become nearly vertical if the sun be low down but strong and unclouded. The axes of the leaves to right and left remain horizontal, but twist so as to face the sun, chiefly at the secondary petiolar and partly at the main pulvini. The pulvini of leaves in an intermediate position partly twist and partly bend in setting the leaf axes in their proper position.

The pulvini of the leaflets respond in a very different manner. When exposed to strong and direct illumination, they cause the leaflets to rise up and fold more or less completely together, thus setting the surfaces of the latter parallel to the incident ray; when the light is weak or diffuse they cause the leaflets to expand horizontally. The pulvini of the leaflets appear to be somewhat more irritable at from 8 to 12 a.m. than they are later in the day. The leaflets commence to rise up a second or two after the sun falls upon them, and in a half to one minute under favourable conditions have risen up their full amount. Owing perhaps to the slightly lessened mechanical moment, the secondary petioles may also rise up slightly, but this is soon readjusted. If the leaflets are shaded after short exposure, they become fully re-expanded in from one to three minutes. Occasionally the reactions are nearly twice as rapid as the above, whilst after prolonged exposure the re-expansion may take place more slowly. If the stimulus is removed before the reaction is complete, the response continues for a short time in the original direction, both a latent period and an after-effect being clearly shown. A series of stimuli of short duration may, owing to the existence of a latent period, be summated and produce a response. Thus, successively exposing to the sun for two seconds and then shading for two seconds, finally causes the leaf to rise up nearly to the full amount, though it takes a longer time for the movement to be completed. If alternately for two seconds in sunlight and four seconds in shade, the leaflet rises up, though only through about 15° to 20° . If alternately for one

second in sunlight and ten seconds in shade, the leaflets remain fully expanded.

The angle which the leaflet assumes is nicely graduated to the intensity of the light to which it is exposed. Thus in only moderately strong sunlight the leaves rise up through an angle of from 30° to 50° , in weak sunlight from 15° to 30° ; whilst if the sun is so shaded by clouds that it can barely cast a perceptible shadow, the leaflets rise up a few degrees only.

When the sun's rays fall somewhat obliquely, but not sufficiently so to cause the plane of the entire leaf to readjust itself at right angles to the direction of the incident ray, in the leaves the axes of which cross the sun's rays to right or left, the further row of leaflets appears to rise up more than the nearer one, so that in each pair of leaflets the angles made between the incident ray and the distal portion of each leaflet is the same, the leaflets apparently responding to the directive action of the incident ray. This appearance is, however, really due to the twisting of the secondary petiole setting its dorsal surface directly facing the sun, for as a matter of fact both sets of leaflets move through the same angle in relation to a perpendicular line falling between them on the petiolar axis to which they are attached.

In the quite young unopened leaflets naturally no sensitiveness to sunlight can possibly be perceived; but in young opened leaflets of about two-thirds the normal size the sensitiveness is even more marked than in adult leaflets, the former folding up when exposed to light of less intensity and expanding fully horizontally only when very completely shaded.

After prolonged exposure to unbroken sunlight for six to eight hours, the leaflets are all completely folded, and re-expand in the shade only very slowly. The petioles are generally in a more or less drooping position, the loss of water by transpiration in spite of the folded position of the leaflets hence having been excessive. The leaflets show a rather weak power of assimilation, which is in some cases barely perceptible, but becomes normal again over night.

If a layer of cold water is interposed between the sun and the exposed leaves, the leaflets rise up as usual but not quite so markedly (5° to 10° less), the difference being due probably to the slight loss by refraction and dispersion as the light passes from the air through the optically denser medium and out again. If sheets of coloured glass are interposed, in all cases the leaflets do not rise up so much as when exposed to direct sunlight; under blue glass the difference being least, under yellow more, and under red glass most marked. When exposed to intense sunlight under blue glass of not too great thickness, the leaflets may fold up nearly to their full extent; whilst when a double layer of thick red glass is interposed they may expand fully horizontally. Sachs and Bert have shown that in red or yellow rays from light of only moderate intensity the leaflets fold together, assuming the nyctitropic position, whereas in the blue rays from light of similar intensity they remain expanded. Hence when the blue rays are weak or absent the leaflets fold together, and when the rays are too intense they again fold together. It is obviously an advantage that the blue rays, when too intense, should cause the leaflets to fold together and hence be protected from excessive photochemical action; but that blue light of only moderate intensity should cause the leaflets to pass from the nyctitropic into the expanded position is only accidentally and indirectly an advantage, owing to the fact that under normal exposure the intensity of the blue rays is a sufficiently accurate measure for the plant of the intensity of the accompanying rays absorbed by the chlorophyll and used in assimilation. The leaflets respond not to the heat but to the light-rays of the sun, and of these rays it is the more refrangible 'chemical' rays which are most effective.

The following experiments show clearly that not only is the pulvinus the motile organ, but it is also the irritable perceptive organ and directly responds to the stimulus exerted by a change in the intensity of the illumination, the leaflet

¹ Sachs, Bot. Zeitg., 1857. Bert, Mém. de la Soc. d. Sci. de Bordeaux, VIII, 1870.

itself playing a perfectly passive part. If a well-defined strip of shade is thrown on the median portion of the secondary leaf, covering all the pulvini but leaving the leaflets exposed to full sunlight, in from two to four minutes the leaflets all become horizontally expanded. If now the leaflets are shaded but the pulvini exposed to sunlight, the leaflets assume the full sunlight position in from one to two minutes. If the leaflets, or the pulvini only, over a portion of a secondary leaf are shaded or exposed to sunlight, this part only responds. If the leaf is in the sunlight-position it is the basal part which should be shaded; but if the leaflets are fully expanded it is the terminal part of the secondary leaf which should be exposed to sunlight, as otherwise the overlapping non-moving leaflets interfere with the movement of the irritated portion and prevent the formation of the sharp line of demarcation between the shaded expanded and exposed folded portions which would otherwise be produced.

When the pulvini alone are shaded, it takes from a half to one minute longer for the leaflets to become fully expanded than it does when the entire leaf is shaded. If the pulvini of the basal pair of leaflets be shaded, the leaflets expand horizontally and remain so even though the whole of the rest of this pair of leaflets and of the entire leaf is exposed to full sunlight. Similarly if one pulvinus only is shaded, that leaflet only to which the shaded pulvinus belongs becomes or remains expanded. The same is the case with a single leaflet or pair of leaflets in all parts of the leaf, but they become or remain expanded only as far as the overlapping leaflets will allow.

If the sunlight be intense and the shadow thrown on the pulvini narrow, the amount of reflected light that reaches the pulvini may be sufficient to cause them to retain a slight angle (5° to 10°) with the horizontal. The interposition of a strip of red or yellow glass between the pulvini and the sun, causes them to expand nearly fully horizontally, whereas if a strip of blue glass is interposed, they remain nearly completely folded together. If the leaflets are completely shaded

from above, but some illuminated from beneath by sunlight reflected from flat mirrors, the leaflets, the pulvini of which are illuminated, rise up, the others remaining horizontally expanded. If the light is somewhat concentrated by means of a plano-concave mirror, the leaflets re-act nearly as actively and rise up nearly as much as when exposed to direct sunlight falling from above.

