INTRODUCTORY LECTURE

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I. PHOTOENVIRONMENT AND ENVIRONMENTAL BIOLOGY

The complex morphogenetical and physiological mechanisms of any living being and all the intricate biochemical–biophysical events, which in their totality constitute the life cycle of an organism, are tuned in a most sensitive way to the environment in which the organism lives. Organism and environment are an inseparable whole. All changes in the environment will ultimately influence the life of the organism.

The environment which is the sum total of the surroundings of living beings is composed of chemical, physical and organismic factors. Light, temperature and water are, of all the physical environmental factors, the most important ones. Light, which in this lecture is our exclusive concern, dominates among the three, as it is, through the mediation of the autotrophous plants, the main source of energy which keeps life going.

The ocean of light which constitutes the photoenvironment initiates in the organisms subjected to it certain photochemical and photophysical processes. These put into motion photosynthesis (in plants), photomorphogenic and phototropistic processes (in plants and animals) and elicit certain behavioural responses (in animals), which, in their turn, are the means by which the organisms adapt themselves to their special photoenvironment.

The molecular biologist and the physiologist study light, as a causal agent, and the organismic responses to it in the laboratory under conditions where the factor 'light' is isolated and constitutes the only variable in an otherwise controlled and constant but unnatural environment. The environmental biologist who wants to find out how the natural photoenvironment influences life and development and how light shapes the ultimate fate of an organism in its habitat has, perforce, to choose a different approach. He must base his research on the knowledge the molecular biologist, the physiologist,
the physico-chemist etc. have gained concerning the causal chain of physiological molecular events light sets in motion in living beings. But the questions he puts to nature are different. The main reasons for this are as follows:

(a) The environmental physiologist has to acquaint himself with light as a physical environmental factor, otherwise he will not know to what the organisms react. He will, therefore, in each habitat, measure the factor ‘light’ in all its aspects (intensity, duration, spectral composition etc.).

(b) He has to take into account that in any natural environment light is not isolated but is only one of a number of environmental factors which operate upon the organism all at the same time, and which in their continuous interaction change each other’s effect upon the organism.

(c) He has to know that an organism fulfills its life cycle in stages by passing through a number of morpho-physiological phases, for example, imbibition, germination, beginning of growth etc. As each phase differs physiologically from the other the same environmental factor as, for example, light, affects each phase differently.

(d) A value judgment is involved in environmental biology. The biologist dealing with the ‘total environment–total organism’ relationship is not only concerned with the cause and effect relation of biological processes. As he studies the response of the whole organism during its full life cycle to environmental conditions as, for example, light, he wants to know if and how the behaviour of plant or animal towards a certain external factor has adaptative value.

II. SCOPE OF THIS LECTURE

Restricting myself as a botanist to plants, the following matters are dealt with:

1. Light as an environmental factor.
2. Photoblastism (photoenvironment and germination).
3. Photomorphoses (photoenvironment and structure).
4. Photomorphogenesis (photoenvironment and development).
5. Photostimulation (photoenvironment and movement).
6. Photoproduction (photoenvironment and production of dry matter).
As it is impossible to deal with all the items exhaustively I will use photoblastism, with which I am personally most familiar, as a kind of case history which will enable me to demonstrate the main basic problems common to all photophenomena. I will additionally deal only with one type of photomorphosis as this will provide the opportunity to stress a certain problem which seems to me to be of importance.

As this is neither a research paper reporting results nor a review the emphasis of this lecture will not be on achievements but on the main problems involved and future avenues of approach, and the citations of literature are not complete.

III. LIGHT CLIMATE

The first task of the biologist who deals with light as an environmental factor is to know the intensity, duration and spectral composition of light and their daily and seasonal changes during the year. Modern text-books of plant ecology (Lundegardh, 1957; Daubenmire, 1959; Walter, 1960) or bio- and agrometeorology (Ashbel, 1957; Foitzik and Hinzpeter, 1958; van Wijk, 1963), or books dealing exclusively with plant and radiation (Sauberer and Härtel, 1959), contain much information about intensity, monthly and yearly changes of global and 'diffuse' (sky) radiation, u.v. radiation, albedo and their global distribution, radiation falling on differently oriented walls and slopes, penetration of radiation in water and snow, radiation under tree canopies, in wheat fields etc.

This accumulated knowledge is satisfactory when considering the relation between light, photosynthesis and dry matter production. But the information about the spectral composition of light is meagre.

In books and papers on plant ecology dealing with light climate one finds little more than a table or a curve of the spectral composition of sunlight and some data concerning the spectral absorption qualities of leaves. Sauberer and Härtel (1959), in their special study 'Pflanze und Strahlung',write: 'Die Vertiefung unseres Wissens über die Zusammenhänge zwischen Licht bezw. Strahlung und Lebensvorgängen bringt uns die Erkenntnis, dass man nun in zunehmendem Masse von den Messungen mit ungefilterten Photoelementen zu Spektralmessungen in bestimmten Wellenbereichen übergehen muss' (p. 132). This is a wish not yet realized.

If we disregard u.v., the meteorologists do not do much better. We find some figures of the yearly and daily course of radiation in
certain spectral areas (see e.g. Henderson and Hodgkiss, 1963) measured for a few years in very few meteorological stations, as, for example, Jerusalem (Ashbel, 1961–3). But all this is insufficient and the following statement of Klein and Shropshire (1964) is correct: 'Neither the energy nor the variations in energy of these regions of natural daylight through the course of daily and seasonal fluctuations has been measured for total sky radiation.' We underwrite fully, therefore, what Brooks (1964) Bot. Rev. 30, 263–89) writes: 'Much very specialized biological and photochemical research is being carried out in laboratories under artificial illumination. This is almost unrelated to the spectral quality of outdoor irradiation from sun and sky.'