Light therefore exercises no directive influence upon the pulvinus of the leaflet; it is only a change in the intensity of the illumination which acts as a stimulus, the movement always taking place in the same direction, no matter how the light falls upon the pulvinus, and the angle through which the leaflets move being dependent upon the intensity of the stimulus.

As is well known, when the intensity of the light to which the plant is exposed falls below a given intensity, the leaf assumes the nyctitropic position; the primary and secondary petioles drooping whilst the leaflets rise up and fold together. When the evenings are bright and cloudless, the leaves begin to close in the tropics after 5 p.m., and by 5.30 p.m. are quite closed, a rough calculation showing that they thereby lose about the equivalent of five to ten minutes' bright midday illumination for assimilating purposes, which is a trifling and perhaps negligible amount. The folding together of the leaflets, along with the diminished temperature and closure of the stomata, besides hindering or preventing assimilation, also interposes a marked check upon transpiration, causing the plant, and more especially the pulvinus, to be temporarily in an even more highly turgid condition than is normally the case. If, when the full nyctitropic position has been assumed, the main pulvinus of the leaf is stimulated by touching the sensitive hairs on its under surface, it gives a marked response, and the turgidity of the upper surface of the pulvinus may be so much greater than that of the stimulated and originally convex surface that the leaf is bent beneath or across the stem, thus reversing the normal position of dorsal and ventral surfaces, and is supported against the action of gravity in this

position for some time. The same stimulation applied to the expanded leaf at midday causes it merely to fall and droop downwards, the fall being largely a passive one, due to the action of gravity being no longer counteracted by the greater turgidity of the convex under-surface of the pulvinus. It must not however be concluded that the sleep-position assumed in the evening is simply due to the general increase of turgidity consequent upon the diminished transpiration. The folding up of the leaflets, which is one of the main factors causing the diminished transpiration, is directly due to the stimulating action of the fading light; for any general increase in turgidity tending to make that of the upper surface more nearly equal to that of the under surface of the pulvinus would tend, not to close the leaflet, but to keep it expanded, were it not overpowered by a more powerful direct stimulus. Besides, were the latter not the case, we should expect to find the leaflets expanding during the night as the normal relation between transpiration and absorption became restored; whereas, as is well known, they remain folded together until caused to expand by the early morning light. The fall of the main and secondary petioles may, however, partly be brought out in the manner above described, for they rise somewhat during the night; but even here the movement is mainly due to the direct stimulating action of the absence of light, for it is only on re-exposure to light of adequate intensity that the normal fully-expanded condition is assumed.

Equally exposed plants of *Mimosa* growing in the one case in dry sandy and in the other in damp humid soil, close at the same time in the evening, and not earlier in the latter case than in the former. If a portion of a plot of plants be kept dry and the rest well watered, with equal exposure, and the plants being to commence with fully expanded, the leaves and the plants in the latter may close five to ten minutes earlier than in the former; but this simply shows that the more turgid plants respond somewhat more rapidly to the stimulus due to the fading intensity of light than do the less turgid ones.

In order to keep the leaflets of *M. pudica* fully expanded, exposure to light of a certain tonic intensity is necessary; exposure to light of greater intensity than this causing a paratonic closure, whilst too feeble illumination causes an atonic closure.

A number of other Leguminosae were examined with regard to the paraheliotropic properties of their leaflets, and though they vary much in degree of irritability and the movement of response is not always of the same kind, nevertheless the general results, especially with regard to the pulvinus being the organ which not only responds to but also perceives the stimulus, were essentially similar to those given by *M. pudica*.

An unnamed *Acacia* (165¹) is nearly as sensitive as *M. pudica* to both contact and exposure to sunlight. Thus the leaflets when lightly tapped rise up and fold together. If exposed to full sunlight they fold completely together in two to three minutes, expanding fully again in five to eight minutes when well shaded. If the pulvini alone are shaded, the leaflets expand nearly completely horizontally, and the movement is but little slower than it is in *Mimosa* under similar conditions. In sensitiveness to contact and to insolation, the leaflets of *Robinia Pseud-acacia* are almost identical with those of the preceding plant. In another unnamed *Acacia* (169¹) the leaflets are not quite so sensitive, a smart rap causing a partial folding, whilst when exposed to full sunlight they are not quite so closely approximated together and when shaded re-expand more slowly.

Dalbergia zeylanica, Roxb., though not sensitive to mechanical irritation, is very nearly as sensitive to, and shows nearly as rapid a response to, exposure to full sunlight, as does *Robinia*.

In *Caesalpinia*, *Dalbergia*, and several *Acacias*, if the leaflets are exposed to full sunlight but the pulvini are shaded, the

¹ The numbers are the Buitenzorg Garden numbers given to enable future identification to be made, specific identification being impossible at the time owing to the lack of flowers and fruit.

former become markedly expanded in a quarter of an hour, and in half an hour are nearly horizontal. If fully exposed to sunlight, the leaflets rise up or twist to their full extent in ten to twenty minutes. The leaflets of several species of *Caesalpinia*, of *Dalbergia linga*, and of *Desmodium velutinum*, D. C., twist, so that the longitudinal axis is at right angles to the lamina or parallel to the sun's rays, the proximal edge of the leaflet being uppermost. At the same time the leaflets may in some cases rise somewhat, but the main and secondary petioles generally droop more or less after prolonged exposure. In this case also the movement of the leaflets is always the same no matter what the angle at which the incident rays fall, the intensity of the light alone acting as a stimulus to movement. Likewise, if the pulvini alone are shaded, the flat surfaces of the leaflets become horizontal, the dorsal (morphologically ventral) surface being directed upwards; but if at the same time the leaf be powerfully illuminated from the side or from beneath, the leaflets, though shaded from the sunlight falling from above, retain their paraheliotropic position.

In *Albizza* sp. ? when exposed to sunlight the leaflets fold forwards and also twist so that the proximal edge is uppermost and the lamina vertical. If the pulvini are shaded, the leaflets begin to expand and twist in five minutes and attain nearly to their normal shade position in fifteen minutes. *Albizza saponaria*, Bl., and *Calliandra haematocephala*, Hsskl., are similar in all respects, with the exception that the movement is slower and takes nearly twice as long before it is completed.

The leaflets of *Cassia montana*, Heyne, when exposed to sunlight fold together forwards, more or less, whilst the pulvinus twists so that the leaflets droop downwards with the under ventral surface directed outwards and in some cases slightly upwards. If the pulvini are shaded, the leaflets begin in ten minutes to expand, and rise up and twist so that the dorsal surfaces face upwards, a nearly normal shade-position being assumed after twenty to thirty minutes. The proximal

surface of the pulvinus, which is uppermost in the sunlight-position, has a moderate amount of red dye in the epidermal cells covering it. Stomata are abundant on the under surface of the leaf, but none are present on the upper. Hence the movement is evidently a means of protection against light alone and not against excessive transpiration; for if the latter were the case we should expect to find the ventral stomatic surfaces being apposed to one another. The outer surfaces of the epidermal cells of the leaflet are curved in outline, the curvature on the upper surface being more marked and conical, on the under flatter and more rounded. This would probably indicate according to Stahl¹ that *Cassia montana* is specially adapted to suit a shady habitat. The sunlight position which the leaflets assume, though sufficient as a protection against not too prolonged exposure, is, owing to the way in which the ventral surfaces are exposed, not so adequate a protection as in the other cases already described.

The bilobed leaf of *Bauhinia*, though slow to react to sunlight, forms nevertheless, owing to the large size of the pair of leaflets of which it is composed, to the manner in which these are hinged together in the median line for a great part of their length, and to the pulvini being partially bifid, interesting material for experimental study. In *B. elongata* the leaflets, when exposed to full sunlight, fold almost completely together, each rising up through an angle of 80° or more. If the pulvinus at the base of the pair of leaflets be shaded, the area shaded being about 1 sq. cm., whilst the area of the leaf left exposed is from 100 to 200 times greater, in a quarter of an hour the leaflets are seen to be expanding, in half an hour they make an angle of 15° to 20° only with the horizon, and in one hour they are nearly horizontal. On then re-exposing fully to sunlight, or on exposing the pulvinus alone, the leaflets begin to rise in five minutes; in ten minutes they have nearly, and in fifteen fully,

¹ Stahl, Ann. d. Jard. Bot. de Buitenzorg, Vol. xiii, 2^e partie, 1896. 'Sammetblättern,' &c.

assumed their normal position. A leaf exposed for eight hours to continuous sunlight showed, if the leaflets were allowed to fold together, a fairly active power of assimilation; but another in which, by shading the pulvinus, the leaflets were caused to remain nearly horizontal, showed after the same time only a moderately active power of assimilation, and in parts faint or none; the next day the remaining portions of the leaflets showed fairly active assimilation. If one half of the pulvinus be removed, the cut surface being smeared with vaseline, the leaflet of that side sinks and can no longer respond to a change in the illumination. The other leaflet, however, still responds, though not quite so markedly as normally.

B. tomentosa, with a much larger leaf and pulvinus, responds more slowly than does *B. elongata*. When the pulvinus is shaded it takes from one to two hours for the two lobes to become nearly horizontal, and, when exposed to sunlight, from a quarter to a half hour to close up to the full extent possible. The leaflets can only close completely together when quite young; when older a slight angle (15° to 20°) always remains between the two leaflets, probably owing to a slight hardening of the pulvinar tissue and to the increased elasticity and incompressibility of the tissue forming the longitudinal hinge between the two lobes. In both *B. elongata* and *B. tomentosa* the pulvini are covered with brown hairs, and both the epidermal and outer cortical layers are dark brown in colour. This is less marked when the leaf is young, and hence probably arises the fact that the quite young leaves fold together when exposed to light of only moderate intensity. In the older, more resistant, stouter, and less transparent leaf, the sensitive pulvinar tissues are largely shielded from the penetration of light, and respond, causing the leaflets to fold together, only when the light is of considerable intensity and the exposure prolonged. The pulvini of the more sensitive leaflets of *Acacia*, *Albizza*, *Dalbergia*, and *Caesalpinia*, are all glaucous and green, and are exposed to the sun's rays in almost every position which the leaflets may assume.

In *Bauhinia*, when the illumination is at all oblique, the folding of the leaf-lobes may cause the pulvini to be shaded and any further movement to cease.

Both *B. elongata* and *B. tomentosa* have an abundance of stomata present on the markedly hairy under epidermis of the leaf, the upper surface being slightly hairy and possessing a few scattered stomata. Hence in the folded position the rate of transpiration can only be very slightly diminished. In *Dalbergia zeylanica*, *D. lingua*, *Albizza saponaria*, *Calliandra haematocephala*, and *Caesalpinia*, stomata are present on the under surfaces of the leaflets only, the upper epidermis having a slightly or markedly thicker cuticle than the under, and being without stomata. In *Albizza saponaria*, *Calliandra haematocephala*, and *Dalbergia lingua*, it follows from the position the leaflets assume, that no checking but rather an increase of transpiration is likely to result when the leaves are exposed to sunlight. In *Dalbergia zeylanica*, the leaflets of which fold together in pairs, even though no stomata are present on the upper surfaces, the folded position of the leaflets will interpose a slight check on transpiration; whilst in *Mimosa* and *Acacia*, owing to the presence of stomata on the upper surfaces and to the overlapping of the leaflets when folded, the check must be very marked. In *Acacia* (165) and in *Robinia Pseudacacia*, stomata are abundant on the under surface and on the outer half of the upper, becoming fewer towards the base of the upper surface of the leaflet, whilst at the base none are present. Hence in these two plants stomata are absent from that part in which, when folded together, there is least chance of any transpiration taking place.

The paraheliotropic position is very evidently assumed solely in order to protect the chlorophyllous layers of the leaflet from exposure to too intense illumination, though it may, as a secondary, and perhaps accidental, effect in a few cases help to guard against excessive transpiration.

PROTECTIVE RED DYE.

In a very large number of cases, and more markedly in the tropics, the leaf, especially when young, is partly shielded from the effects of exposure to light by the presence of a protective red dye. Stahl, in a recent publication¹, has expressed certain theories with regard to the function of erythrophyll in plants, which cannot be passed over without criticism. In opposition to the generally accepted view, Stahl holds that the importance of the red dye is that it acts, not as a protection against light at all, but first, as a warning or frightening (*abschreckende*) colouration, and secondly, and most importantly, as a heat-absorbing medium.

As regards the importance of the red dye as a frightening colouration, Stahl himself shows that it only applies to higher animals in which the powers of vision, and more especially of colour-perception, are well developed; and even then the deterrent effect is by no means marked, and ceases to become evident when the animal is hungry. Obviously, with animals such as snails, the main depredations of which are carried on in darkness or in partial obscurity, when the red colouration cannot be distinguished, it can hardly exercise any deterrent effect in virtue of its colour. It may safely be concluded that any value of the red dye as an '*abschreckende*' colouration is quite accidental and secondary, though it may in some cases be of undoubted use to the plant. A similar instance, in which a special peculiarity developed for a particular purpose has acquired accidentally a minor secondary importance, is afforded by *Mimosa pudica*. In this plant the folding up of the sensitive leaflets, which takes place when the plant is agitated by the wind, is undoubtedly of primary importance as a protection against mechanical injury or drought, to both of which the plant is very sensitive and liable. When a browsing animal, such as a goat, approaches a clump of

¹ Stahl, Ueber bunte Laubblätter: Ann. d. Jard. Bot. de Buitenzorg, Vol. xiii, 2^e partie, p. 137, 1896.