Dr W.H.Klein, of the Smithsonian Institution, is at present organizing a programme of absolute R and FR measurements to fill this gap. As it becomes increasingly clear that Red–Far Red (R–FR) reversible low energy reaction is at the root of a great many physiological events, and as other morphogenic photomechanisms bound to certain spectral regions slowly become unravelling we urgently need the following data with special emphasis on R and FR:

1. Reliable and detailed measurements of the spectral composition of sunlight all over the globe.
2. The changes in spectral composition from morning to evening throughout the year.
3. The changes in spectral composition as a function of habitat, that is the spectral composition as dependent on exposition of slopes, in caves, inside various plant communities etc.
4. The change in spectral composition of sunlight at different depths of soils of various composition. There are some such measurements (see Sauberer and Hartel, 1959, and Wells, 1959) but they are wholly insufficient.

As the light energies needed to put in motion certain physiological reactions are very low we should also know more about moonlight and its spectral composition.

IV. PHOTOBlastism

The life cycle of all higher plants starts with germination. During germination the dispersal unit passes from dormancy to a state of intense physiological activity in a few hours. When dormant, the dispersal unit is highly resistant to external factors. It can be put into boiling water, concentrated acids etc. without loss of embryo-viability.
The essential core of the dispersal unit, the embryo, is thus protected against adverse external conditions.

When germination has started the embryo loses its high degree of resistancy. Through inhibition and the beginning of growth the embryo, transformed into a seedling, takes up intimate metabolic contact with its surrounding, and is from thereon submitted to the dominant influence of its environment from which it is more or less physiologically isolated during dormancy.

Germination is therefore a most critical period in the life of a plant, as time and place of germination are of decisive importance for the survival of individuum and species. The more extreme the environment—as in deserts—the more important becomes timing and topography of germination.

Accordingly, evolution has forced plants to develop a great variety of germination controlling mechanisms which permit plants to germinate only at the most appropriate time of year and in those habitats best suited to the special ecological requirements of the species.

One of the means of germination control is photoblastism, that is the influence light exerts upon germination. Photoblastism can be positive or negative. In other words the germination of some seeds is stimulated, of others inhibited by light. There are also seeds which are light independent in germination.

A. Positive photoblastic reactions

1. Light action in various spectral regions

We take as a point of departure the germination of lettuce seeds var. 'Grand Rapids'. When germinated in the darkness at 26°C, only a small percentage of the seeds germinate. When given a short illumination of white light full germination is obtained. Continuous white light has the same effect as a short illumination (Table 1) but, whereas with short illumination germination is directly proportional to the amount of light up to the maximum saturating amount, germination under continuous illumination is inversely proportional to light intensity (EVENARI and NEUMANN, 1953; EVENARI, 1956, 1964).

With other photoblastic seeds this difference between the effect of short and prolonged illumination is much more pronounced. The germination of the acid treated dispersal units of Oryzopsis miliacea, for example, is promoted by a single short illumination with white light but inhibited by continuous light even below the level of dark germination (KOLLER and NEGBI, 1959).
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Since the classic paper of Borthwick et al (1952), we know that the effect of short-duration white light upon germination is based on a reversible photoreaction put into motion by the red wavelength (around 660 nm) and the far red (around 730 nm) part of the spectrum. The reversibility of this reaction can be easily demonstrated with

**Table 1. Germination percentages of lettuce seeds ‘Grand Rapids’ at different temperatures (°C) in darkness (D) and in continuous white light (L, 130 ft-cd).**

<table>
<thead>
<tr>
<th>Temperature</th>
<th>D</th>
<th>L</th>
</tr>
</thead>
<tbody>
<tr>
<td>10</td>
<td>72</td>
<td>97</td>
</tr>
<tr>
<td>18</td>
<td>75</td>
<td>100</td>
</tr>
<tr>
<td>20</td>
<td>72</td>
<td>97</td>
</tr>
<tr>
<td>24</td>
<td>13</td>
<td>98</td>
</tr>
<tr>
<td>38</td>
<td>8</td>
<td>87</td>
</tr>
<tr>
<td>31</td>
<td>3</td>
<td>70</td>
</tr>
</tbody>
</table>

lettuce seed ‘Grand Rapids’. The photoreaction is mediated by the chromoprotein phytochrome which has an R absorbing (P_{660}) and an FR absorbing (P_{730}) interconvertible form

\[ P_R \xrightleftharpoons{R}{FR} P_{FR} \]

(Red = R, Far Red = FR, White Light = W, Darkness = D, Blue = B)

As long as \( P_R \) is preponderant, germination cannot take place. If by irradiation with R the equilibrium is driven towards \( P_{FR} \), the pathway to germination is open. If by irradiation of \( P_{FR} \) with FR the process is reversed, germination is again inhibited.

One of the main problems of future research in this field is the question of whether there is only this photoreaction. If another photoreaction is involved, is it mediated by phytochrome or is another pigment involved?

It seems certain that there are at least two photoblastic mechanisms: a low energy one (10^{-2} J/cm^2), identical with the R-FR mechanism, and a high energy one (more than 1 J/cm^2).

The presence of the high energy reaction can be demonstrated in various ways. Lettuce, var. ‘Progress’, do not require light for their germination. They germinate equally well in light and darkness. By treating the seeds with a certain concentration of coumarin which
inhibits their germination in darkness, they become photoblastic and
the latent low energy reversible R–FR mechanism becomes active.
R stimulates germination, overcoming the inhibitory influence of
coumarin, FR inhibits. When coumarin untreated ‘Progress’ seeds
are illuminated with short FR, germination is not affected. Prolonged
FR, however, nearly completely inhibits germination and the reactivity
of the seeds towards subsequent application of R decreases with
increasing duration of the FR treatment (Evenari, 1964).