M. pudica, and agitates any part of it at all strongly, the green appearance disappears at once, and only an apparently withered clump, in which the hard and prickly stems are most conspicuous, remains; the consequence being that the animal either turns away or passes through the clump of *Mimosa* to reach more congenial and less bewildering pasturage. In a country with many browsing animals this peculiarity cannot fail to be of considerable, though only accidental, importance.

As regards the second part of Stahl's theory, there is no doubt whatever that the presence of erythrophyll in the cell-sap will cause a leaf to absorb more light, and also more heat, than it would otherwise have done; but the question is whether the heat-absorbing property of the red dye is not merely secondary, and, perhaps, in many cases, a disadvantage to the plant. In the case of alpine plants, Kerner von Marilaun¹ had already pointed out that the heat-absorbing power of the red dye may be of accessory importance to its light-protective function.

Engelmann² has shown that the red pigment erythrophyll allows, in a typical case, about 90 per cent. of the orange rays which are most useful for assimilation, 10 to 30 per cent. of the green and yellow which are least useful, 50 per cent. of the blue which are somewhat more useful, and 80 per cent. of the violet, rays to pass through.

Pringsheim³ found that when exposed to concentrated blue or green sunlight in the presence of oxygen, the chlorophyll-grains over an exposed area of an end-cell of *Chara* are killed and bleached in 5 minutes; whereas when exposed to the concentrated red rays and kept cool, they remain living for a longer time, only beginning to bleach after 20 minutes' exposure. The red dye therefore, whilst allowing as much as possible of the light useful for assimilation to pass through, absorbs as much as possible of the rays exerting the greatest photo-chemical effect upon the chlorophyll and

¹ Pflanzenleben, Bd. i, p. 364.

² Engelmann, Bot. Zeit., June, 1887.

³ Pringsheim, Pringsh. Jahrb., Bd. xii, 1882, pp. 326-344.

the protoplasm. Were the primary and most important function of the red pigment to act as a heat-absorber, it would be natural to expect that it should show a marked absorption of the dark heat-rays which do not appear to be used in chlorophyllous assimilation, instead of its absorbing for the most part the green and yellow rays, in which the heating effect is comparatively slight. Engelmann (l. c.) does not, however, ascribe any power of absorbing the dark heat-rays to erythrophyll. Stahl (l. c.), it is true, finds that red leaves, when exposed to dark heat-rays, show a rise of temperature of from 1° to 2° over similar green leaves similarly exposed. The explanation of this probably lies, however, in another observation of Stahl's, namely, that red leaves have fewer stomata than the green ones, the consequently lessened transpiration in the red leaf being probably the cause of the difference in temperature. It is extremely probable that in the water distributed throughout its substance, the leaf possesses as sufficiently powerful an absorbent of the dark heat-rays as is needful. The very fact that in spotted leaves the red areas contain fewer stomata than do the neighbouring green ones, is very strongly in favour of the view that the slight additional absorption of heat and consequent acceleration of transpiration is a disadvantage which needs to be guarded against, and which is in this manner adequately compensated for. As Stahl shows, green leaves or green areas of the leaf, when exposed to *sunlight* in *dry* air, give off more water-vapour than red leaves of the same plant or red areas of the same leaf do.

Kerner von Marilaun¹ mentions that *Satureja hortensis*, grown fully exposed to sunlight in his alpine garden, develops an even greater abundance of the protective red dye and flourishes, whilst *Linum usitatissimum* remains green, grows badly, and dies before flowering. From this he concludes that the red pigment is important as a protection against intense illumination. Stahl (l. c.) finds that, in the

¹ Pflanzenleben, Bd. i, p. 364.

Alps on clear nights, *Linum* is unable to empty its leaves of starch, whilst *Satureja* does so, and hence concludes that this is due to the red leaves being warmer during the night, an assumption which is not justifiable without direct experimental evidence, for it has yet to be proved that the red pigment has any special power of absorbing dark heat-rays: moreover, in correlation with the fact that the red leaf absorbs heat in slightly greater amount than a green one does, it would be natural to expect that the former would also radiate heat more rapidly than the latter when the temperature falls during the night. The above observations cannot be said to point one way or the other. All they show is that *Satureja* is more adaptable to an Alpine habitat, and with this adaptability the presence and increased formation of the red dye may be a more or less important correlative factor; whilst *Linum*, under such conditions, is unhealthy, and amongst other signs of sickness a weakening of the translocatory powers may be one symptom. Costerus¹ has, however, shown that, in most tropical plants, but little starch is removed during the night; so that in the tropics, at any rate, the retention of an abundance of starch in the leaves over night is a normal phenomenon, and does not indicate that the plant is in an unhealthy condition.

Stahl supposes that in the tropics the heat-absorbing function of the red pigment is to increase the amount of transpiration, and in the plants of temperate regions to raise the temperature of and hence give rise to more active metabolism in, more especially, the young growing organs. He points out that in the tropics many plants affecting shady habitats have a marked and deep red colouration, and that in many cases the red dye is present only in the under epidermis or spongy mesophyll. The explanation of the presence of a marked red colouration in the leaves of many shade-plants is readily explained as being necessary to guard against the partial or complete assimilatory inhibition to

¹ Costerus, Ann. d. Jard. Bot. de Buitenzorg, p. 73, Vol. xii, Pt. I, 1894.

which such shade-plants are especially liable when accidentally exposed to prolonged intense illumination.

In trees or shrubs growing more or less in the open and with foliage which is red when young, it can plainly be seen that the young foliage formed in more shaded positions is less red than that which is more exposed ; whereas according to Stahl's theory the reverse should be the case. The more exposed leaves also retain their red colour longer and to a later stage of development than the shaded ones, in those cases in which the leaves lose their red colour when adult, as is shown well by *Ancistrocladus VahlII*. Owing to the tonic stimulating action which light exercises, the more exposed leaves are larger, broader, and develop more rapidly, than very much shaded ones. Hence, owing to the chlorophyllous tissues developing and reaching their adult and most resistant condition more rapidly, the red colouration may disappear from the more exposed leaf in an actually slightly shorter time, though it persists to a later stage of development and size in the more exposed leaf than in the markedly shaded one.

That many plants growing in the shade form a greater or less amount of red pigment is quite true: but in all the cases observed the red colour is most marked when the plant is growing in more exposed situations, and in extremely shady habitats it may almost or entirely disappear. The inference simply is that such plants are extremely sensitive to and readily injured by exposure to light of at all marked intensity: whilst it has already been clearly established that very marked differences do actually exist in the sensitiveness of different plants to light in correlation with the amount of exposure to which they are subjected in their natural habitat.

In the Filicineae it is possible to formulate the general rule that hygrophilous Ferns growing in damp and shady places are always green; whilst in more or less xerophilous Ferns, growing in more exposed and drier habitats, a marked red colouration is frequently present. Thus in *Blechnum orientale*, growing in an exposed and rather dry situation in the gardens at Peradeniya, the young leaves have a marked red coloura-

tion, and are at the same time protected from excessive transpiration by the presence of numerous stalked mucous glands of epidermal origin. The red colouration is most marked when the leaf is nearly fully expanded and about two-thirds its full adult size, being less marked in the young inrolled leaflets than in the still young but just expanded ones. As the leaf becomes adult, the red colour rapidly diminishes from the base upwards, and the mucous glands wither away and disappear. The red dye is formed in the mesophyll-layers only, and chiefly and most markedly in the cells of the palisade-parenchyma. As the dye disappears the special protection which the mucous glands afford against excessive transpiration is no longer needed, and the glands dry up.

As regards the cases in which the red dye is present only in the under epidermis or in the spongy mesophyll, it must be remembered that in many such cases the young leaves expose their ventral surfaces to the light. Thus in *Musa*, the young leaves are vertical and rolled up with the ventral (under) surface outermost; and in one variety of *Musa* a red dye develops on the under exposed surface, disappearing as the leaf unrolls and expands horizontally. The adult leaves of *Musa* (see above, p. 440) are quite resistant to even prolonged insolation, but the exposed portions of the young leaves are more sensitive, and may have their power of assimilation weakened or temporarily inhibited by a full day's insolation.

In *Uncaria sclerophylla* the young leaves have a red dye in the under epidermis only, which is also covered by adpressed sclerotic hairs. The young leaves are at first folded longitudinally, with the under (ventral) surfaces outwards; and commonly even as they expand and before the fixed light position is taken up, the ventral surface is more exposed than the dorsal. The red dye acts as a protection against sunlight, whilst the adpressed hairs guard against excessive transpiration. The dye begins to disappear when the leaf is from one-third to one-half its full adult size, and is almost entirely gone when two-thirds grown. Young expanded

leaves (5 cm. long by 2.2 cm. broad) show normally a weak but distinct power of assimilation, but after eight hours exposure to full sunlight, with the dorsal surface upwards, assimilation is faint or absent, some leaves being fatally injured; whilst if the ventral surface, exposure of which in an adult leaf of a shade-plant sensitive to exposure produces more effect than does exposure of the dorsal surface, is subjected to insolation for the same time, a weak or faint power of assimilation is shown, and the leaves all recover and show next day a normal weak power of assimilation. In a fully adult green leaf (13.5 cm. long by 6.5 broad) after eight hours' exposure, a moderately to fairly active power of assimilation was shown.

An unnamed epiphytic Aroid, growing in the Canarien Allée near the main entrance of the Buitenzorg Gardens, has the young leaves rolled up vertically with the ventral (under) surface outwards, a red dye being present in the spongy mesophyll-cells and also around the vascular bundles. As the leaf expands horizontally, dorsal surface upwards, the red dye lessens in amount; but in adult leaves a slight amount is still present. In other plants the red dye might remain in this position in the adult leaf as a vestigial survival of that present in the young leaf, and without necessarily having any functional importance.

In many Scitamineae it is the under surface of the leaf which is red. *Alpinia officinarum*, Hance, has a purplish-red colour, on the under surfaces only, of the nearly vertically erect leaves. From the very young leaves the red colour is absent; it appears as soon as the leaf is exposed, and is most marked when from one-third to one-half full grown; after this it decreases in amount, disappearing at the edges and sides first, and finally in the fully adult leaf being totally absent. *Belemcanda chinensis* is exactly similar with regard to the distribution and appearance of the red dye, but the dye does not commence to disappear until after the leaf is fully adult and the young sensitive growing tissues no longer need that protection from light which, owing to the marked

exposure, when young, of the ventral surface to illumination, was peculiarly necessary. In various Zingibers, Marantas, &c., in which the under surface of the leaf is red, the leaves when adult are horizontal with the ventral surface downwards, and the red pigment disappears in the post-adult stages. In some cases the leaves remain partly erect, in which case a slight red colouration may persist on the under surface.

When exposed to strong illumination, *Mimosa pudica* acquires a distinct reddish colouration on the upper exposed surfaces of the petioles and younger branches, which is slight or absent in the young still folded leaflets; in the adult leaves the red colouration is especially marked, but is restricted to the under surfaces of the leaflets. In shaded plants the red colouration is but slight or absent, and this is commonly the case in plants grown in European hot-houses. The red dye is formed in the epidermal cells at the edges of the leaflets and in those parts of the under surface which are exposed when the overlapping leaflets are all folded together. At the apex of the leaflet the under epidermis has a thicker outer wall and cuticle than the upper epidermis, but in the basal part of the leaflet this difference does not exist; if anything, the upper epidermis and cuticle are here slightly thicker than the under. On the basal pair of leaflets the under epidermis and cuticle, which are outermost and entirely exposed when the leaflets are folded, are thicker than the upper all over the leaflet. On the upper surfaces of the leaflets, stomata are abundant and increase in number towards the apex, being especially abundant at the extreme apex. The average number of stomata on the under surface is slightly greater than on the upper, but not quite so abundant as at the apex on the upper surface. On the under surface at the apical one-eighth to one-twelfth of the length of the leaf, i.e. over the portion which, being exposed when the leaflets fold together, has a protective red pigment, no stomata at all are present. Of the basal pair of leaflets belonging to one of the outer petioles, the outer one is generally larger and better developed besides being more exposed than the inner, and

in it the adaptive modifications are most markedly developed. The entire under surface is markedly red and hairy. The outer wall and cuticle of the epidermal layer, all over the under surface of the leaflet, are thicker than on the upper surface. Stomata are present all over the under surface, but only one-third to one-fifth, or less, of the number present on the upper surface, and the guard-cells have markedly thickened and cuticularized walls. On the upper surface stomata are abundant all over the leaflet, being less abundant at the base and especially abundant at the apex.

When therefore the leaflets of *Mimosa* are folded together, only the red and hairy parts of the under surfaces of the overlapping leaflets are exposed, whilst the fully exposed under surfaces of the basal pair, and the exposed edges of the other leaflets, are markedly red and hairy and contain as compared with the upper surfaces but few or no stomata. The red dye protects the exposed portions of the more sensitive under surface from any excessive photo-chemical action caused by the unnatural exposure, whilst at the same time transpiration is reduced to a minimum.

The leaf of *Mimosa* is very thin, consisting besides the upper and under epidermis, of a single layer of palisade-parenchyma with large and numerous chlorophyll-grains, and of two or three layers of spongy mesophyll. The plant is very sensitive to drought and is readily injured by it, the least scarcity of water causing the leaflets to fold and to remain folded for some time after the plant has been fully supplied with water again; whilst if the drought be at all prolonged the leaflets may never recover or re-expand. It is hence obviously an advantage that, whenever a wind of sufficient velocity to agitate the leaflets is blowing, any excessive and injurious transpiration which it might cause should be guarded against by the mechanical stimulation causing the leaflets to fold together. At night-time the folded position of the leaflets and the hairiness of the exposed portions act as a protection against the loss of heat by both transpiration and radiation.