There is much further proof of the existence of high energy reaction.
We cite only one more instance. Kadman-Zahavi (1960) found in
Amaranthus retroflexus where, as in Oryzopsis miliacea short W
stimulates and continuous W inhibits (at 26°, for example, the ger-
mination percentages are: D 32 per cent, single short W 92 per cent,
continuous W 3 per cent), that the low energy reversible R–FR
mechanism is active. But prolonged FR, if given for a long enough
period, inhibits irreversibly (Fig. 1a). The seeds recovered from this
inhibition when they were put into darkness after illumination with
FR (Fig. 1b, c).

Hendricks and co-workers (1959) are of the opinion that the high-
energy reaction is mediated by phytochrome through simultaneous
continued excitation of both pigment forms. Certain experiments
speak against this theory. We cite only one: Lettuce seed var. ‘Reine
de Mai’, which are normally not light-dependent as the above cited
var. ‘Progress’, are made light-requiring by FR irradiation (4·5 J/cm²).
The FR inhibition is cancelled by R (2·3 J/cm²). This is the usual

When a dark period is intercalated between R and FR, FR loses its
reversing influence as a function of the length of the dark period. This
is known for many seeds possessing the R–FR mechanism and
happens because P_{FR} puts into motion a chain of biochemical reactions
leading to germination. If that chain had enough time to proceed to a
certain point it cannot be reversed even by converting all the pigment
to P_{R}. With ‘Reine de Mai’ seeds the length of the dark period needed
to make short, low energy FR ineffective is approximately 15 h at 20
and 25° C. When prolonged high-energy FR is given after such a dark
period it inhibits germination more or less completely. As this happens
when, as Rollin says, ‘l’intervention du phytochrome est terminée’
it is probable that the high energy reaction is independent of the
reversible R–FR mechanism.

Mohr and Appuhn (1963) report similar results and conclude that
the low- and high-energy systems are mutually independent; but both control the production of a substance B which—when it reaches a certain threshold value—puts germination into motion. This is one possible explanation of the facts. (For another one see Evenari, 1957.)

Other indications point in the same direction, that is the presence of at least two independent photoreactions.

![Germination percentages of seeds of Amaranthus retroflexus.](image)

**Fig. 1.** Germination percentages of seeds of *Amaranthus retroflexus*. Curve *a*: seeds kept for 2 days in darkness, transferred to prolonged FR for different lengths of time (abscissa) and then illuminated with 32,000 meter candles sec of W. Curve *b*: as *a*, but seeds kept for 2 days in prolonged FR (10,700 m-cd), transferred for different lengths of time to darkness (abscissa) and then illuminated as in *a*. Curve *c*: as *b*, but intensity of prolonged FR 4280 m-cd (after Kadman-Zahavi, 1960).

(a) Blue light (around 440 nm) of high energy affects the germination of many photoblastic seeds. Blue light is also active in other morphogenic reactions. We cite only the development of fern gametophytes (Mohr and Barth, 1962; Miller and Miller, 1964). But, as in the case of etiolated pea segments, the blue effect was reversed by FR (Bertsch, 1963) it could be that the B effect is mediated by phytochrome which absorbs in the B-region. However, the question remains open.
(b) The germination of the achenes of *Artemisia monosperma* is promoted by short and continuous irradiation with R, FR, blue, green, yellow and white light. The R promotion is not cancelled by FR (Koller, 1963; Koller et al., 1964, Table 2).

Although phytochrome absorbs in the green and yellow the absorption coefficient in these regions is very small in comparison with the absorption in R, FR and B.

The question now arises as to whether the presence of high and low energy reactions can explain the different behaviour of certain seeds in continuous and short-time illuminations with W. We will take as an example the case of dispersal units of *Oryzopsis miliacea* (Koller, 1963; Négbi and Koller, 1964). As stated already, at certain temperatures continuous W inhibits, short W promotes germination. But continuous W inhibits only as long as the seeds are irradiated. Transfer to D after continuous W promotes germination. This promotion is reversed by short FR or continuous W. Continuous FR and B inhibit germination and prevent subsequent germination in D. The low-energy R–FR mechanism is active in the dispersal units. It is responsible for the promoting effect of short W as the R present therein is preponderant over B and FR which are also contained in short W because the equilibrium favours P_{FR}. Continuous FR and B inhibit germinations. Continuous W inhibits because the R part of it keeps the phytochrome system at P_{FR} and does not permit the B and FR contained in continuous W to cause light irreversible inhibition of germination. The presence of the high-energy FR–B system, in its turn, prevents P_{FR} from setting into motion the physiological processes leading to germination. This block is removed by transfer to D when the presence of P_{FR} brings about germination. The example given

<table>
<thead>
<tr>
<th>Temperature °C</th>
<th>Blue</th>
<th>Green</th>
<th>Red</th>
<th>Far-Red</th>
<th>White</th>
<th>Darkness</th>
</tr>
</thead>
<tbody>
<tr>
<td>10</td>
<td>80</td>
<td>86</td>
<td>97</td>
<td>86</td>
<td>90</td>
<td>4</td>
</tr>
<tr>
<td>15</td>
<td>94</td>
<td>95</td>
<td>97</td>
<td>85</td>
<td>98</td>
<td>5</td>
</tr>
</tbody>
</table>
PHOTOENVIRONMENT

shows how difficult it is to understand the complicated action of white light even when we know how its spectral components act. It must therefore be one of the future tasks of photobiology not only to study isolated spectral regions but to find out how they interact when applied together as is the case in white light.

2. Skotodormancy

When lettuce seeds ‘Grand Rapids’ are irradiated with short W or short R at different times of dark imbibition, light becomes less and less effective in promoting germination (Fig. 2). After about 3–4 days in darkness the seeds have lost their reactivity towards light. They become skotodormant, that is, prolonged darkness has produced a secondary dormancy in the imbibed seeds which cannot be broken any more by light (Evenari and Neumann, 1953). Skotodormancy is broken by a low-temperature treatment of various duration, after which the seeds react again to R–FR. The same has been reported for many other photoblastic seeds (Evenari, 1956, 1964).

What happens during imbibition in darkness that changes the seed’s reactivity towards light? This question leads to the broader one

![Fig. 2. Germination percentages of lettuce seeds var. ‘Grand Rapids’ when irradiated for 5 sec (a) and 60 sec (b) with 250 ft-cd of white light after different imbibition times (after Evenari et al., 1953).](image-url)
of the influence of a dark period on germination in general. We can differentiate between the following modes of action:

(a) A dark period after short R permits the physiological processes initiated by R to proceed so that they cannot be reversed any more by R.

(b) A dark period after prolonged FR restitutes the reactivity towards FR. This is the case with *Amaranthus retroflexus* (Fig. 1). This can be explained by the dark conversion of $P_R$ to $P_{FR}$.

(c) A prolonged dark period eliminates or inactivates the R–FR mechanism. What happens in this last case is open to speculation. Do the physiological processes proceeding during dark imbibition, as indicated by a changing respirational activity, affect phytochrome directly? Does dark imbibition lead to the accumulation of substances which inhibit the R–FR mechanism and which are removed by a cold treatment? No answer can be given but it seems very worthwhile to attack this question.

3. Interaction of temperature and photoblastism

The influence of light upon germination is in most cases a function of temperature, although there are dispersal units which at all temperatures are consistently positively photoblastic, as, for example, the

<table>
<thead>
<tr>
<th>Temperature</th>
<th>D</th>
<th>L</th>
</tr>
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<tbody>
<tr>
<td>9</td>
<td>o</td>
<td>80</td>
</tr>
<tr>
<td>13</td>
<td>o</td>
<td>61</td>
</tr>
<tr>
<td>19</td>
<td>o</td>
<td>79</td>
</tr>
<tr>
<td>20</td>
<td>o</td>
<td>76</td>
</tr>
<tr>
<td>22</td>
<td>o</td>
<td>82</td>
</tr>
<tr>
<td>26</td>
<td>o</td>
<td>72</td>
</tr>
<tr>
<td>31</td>
<td>o</td>
<td>29</td>
</tr>
</tbody>
</table>

seeds of *Diplotaxis Harra* (Table 3). We will disregard the effects of alternating temperatures and only deal with the effects of constant temperatures and non-periodic temperature changes.
The dark germination of lettuce seed 'Grand Rapids' is very high over the temperature range 10–20°C, and consequently the difference between light and dark germination is relatively small. Higher temperatures cause a decrease in germination percentages of seeds but the decrease is sharper in darkness than in light so that the maximum promoting effect of light is found around 25–30°C (Table 1). If we consider seeds which germinate in darkness as having 'escaped' photosensitivity of germination, this means that decreasing temperatures remove more and more seeds from photosensitivity.

With increasing temperatures the photomechanism becomes increasingly inefficient and is unable to overcome the germination block imposed by higher temperatures. Temperatures can in some cases also change the sign of the photoblastic response. Seeds of *Amaranthus caudatus*, for example, are, with continuous illumination, positively photoblastic at higher and negatively photoblastic at lower temperatures.

**Fig. 3.** Germination percentages of seeds of *Amaranthus retroflexus* at different temperatures. *a*, in darkness; *b*, with a short, single illumination of white light; *c*, with continuous illumination of white light (100 ft-cd) (after Kadman-Zahavi, 1960).
The high- and low-energy reactions are differently affected by temperatures, a fact speaking for their mutual independence. Acid-treated dispersal units of *Oryzopsis miliacea* at 20°C are positively photoblastic both under continuous white light and with a short white illumination. At 26° and 30°C they are negatively photoblastic under continuous illumination but remain positively photoblastic with a short illumination (Koller and Negbi, 1959).

In *Amaranthus retroflexus* (Kadman-Zahavi, 1960), a single short illumination applied between 20–37°C produces a positively photoblastic effect the size of which is temperature dependent. Continuous illumination, however, has a negatively photoblastic influence at the lowest temperature, changes over to a positive effect between 26–36°C and has no effect at 37°C (Fig. 3).

The temperature of the dark period before or after irradiation has also a profound influence on the light effect. We cite only one case of the many known. The seeds of *Hyoscyamus desertorum* (Koller, 1963) do not germinate in D at temperatures between 15° and 30°C. In continuous light germination occurs only at the higher temperatures whereas at the lower temperatures continuous light does not promote germination. The seeds need a combination of high temperatures and light for germination (Table 4).

### Table 4. Effects of continuous light (L) or darkness (D) applied at different temperatures (°C) on the germination percentage of seeds of *Hyoscyamus desertorum* (after Koller, 1963).

<table>
<thead>
<tr>
<th>Temperature °C</th>
<th>L</th>
<th>D</th>
</tr>
</thead>
<tbody>
<tr>
<td>15</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>20</td>
<td>2</td>
<td>1</td>
</tr>
<tr>
<td>25</td>
<td>60</td>
<td>10</td>
</tr>
<tr>
<td>30</td>
<td>64</td>
<td>3</td>
</tr>
</tbody>
</table>

When the seeds were pre-treated with sub-optimal temperatures of 15° and 20°C in D or L and then transferred to 30°C in L the pre-treatment in D did not affect the subsequent high germination in 30°C L, whereas the pre-treatment with sub-optimal temperatures in L inhibited germination under subsequent optimal conditions.
Pre-treatment at 10°C, whether in L or D, did not inhibit later germination at 30°C (Table 5).