On the upper surface of the pulvinus the epidermis bears some resemblance to a columnar epithelium, the outer ends of the cells being rounded or conical, whilst the cell-cavity is filled with a red sap. This layer probably acts as a protection to the sensitive pulvinar tissues, preventing them from being too readily affected by light falling from above. As has been already shown, the pulvinus is, probably owing to this fact and to the transparency of the pulvinar tissues, almost or quite as readily affected by illumination from beneath as from above; the only condition necessary being that the light when it reaches the sensitive pulvinar tissues shall be of sufficient intensity to act as a stimulus.

From the foregoing it is clear that the red colouration found on the parts of the under surfaces of the leaflets of *Mimosa* which are exposed when folded, comes under the same category as in the plants previously mentioned, being for the purpose of shielding the transparent spongy mesophyll, in which the higher processes of synthetic metabolism, as distinguished from the simpler primary assimilatory processes, are probably especially active, from the injurious effects of the exposure to which it might wholly or in part be liable when the leaflets are folded together.

In some cases, however, such as in certain Begonias, in which the leaf is horizontally expanded and the red dye is present only on the under surface in the adult leaf, Stahl's interpretation of the functional importance of the red colouration may be the correct one; for even excluding all such cases occurring in cultivated garden-plants in which the peculiarity might be due to artificial selection, still cases remain for which this explanation does not suffice. Granting that the red pigment must always be formed for a useful and definite purpose, its well-defined and apparently purposeful distribution precluding the idea of its being an accidentally coloured useless waste product of metabolism, it is difficult to see in such cases, even though they are but few in number, what other useful function it could possibly have.

As regards the young hanging-foliage of certain tropical

trees, Keeble¹ has already shown that the hanging position acts as a protection against excessive transpiration which is very apt to injure the young leaves, and that when in addition a red dye is present the decomposition of the chlorophyll by exposure to strong light is thereby largely prevented. The temperature-determinations which Keeble made at the upper and under surfaces of red and green insolated leaves of *Amherstia nobilis*, seem to point to the following explanation. On the upper surface of the red leaf the temperature averages 1°C higher than on the upper surface of the older green leaf, owing to the transpiration being less and the absorption of heat being greater in the former case than in the latter; whilst at the under surface of the green leaf the thermometer averages a degree above that beneath the red leaf, owing to the green leaf being more transparent to radiant heat than the red one is. Any injurious increase in the rate of transpiration, which might be caused in the young red leaves by the slight increase in the power of heat-absorption which the red colouration gives them, is prevented by their overlapping and hanging position.

It is evidently of considerable interest to know exactly what power of assimilation the young leaf possesses when in the hanging position. The following observations made in the usual manner elucidate this point, the measurements in length (L) and breadth (B) being given in terms of those of the fully adult leaf:—

Saraca declinata, L $\frac{8}{17}$, B $\frac{6}{11}$. Very pale yellowish green, apical half pinkish white. No power of assimilation perceptible except along the veins, here the chlorophyll grains are small pale yellowish green and faint evolution of O is shown. L $\frac{4}{7}$, B $\frac{7}{11}$. Pale yellowish green, distinctly green along the veins, apical portion pinkish white. Chlorophyll-grains moderately large, weak assimilation, moderately active at base near ribs, in apical portion faint or imperceptible.

L $\frac{5}{7}$, B $\frac{8}{11}$. Chlorophyll-grains fairly large and green, assimilation active to moderately active, leaflets green and expanding.

¹ Annals of Botany.

Brownea capitellata, $L \frac{1}{2}$, $B \frac{5}{13}$. Midrib pale green, leaf inrolled longitudinally, chlorophyll-grains quite small and pale yellowish colour, no assimilation perceptible. $L \frac{11}{16}$, $B \frac{8}{13}$. Leaf just unrolled, pale brownish green along veins, here in parts faint assimilation, in rest of leaf none and only faint greenish colouration. $L \frac{13}{16}$, $B \frac{10}{13}$. Expanded and nearly fully green, assimilation moderately to quite active.

Amherstia nobilis, Wall, $L \frac{5}{14}$, $B \frac{8}{15}$. Chlorophyll-grains small and pale yellowish green. No assimilation perceptible. $L \frac{1}{2}$, $B \frac{4}{7}$. Assimilation weak to imperceptible. $L \frac{19}{28}$, $B \frac{9}{15}$. Chlorophyll-grains fairly large, still somewhat yellowish green, assimilation weak. $L \frac{25}{28}$, $B \frac{14}{15}$. Still quite red but reddish colour disappearing at apex, and leaflets commencing to rise and expand. Chlorophyll-grains fairly large and yellowish to nearly normal green, assimilation weak to moderately active. Leaflet on cut branch in water exposed for five hours to full sunlight slightly fading in colour, assimilation imperceptible, being next day weak to moderately active. $L \frac{1}{1}$, $B \frac{1}{1}$. Adult fully green leaf, assimilation active. Leaflets on cut branches insolated for five hours show fairly active assimilation, but after a whole day's insolation, assimilation is fairly active, to weak or in some cases imperceptible, next morning being fairly active.

In *Amherstia* it is only when the red colour disappears and the leaf is expanded and green that assimilation becomes fully active. In the hanging position the assimilatory power of the leaflets being feeble or absent, the loss to the plant, by the non-exposure of the leaflets to light, of material which might possibly have been assimilated, is but trifling; whilst the gain, in the protection afforded against excessive transpiration or exposure to strong illumination and in the rapidity with which the young leaflets are thereby enabled to develop, is very great. If branches of *Amherstia* are bent so that the red hanging foliage-leaves are exposed to as much sunlight as possible, and the leaflets are supported on wires and spread out in a horizontal position, they may wilt or fade at the edges or tip or over irregular areas in the lamina, the growth of the leaflets is retarded and at the same time the exposure to excessive illumination causes a distinct

retardation of the growth and turning green of the chlorophyll-grains. If the leaflets are merely spread out horizontally, but not otherwise exposed, so that the rate of transpiration is markedly increased, they may become wilted, and their development and rate of growth is slightly retarded. This is hence certainly a case in which any power of increasing the rate of transpiration which the red dye may possess in virtue of its feeble action as a heat-absorbing medium, does not seem to be of any advantage but rather a slight disadvantage to the plant, were it not guarded against by the hanging and overlapping position of the leaflets; whilst the protection which the red dye affords against the retarding action that light of too great intensity exercises on the growth and development of the young and especially sensitive chlorophyll-grains is clearly of the highest importance. The young leaf is not to be regarded as an assimilatory organ, the metabolism of which demands a large supply of mineral salts and hence also of water, but as a growing organ to which nourishment is supplied in soluble and concentrated form, and in which a comparatively small amount of transpiration suffices, along with the strong osmotic currents maintained by the continual removal of the supplied food-material, to provide it with all it requires.