This case is quite interesting as it shows that light which promotes germination at higher temperatures blocks the promoting light effect if applied as a pre-treatment at sub-optimal temperatures. These same temperatures, when applied in darkness, do not affect later germination at optimal temperatures.

**Table 5. Germination percentages of seeds of *Hyoscyamus desertorum* at 30°C in light after having been pretreated for 16 days at various temperatures in darkness (D) and continuous light (L) (after Koller, 1963).**

<table>
<thead>
<tr>
<th>Pretreatment</th>
<th>Germ. %</th>
</tr>
</thead>
<tbody>
<tr>
<td>1–7°C L</td>
<td>56</td>
</tr>
<tr>
<td>1–7°C D</td>
<td>48</td>
</tr>
<tr>
<td>15°C L</td>
<td>9</td>
</tr>
<tr>
<td>15°C D</td>
<td>54</td>
</tr>
<tr>
<td>20°C L</td>
<td>17</td>
</tr>
<tr>
<td>20°C D</td>
<td>68</td>
</tr>
<tr>
<td>—</td>
<td>62</td>
</tr>
</tbody>
</table>

If we disregard the influence which temperature exerts on those physiological events leading to germination which are initiated by the photoreaction and are, as biochemical processes, temperature dependent, it is obvious from the few examples given that temperature interacts with light in various ways and affects the high- and low-energy photomechanisms differently. But the main questions which we must ask in each case and mostly cannot answer with certainty are:

(a) Does temperature affect the pigment system or systems directly influencing their equilibrium?

(b) Does temperature act in converting a pigment precursor to an active pigment?

(c) Does temperature change the direction of the chain of physiological events leading to germination causing it to by-pass the photoreaction?

(d) Does temperature push the biochemical–physiological events directly initiated by the photoreaction into a different direction?
4. Coats and light effect

In many cases coats (hulls, fruit or seedcoats, endosperm) enveloping the embryo enforce upon it germination control by light and temperature limiting germination conditions to a quite narrow range of temperatures in co-operation with certain conditions of illumination. When the embryos are freed of their coats these controls are to a great extent eliminated (Table 6).

**Table 6. Germination percentages of seeds and embryos of Bidens radiata at various temperatures (°C) in darkness (D) and light (L) (after Rollin, 1963b).**

<table>
<thead>
<tr>
<th>Temperature</th>
<th>10</th>
<th>15</th>
<th>24</th>
<th>25</th>
<th>26</th>
<th>28</th>
<th>30</th>
<th>33</th>
<th>35</th>
<th>37</th>
<th>39</th>
</tr>
</thead>
<tbody>
<tr>
<td>Seeds L</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>95</td>
<td>100</td>
<td>100</td>
<td>100</td>
<td>100</td>
<td>70</td>
<td>40</td>
<td>0</td>
</tr>
<tr>
<td>Seeds D</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>10</td>
<td>52</td>
<td>80</td>
<td>100</td>
<td>100</td>
<td>79</td>
<td>45</td>
<td>7</td>
</tr>
<tr>
<td>Embryos L</td>
<td>100</td>
<td>100</td>
<td>—</td>
<td>100</td>
<td>—</td>
<td>—</td>
<td>100</td>
<td>—</td>
<td>64</td>
<td>27</td>
<td>0</td>
</tr>
<tr>
<td>Embryos D</td>
<td>100</td>
<td>100</td>
<td>—</td>
<td>100</td>
<td>—</td>
<td>—</td>
<td>100</td>
<td>—</td>
<td>70</td>
<td>39</td>
<td>0</td>
</tr>
</tbody>
</table>

The morphological nature of the coats can be quite different. In lettuce seeds the restricting envelope is the membrane-like endosperm consisting of two cell layers (Evenari and Neumann, 1952). This is proved by decoating experiments and by deuteron irradiation (Klein and Preiss, 1958a) which penetrates to the endosperm but not to the embryo and has the same effect as decoating. As deuteron radiation is generally destructive, it may be assumed that it influences germination by removing the restricting influence of the endosperm.

The achenes of Bidens tripartita (Rollin, 1956) possess a fruit coat which restricts germination in L and D at constant temperatures, apparently because of its impermeability to oxygen. The seed coat contains a germination inhibitor. Its inhibiting action is overcome by light. The coats of the dispersal unit of Betula pubescens and B. verrucosa restrict likewise germination. This is explained by the authors (Black, 1956; Black and Wareing, 1959) by supposing that the coats contain a germination inhibitor and at the same time restrict the oxygen supply to the embryo. The inhibitor increases the oxygen requirement of the embryo. In the unchilled dispersal units the germination block imposed directly and indirectly by the coats through their inhibitor content and partial impermeability to oxygen is overcome by light.
Experiments with lettuce seeds 'Grand Rapids' suggest to their authors (Ikuma and Thiman, 1963) that the endosperm membrane restricts germination mechanically by not enabling the root tip to penetrate it. The photomechanism, in their opinion, activates an enzyme 'whose action enables the tip of the radicle to penetrate through the coat', probably by its cellulytic orpectolytic activity. If this is true, all the agents (high temperatures, prolonged FR, certain concentrations of coumarin etc.) which inhibit germination of the whole achene or the embryo surrounded by the endosperm membrane but do not impede growth of the isolated embryo, would directly or indirectly prevent formation or activation of the enzyme. It will be an important task of future research to clear up this point.

5. The site of photosensitivity
Although the endosperm imposed germination restriction of lettuce seed 'Grand Rapids' are overcome by the low-energy photomechanism, the endosperm is not the seat of photosensitivity. The proof lies inter alia in the following experiment: Achenes, irradiated on one side with R and then on the other side with FR, reacted no differently to seeds irradiated with both radiations on the same side, one being given after the other (Klein and Preiss, 1958b).

Cutting experiments and shading of different parts of the seed (Ikuma and Thimann, 1963) have made it probable that the hypocotyl end of the embryo is the site where the seed’s photosensitivity is located. It is also probable that in other photoblastic seeds the embryo is the photosensitive site (see Evenari, 1956, 1964).

6. Environment during ripening and its influence on photoblastism
There are very few data in the literature concerning the influence of photoenvironment during the ripening of the seeds, when they are still on the mother plant, upon their germinability later on (Lona, 1947; Jacques, 1957; Heslop-Harrison, 1959; Koller, 1962). But apparently this influence is quite strong. I would like to demonstrate this in the case of Diplotaxis Harra.

Diplotaxis is an annual-biannual desert plant of the Negev Highland. We collected seeds near our desert research station at Avdat in 1960 and 1962, and in 1962 grew plants from these seeds in the experimental plot of our Department in Jerusalem. In April 1962 seeds were collected from these plants. The germinability of seeds of the
Avdat and Jerusalem stocks was very different. We will refer here only to the main differences concerning their photoblastism.

Both stocks are positively photoblastic and light requiring in their germination. But, whereas at 26°C the Avdat (1960 and 1962) seeds need continuous light or at least an 8-h light period for full germination (continuous W of an intensity of 6–800 ft-cd causes full germination, 1/64 ft-cd already stimulates, R works like W) and a short illumination has no or very little effect, the Jerusalem (1962) seeds are already stimulated by 1 sec of W (280 ft-cd) and 2 mins brings them to full germination. Short R has the same effect.

Another difference between the two stocks is that after 5 days of dark imbibition the Avdat seeds enter complete dark dormancy which is not broken by continuous light, whereas the Jerusalem seeds are only part dormant after the same treatment. We did not know what was the reason for this different germination behaviour until we carried out the following experiment.

Table 7. Germination percentages of various stocks of seeds of *Diplotaxis Harra*. The light source was a fluorescent bulb. The experiment was carried out at 26°C in February 1964 (after Evenari, original).

<table>
<thead>
<tr>
<th>Germination conditions</th>
<th>Avdat 1960</th>
<th>Jerusalem 1962</th>
<th>Long day</th>
<th>Short day</th>
</tr>
</thead>
<tbody>
<tr>
<td>Continuous white light</td>
<td>60</td>
<td>92</td>
<td>95</td>
<td>99</td>
</tr>
<tr>
<td>Darkness</td>
<td>0</td>
<td>2</td>
<td>0</td>
<td>2</td>
</tr>
<tr>
<td>30 min white light starting with imbibition</td>
<td>6</td>
<td>74</td>
<td>5</td>
<td>50</td>
</tr>
<tr>
<td>Continuous white light after 5 days in darkness</td>
<td>1</td>
<td>22</td>
<td>14</td>
<td>47</td>
</tr>
</tbody>
</table>

We grew *Diplotaxis* from 1960 seeds in Jerusalem during the 1963–4 growing season in the experimental fields of the department, under long days (20 h of daily light) and short days (8 h of daily light). When we tested the photoblastism of the seeds collected from short- and long-day plants it was seen that the long-day seeds reacted more or less like the Avdat seeds and the short-day ones like the Jerusalem seeds (Table 7). This proves that the photoenvironment under which the seeds ripen is one of the factors which determine their photoblastism decisively.
In this case, as in similar ones studied by other authors, the history of the seeds, that is the environment through which they passed during ontogenesis on the mother plant, determines their physiological reactions later on. It would be worth while to find out how far other photomorphogenic phenomena are influenced by the same 'historical' factor.

Another interesting question arises in connection with this problem. Is the germination of the seeds only affected by the environment during seed maturation or does the environment of the mother plant before fertilization also influence the seed's germinability? We are now investigating this question.

B. Negative photoblastic reactions

Although the sign of photoblastism is a function of temperature, energy and spectral composition of light, it is still practical to divide the photoblastic dispersal units, according to their preponderant reaction to white light, into positively and negatively photoblastic ones.

1. Light action in various spectral regions and temperature effect

The germination of the seeds of *Phacelia tanacetifolia* (Rollin, 1963b) is, at 22°C, inhibited by W as long as the seeds are exposed to light. When transferred from W to D after 12 h the seeds germinate fully—after 48 h about 50 per cent, and after 7 days about 12 per cent still germinate. R inhibits germination during the first hours of imbibition. A maximum of sensitivity is reached during the second to third hour. When, after prolonged irradiation the seeds are transferred to D, germination takes place.

FR (710 nm) and B (two peaks, one at 448 the other at 508 nm) inhibit germination, but only when applied during the seventh to fifteenth hour after the start of imbibition. These wavelengths, too, inhibit only as long as the seeds are irradiated. Recent work in our department by Richter has shown that green (514 nm) also inhibits germination. The seeds are much more sensitive to FR in comparison with B as 3·3 μw/cm² are necessary to produce 50 per cent inhibition in FR and 30 μw/cm² in B. Obviously the pigment or pigments involved must be continuously excited in order to block germination. In D they revert to their initial state, freeing the pathway to germination.

The fact that the time-tables for the R inhibition, on the one hand,
and the FR-B inhibition, on the other, differ so much seems to show that we deal here, as in the case of the positively photoblastic seeds, with two different processes. There are two more indications pointing to the same conclusion:

(a) The R inhibition is strongly temperature dependent. At temperatures lower than 10°C, R ceases to inhibit. FR and B inhibition is temperature independent, as even at 5°C the seeds are still inhibited to about 70 per cent.