If the primary function of the red dye in the tropics were to increase the amount of transpiration, then it would be only natural to expect that it would be formed in greatest abundance where the temperature is lower and the air more nearly saturated with water-vapour. The very opposite is however the case. Thus at the foot and sides of the volcanic mountain of Gedeh, and in the valleys around, very many plants have a reddish colour, especially in the young leaves. As one ascends this becomes less marked, until at Tjibodas and in the forests above it (4,500 ft. to 6,500 ft.), the number of plants showing a red colouration, and the intensity of the latter when present, reach a minimum. The vegetation at this elevation is almost entirely green, a few plants only, especially if growing in open clefts or glades in the forest,

having more or less reddish young leaves. Yet it is just here where a power of stimulating transpiration is apparently most needed; for at this elevation the air is, during the greater part of the time, at or near saturation-point. On the other hand if the red pigment acts as a protection against sunlight, it is easy to understand why here, where the sun rarely shines for more than a few hours daily and then generally through a haze of clouds, the protective red pigment should almost entirely disappear; for it is just the more refrangible photo-chemical rays which the air saturated with water-vapour absorbs in greatest amount.

At the summit of Pangerango (10,000 ft.) and for a few hundred feet below, the plants are in one or more characteristics markedly xerophilous (hairs, wax, thick epidermis and cuticle, few stomata, mucilaginous or fleshy tissues, reduced leaf-surface, &c.), and very many have a pronounced red colouration either in the young leaves and shoots or in the adult leaves as well. Here, just above the cloud-belt, the exposure to light is greater both in amount and intensity; whilst the drier air, the lower atmospheric pressure, and the more prevalent wind, all render the rapid evaporation of water easy. From too intense exposure to light the plants protect themselves largely by means of the red pigment; whilst the xerophilous character which the plants assume guards them against excessive transpiration, to which the difficulty of absorbing water in sufficient amount when the ground-temperature is low but the temperature around the aerial parts relatively high, a frequent occurrence at such elevations, renders them especially liable. It appears therefore that where transpiration is easy but the exposure to light great, the red colouration is most marked, but where transpiration is difficult and the exposure slight, it diminishes or disappears.

In Java at the commencement of the wet S.W. monsoon and in Ceylon at the rainy commencement of both monsoons, the vegetation acquires a more marked reddish tinge than in the dry periods between the monsoons. This is, however,

simply due to the fact that the young foliage, which in most tropical plants is more or less tinged with red, is very much more abundantly formed at this period than during the dry season. Even during the wet season in West Java, there is almost always bright sunlight until mid-day, lasting often till 3 or 4 p.m., and occasionally all day; so that the young foliage which the rain has caused to be produced in such abundance is exposed for six hours on the average to very bright illumination, the sunlight from 9–12 being the brightest of the day. Hence the protective red colouration is perhaps quite as necessary during the wet season as during the dry.

An interesting fact noticed by Stahl (*l. c.*) is that in the adult leaf the guard-cells of the stomata are always without any red dye even though it may remain present in the epidermal cells of the upper surface. The importance of this Stahl concludes to be that the guard-cells remain cooler, transpire less, keep open longer, and hence promote transpiration and assimilation. However, Stahl also points out that in many plants, especially in spring, the epidermal cells immediately around the stomata have a red sap, and are thereby enabled to heat the points at which the water-vapour escapes and hence the guard-cells also.

Instead of adopting either of these contradictory explanations, it is perhaps simpler if we regard the absence of the protective red dye from the guard-cells of the stomata as being due to the fact that they are essentially organs which react to light: hence it is important that they should be exposed to the same intensity of light as is falling on the surface of the leaf in which they are present, even though a certain risk of permanent injury may thereby be incurred.

Wiesner¹ states that a portion of the light absorbed by the chlorophyll goes to warm the chlorophyll-grain, and hence the surrounding parts also; so that even if we accept Stahl's view, the absence of the red dye from the guard-cells may simply be due to the fact that the greater amount of chloro-

¹ Wiesner, Sitzungsbericht d. K. Akad. der Wiss. zu Wien, Bd. lxxiv. p. 1876.

phyll which they contain enables them to dispense with any special and very much less efficient heat-absorbing medium such as erythrophyll.

That the stomata are markedly sensitive to and may be injured by prolonged exposure to sunlight, so that the presence of a protective red dye in the guard-cells might possibly under given conditions of exposure be an advantage to the plant, is shown by the following observations. The adult leaves of a number of plants having stomata on both surfaces were exposed to bright sunlight, in some cases the upper and in others the under surface being the exposed one: the epidermis was then removed and examined under optimal illumination by the Bacterium-method to ascertain whether the assimilatory powers of the chlorophyllous guard-cells were affected in any way. The guard-cells are rather sensitive to the action of prolonged sunlight; and often four to five hours' exposure, especially when it is the under surface which is exposed, is sufficient to inhibit their assimilatory activity, the power as a general rule returning again in from a few hours to a day, if placed under conditions which permit of recovery. With longer exposure, and especially if subjected to the cumulative effects of exposure extending over several days, the chlorophyll-grains are more or less completely bleached, and may be in a condition of permanent light-rigor from which no recovery is* possible. It is commonly the case that in exposed leaves which have been for some time adult but which are still quite vigorous, no power of assimilation can be detected in the guard-cells of the stomata, if any, on the upper surface; and this may still be the case, especially in well-exposed leaves, even if previously kept under conditions which permit of recovery, the chloroplastids in such cases being in a condition of permanent light-rigor. The guard-cells from the under surface of normal leaves, when examined in the morning, almost without exception show a more or less marked power of assimilation, and this persists until the decline of the leaf commences.

Bearing these facts in mind, it is easy to understand that, in much exposed and horizontally expanded bifacial leaves, it should be an advantage to the plant to have the stomata restricted entirely or almost entirely to the under surface of the leaf; whereas in an erect leaf, or one growing in the shade, the stomata tend to be more evenly distributed over both surfaces. It is interesting to notice that in a bifacial leaf, with more than one layer of palisade-parenchyma, owing to the stomata being more abundant on the under surface of the leaf, the amount of assimilation performed by the different layers of the palisade-parenchyma tends to be equalized under normal conditions of exposure and illumination, the deeper layers coming into contact with air containing a higher percentage of CO_2 ¹, whilst the upper ones are exposed to stronger illumination.

Stahl mentions that the marked red colouration which the stigmas of many anemophilous plants show, may be for the purpose of raising the temperature of the stigma, and hence aiding the growth and germination of the pollen, on which, according to Stahl, light exercises no perceptible influence. In a previous paper² it has however been shown that exposure to light of marked intensity exercises a distinct influence on the germination of the pollen-grain, and more especially retards the growth in length of the pollen-tube. Hence, considering the generally much exposed condition of the stigmas of anemophilous plants, it is very evident that the red dye even in this case may be of paramount importance as a protection against the inhibitory action which strong light exercises on the growth and elongation of the pollen-tube.