(b) R ceases to inhibit at low oxygen tensions whereas FR and B inhibition is independent of oxygen tension as, in an atmosphere containing 1 per cent O₂, FR germination is 12 per cent, D germination 69 per cent and R germination 68 per cent. The question arises if, in Phacelia, the reversible R–FR photomechanism is present. Besides the fact that the wavelength of the inhibiting R is the same as for the promoting R in positively photoblastic seeds, one experiment of ROLLIN (1963b) indicates that this system is active. When Phacelia seeds are irradiated with continuous light of a 600–800 nm wavelength (containing, therefore, R and FR) germination is less inhibited than by R and FR alone. ‘Il semble qu’indépendamment de son action inhibitrice la lumière rouge sombre puisse diminuer l’effet de la lumière rouge clair.’ But SCHULZ and KLEIN (1963) come to the conclusion that the phytochrome system does not exist in Phacelia. This is based on the following facts:

(1) In addition to R, FR and B, near u.v. (320–425 nm) and far u.v. (254 nm) also inhibit germination.

(2) R and B and R and FR, when given simultaneously, inhibit synergistically.

The question of the pigment or pigments involved therefore remains open.

The germination of the negatively photoblastic seeds of Nemophila insignis is also inhibited by R, FR and B at temperatures higher than 20°C, and the photoblastism of this species seems mutatis mutandis to be similar to that of Phacelia (ROLLIN, 1963b).

The germination of the decoated seeds (i.e. embryos enclosed in their intact inner seed membrane after the removal of the hard outer part of the testa) of Citrullus colocynthis is inhibited by continuous W at temperatures below 25°C (KOLLER et al, 1963). Intensities as low
as 2 ft-cd are effective. Above 25°C the decoated seeds germinate equally well in D and L. B seems to be the most inhibiting spectral region.

2. Coat effects and site of photosensitivity

When seeds of *Phacelia* are exposed to light and then seed coat and endosperm cut off in different places they germinate fully even after 5 days in light, provided the seed coat was removed at the radicular end of the embryo. Cutting off seed coat and endosperm at the cotyledonary end has a weak influence; removal of the seed coat at other places has no effect at all on germination (ROLLIN, 1963b). High oxygen tensions lead to germination of the intact seeds in continuous W.

In *Citrullus* the removal of the inner seed membrane removes photo-inhibition; but the growth of the naked embryo is greatly reduced by continuous W (KOLLER et al, 1963).

In repeating an old experiment of GASSNER, BÖHMER and EVENARI (cited in EVENARI 1956) the authors found that they could duplicate the coat effect by enclosing the naked embryo in moist filter paper. Its germination was then inhibited in W but not in D. Shading and light spotting of various parts of the seeds proved that the radicular end of the embryo was the site of light perception. The same was shown for the negatively photoblastic dispersal units of *Calligonum comosum* (KOLLER, 1956).

In summing up the question of the site of sensitivity to light in positively and negatively photoblastic seeds we may say that all the evidence points to the radicular part of the embryo and not the seed coat as the seat of photoperception.

The problem of the function of the coats, however, is not solved. It may be that the theory of IKUMA and THIMANN fits the case of lettuce seeds. But is it applicable to other cases as, for example, *Citrullus* or *Phacelia*? Could it explain the fact that wet filter paper, which does not offer any mechanical resistance, can play the role of the coats?

Is the function of the coats—at least in some cases—best explained by assuming that they affect the exchange of gases or/and the need of the embryo for oxygen? In cases like that of *Citrullus*, where W restricts even the growth of the naked embryo, is there not an additional factor involved?

We are left with many questions and feel that here is an area which needs a new approach with modern methods.
C. Ecological implications of photoblastism

It is one of the tasks of photobiology, when dealing with the natural photoenvironment, to assess the survival value of the photomorphogenic processes involved. We therefore will now consider in what way photoblastism as a mechanism controlling germination affects the ecological behaviour of plants. This can be done by restricting germination to:

1. Certain soil types;
2. Certain amounts of rainfall;
3. Certain densities of covering vegetation;
4. Certain depths of the germination medium;
5. Certain osmotic potentials of soils.

Germination controlling mechanisms affect plant life under natural conditions in still another way. When the positively photoblastic lettuce seeds are germinated at 27°C in darkness a certain percentage will germinate. They are those which have 'escaped' light control. The percentage of these dark germinators changes with after-ripening, storage conditions etc. The same is true for most other positively or negatively photoblastic seeds where a certain percentage will always germinate under light conditions adverse to the germination of the majority. This means that in a given population of seeds the individual seeds are in different physiological stages or, we may say, indifferent stages of dormancy and—to state it in exaggerated terms—the optimal constellations of external conditions needed for germination differs for each. As there are many germination controlling mechanisms besides photoblastism, for which this is true, the variety of conditions under which some of the seeds out of a given population will germinate is great. This is the main reason why seeds of wild plants never germinate uniformly and why their germination under natural conditions is spread over many years, as in each year only a certain percentage meets appropriate germination conditions. The manifoldness of germination conditions thus created raises the probability of survival. There is an indirect proof for this statement.

The dispersal units of the oldest cultivated plants like wheat and barley are not light-requiring and germinate uniformly, because man has, by unconscious selection, removed most of their germination controlling systems, as, for example, photoblastism. The wild species
like *Triticum dicoccoides* and *Hordeum spontaneum* still possess these mechanisms. Their loss is apparently one of the reasons why the cultivated cereals are unable to survive and quickly disappear when left to themselves (Koller, 1964).

We will discuss here only some specific cases where the survival value of photoblastism can be demonstrated. *Juncus maritimus* var. 'arabicus' grows in the Negev desert on banks of brackish puddles and swamps. As its seeds are absolute light requirers over a broad range of temperatures they can neither germinate in too deep a layer of water nor under a dense cover of vegetation, a fact which restricts them to their typical habitat (Tadmor et al., 1958). *Calligonum comosum* grows on coarse sand and gravel along wadi beds of the Negev desert and on sand and gravel fields of the Wadi Araba, where water conditions on the surface are very bad even directly after a heavy rain. The seeds of this species are negatively photoblastic at all temperatures tested (Koller, 1956). This restricts their germination to a certain depth below the soil surface, where light does not reach the seeds any more.