In the case of alpine and arctic plants, the slight additional absorption of heat which the red dye causes, may be of some use; but in all cases, other things being equal, an increased absorption of heat means an increased transpiration, which,

¹ Blackman, On the Path of the Gaseous Interchanges in the Leaf: Proceedings of the Royal Society, 1896.

² Observations on the Pollen-tube: Trans. Liverpool Biol. Soc., Vol. ix, 1895.

in alpine plants without a marked xerophilous¹ habit, might be distinctly injurious, owing to the difficulty of absorbing water from the cold ground in sufficient amount to cope with the rapid evaporation caused by the low pressure and dryness of the air. Besides, the insolation-temperature in alpine regions is already sufficiently high: it is at night and when shaded that an absorption of heat might be of considerable use.

In *Haematococcus* and similar forms the light-protecting function of the red dye is probably the most important one; for, as Schröder² and Klebs³ have shown, the common presence of a red dye in the resting-spores of many Algae is of importance as a protection against the decomposition to which the chlorophyll in such cases is especially liable when exposed to light. Thus the green zygotes of *Hydrodictyon* may remain living if dried in darkness, but if exposed to light become decolorized and die.

Stahl considers the fact that the red colouration, which the young shoots of plants growing in cold climates generally show in spring, commonly disappears on the advent of the first few warm days, as being conclusive evidence pointing to the red dye being of importance as a means of raising the temperature of the young growing parts. It is however just when the temperature is low that the chlorophyll-grain is most liable to the decomposition induced by the action of light⁴, and when the light, if sufficiently intense, most markedly retards the development and turning green of the etiolated chloroplastid.

If plants of *Elodea canadensis*⁵ or *Utricularia vulgaris* are immersed in weak sugar-solution kept at ordinary room-temperature and exposed to strong light, they may show a marked tendency to form a red dye, whereas in water or

¹ Lazniewski, Beiträge zur Biologie der Alpenpflanzen: Flora LXXXII, 1896, pp. 224-267.

² Schröder, Bot. Untersuch. Tübingen, Bd. ii, Hft. 1, 1886.

³ Klebs, Bot. Untersuch. Tübingen, 1883, Bd. i, Hft. 2.

⁴ See Assim. Inhibition: Journal Linnean Society, 1896, p. 390 (Coniferæ).

⁵ Assim. Inhib.: Journal Linnean Society, Vol. xxxi, 1897 (Botany), p. 567.

diffuse daylight but little or none is formed. Hence under conditions in which the chlorophyll-grain tends to become unhealthy and its assimilatory activity to become inhibited¹, a red dye protecting it from the effects of excessive exposure to which it is now specially sensitive, tends to be formed. The non-formation of the red dye under exposure to weak diffuse daylight, is strong though not conclusive evidence that the red dye is not merely an accidental metabolic product formed under these peculiar conditions of nourishment. Obviously, since the plants are submerged, it cannot possibly be for the purpose of increasing what is non-existent, i. e. transpiration, nor can it perceptibly raise the temperature of a submerged water-plant. When a red colouration is present in underground parts (Beet-root, &c.) which are not exposed to light or only to very faint illumination, it may very possibly be a waste metabolic product accidentally produced, and perhaps without any special function.

J. C. Costerus² finds that in most tropical plants before 6 a.m. an abundance of starch is present, that it decreases rapidly until 7 a.m., then increases again and reaches a maximum in some plants at noon, and in others not until 4 or 5 p.m. During the night but little starch is removed, and Costerus concludes that light probably exercises a most important influence in favouring the translocation of carbohydrates. Pick³, on the other hand, long ago came to the conclusion that light inhibits or retards the translocation of carbohydrates, and that the red dye is developed as a protection against this action of light. Pick's interpretation of the function of the red dye has already been shown⁴ to be only a special and less important case of its general protective function. The slow removal of the accumulated starch at night, and its rapid diminution in the early morning when exposed to light, are not necessarily due to any direct

¹ Loc. cit. footnote 5, p. 477.

² Costerus, *Ann. d. Jar. Bot. de Buitenzorg*, p. 73, Vol. xii, Pt. I, 1894.

³ Pick, in *Bot. Centralblatt*, XVI, pp. 9-12.

⁴ *Linnean Soc. Journal*, 1896 (Bot.), p. 445.

influence of light on translocation, but may be indirectly due to the light causing a markedly increased transpiration, and so increasing the velocity of the conduction-currents as to rapidly remove the soluble carbohydrate as fast as it is formed, thereby permitting of the rapid solution and removal of the accumulated starch. At the same time it is in the early morning, as the temperature rises, and before the light becomes too strong, that growth is most active, and the stored material is most rapidly used up.

There can be little doubt that, both in the tropics and in temperate climes, the main and primary function of the red dye, when present in exposed parts, is to act as a protection against light of too great intensity; though in all cases its presence at the same time confers upon the plant a slightly increased power of absorbing heat. For calling attention to this latter possibility Stahl deserves full credit from both the physiologist and the biologist: in a few cases, such as in the horizontal leaves of shade plants having the red colouration present on the under surfaces only, the relatively slight heat-absorbing power of the red dye may, by secondary adaptation, have become its most important function.

SUMMARY.

In tropical plants full and prolonged insolation may markedly affect or temporarily inhibit the functional activity of the assimilating parts. If the stoppage be temporary, it is generally accompanied by but little change in colour; but if permanent, the colour of the chlorophyll-grains is markedly affected, and they may be completely bleached. Different plants show very different resistant powers, shade-loving plants being, as might naturally be expected, the least resistant.

The leaves are protected against the injurious effects of excessive exposure by the presence of a red dye and by active or passive paraheliotropic movements. The active movements are best shown by the motile leaves of the Leguminosae, the pulvini being the motile and irritable

perceptive organs. In *Mimosa pudica* the irritability is very marked and well differentiated, the main pulvini responding to the direction of the light in a diaheliotropic manner, the pulvini of the leaflets responding to the intensity only of the illumination, being paraheliotropic in intense light, diaheliotropic in diffuse daylight, and nyctitropic in very weak light or darkness. It is mainly to the photochemical rays, which are most active in inducing the decomposition of chlorophyll, and in inducing light-rigor, that the pulvinus of the leaflet responds.

The red pigment acts mainly and primarily as a protective shield against the more refrangible rays (green and blue). It has also a feeble heat-absorbing power, which may, in a few cases, possibly be of considerable or even primary importance.

Ewart, Alfred J. 1897. "The effects of tropical insolation." *Annals of botany* 11, 439–480. <https://doi.org/10.1093/oxfordjournals.aob.a088663>.

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