*Salsola volkensii* is one of the very few summer growing desert annuals. It is a ruderal plant as its habitat is freshly disturbed soils where the 'normal' winter vegetation is destroyed and where, therefore, there is no competition with other plants for water (Negbi and Evenari, 1962). The moment the habitat is settled with other plants, *Salsola* disappears. *Salsola* is characterized by a curious kind of heterocarpy. It possesses dispersal units with green chlorophyllous and with yellow achnorphyllous embryos. 'Green' fruits are aphotoblastic and germinate in light and darkness over a very wide range of temperatures. Their germinability is already high directly after harvesting and they do not need any period of after-ripening; but they lose their germinability and viability very fast. The yellow fruits, on the other hand, germinate very badly after harvesting, and this only over a very narrow temperature range, are positively photoblastic under all germination conditions, have a protracted after-ripening period and do not lose their germinability with up to 5 years of storage but rather increase it with age.

The aphotoblastic green fruits are the ones which germinate in the field immediately after they fall off the mother plant with the first rain. They germinate when covered by the litter of the mother plant as they do not require light for germination. The yellow fruit do not germinate during the first year and will, for lack of light, not germinate when the formerly disturbed soil is occupied by other winter growing vegetation
or when covered by soil. They start germination immediately, even after several years, when the soil is again disturbed and the fruits are brought to light (Negebi and Evenari, 1962; Negebi and Tamari, 1963).

We mention briefly only one more case where the photoblastism of seeds has ecological importance. The seeds of various species of Chenopodium germinate better in light with an R:FR ratio similar to that of sunlight than in light with an R:FR ratio typical for sunlight which has passed through green vegetation. This, apparently, is a factor-limiting germination in the shade of other plants and causes full germination in habitats without shade, especially as the limiting influence of low versus high R:FR ratios is apparent over a wide range of energies and photoperiods as 'the restrictive influence of low as compared with high R:FR ratios was obtained over a wide range of energies and with different photoperiods' (Cumming, 1963).

V. PHOTOMORPHOSES

We will deal here with only one of the many interesting effects of light on anatomical structure, that is sun and shade leaves.

It has been known for a long time that the size, shape and anatomical structure of tree leaves exposed to the sun and of those growing in shade is very different. Sun leaves are mostly smaller, more deeply lobed, more hairy, have shorter petioles and are more densely veined, are thicker in cross section and have a more differentiated mesophyll with well developed palisade cells, which in extreme cases of shade leaves are missing altogether. Leaf epidermis cells and stomata are mostly smaller and more numerous per unit. In sun leaves the anticlinol walls of the epidermis cells are mostly straight, in shade leaves they are convolute (Schramm, 1912; Penfound, 1931; Schröder, 1938; Wylie, 1951; Anderson, 1955; Cormack, 1955; Talbert and Holch, 1957; Stalfelt, 1956; Hughes, 1959).

Many authors regard the sun leaves as xeromorphic and the shade leaves as mesomorphic or even hygromorphic. The differences between sun and shade leaves are not due to differences in the development of the leaf primordia as this is the same for sun and shade leaves (Thomson and Miller, 1962, see also Blackman, 1961). At a relatively late stage the further differentiation of the shade leaves is inhibited. They could therefore be regarded as immature sun leaves.

Cell division, cell expansion and cell differentiation are involved, but to varying degrees as the differences in cell division are less
pronounced than those concerning elongation, expansion and differentiation (Watson, 1942; Isanogle, 1944; Maksymowych, 1963).

Shading experiments carried out by many authors (Penfound, 1931; Wassink et al, 1956; Hughes, 1959; Pieters, 1960; Wassink, 1960; and others) have shown that the main parameter responsible for the different structures of sun and shade leaves is light intensity. But this does not exclude other contributing factors such as temperature, relative humidity of the air etc.

We do not know by what mechanism light intensity produces the anatomical-morphological changes in the leaves. Does the osmotic potential change under the influence of the various light intensities as has been proposed by some authors? To what degree are growth hormones involved?

We also do not know if the main causal agent is the total energy flux of white light or only the light intensity in certain spectral regions contained in white light. Is, perhaps, the ubiquitous R–FR mechanism involved, at least in that phase which leads to differences in lateral expansion and different sizes of leaf blades without a change in the amount of dry matter (Hughes, 1959)?

There is another interesting facet to our problem. How does the same light intensity, which in sun leaves inhibits the expansion of the epidermal cells in the periclinal direction, stimulate the growth of the palisade cells in the anticlinal direction?

As there are no answers to our questions we can only underwrite the statement of Hughes (1959): 'It is surprising how little information is available... on a subject so fundamental as the basic understanding of leaf morphogenesis.'

It would be most beneficial to gather together the missing information, not only because we need to know more about the aetiology of leaf morphogenesis but for the following reasons as well:

(1) The problem of sun and shade leaves touches upon another of the vast unanswered questions of biology (i.e. the aetiology of xeromorphism).

(2) Sun and shade leaves differ in their physiological activities such as transpiration (Maximov, 1929; Stalfelt, 1956) and photosynthesis. It has been shown for photosynthesis that sun leaves, for example, have higher maximum rates of photosynthesis than shade leaves (Pieters, 1960) and that in shading experiments the net assimilation rate (g/cm²/day) increases and the chlorophyll content per cm² decreases with increasing light intensities (Wassink
et al, 1956; WASSINK, 1960). These facts have great ecological importance as adaptations to changing environmental conditions. As in this case, environment, structure and function are most clearly interconnected, it would be a classical example for an investigation into the causal chain linking the three together.

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