Zeitschrift: Berichte der Schweizerischen Botanischen Gesellschaft = Bulletin de la Société Botanique Suisse

Herausgeber: Schweizerische Botanische Gesellschaft

Band: 46 (1936)

Artikel: The light climate of Woodlands

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DOI: https://doi.org/10.5169/seals-31048

The Light climate of Woodlands.

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Eingegangen am 3. November 1935.

The problem of light efficiency as it affects plant life has naturally been the subject of repeated enquiry and Professor Rübel has been one of those who have contributed notably to our knowledge of this subject.

The difficulty that has however always been encountered concerns the technique of light estimation. The methods that have been generally adopted have measured the photochemical rays regardless of the value which they have for photosynthetic activity. The chief asset of the earlier investigations is that the methods employed facilitated the integration of the available radiant energy over an appreciable period of time, a matter of some importance in view of the changing intensities within a plant community even when the external illumination is approximately constant. The movement of sun-flecks with the changing position relative to the incidence of the suns rays; the differing permeability of a leaf canopy for light when the laminae take up new positions of equilibrium in gusts of wind, illustrate causes of variation in light intensity within a community which may diminish the value of short duration determinations as an indication of the average illumination available for photosynthesis. In this connection it is worth recalling the experiments of Warburg which shewed that intermittent illumination was more effective than continuous illumination.

The prime need of the ecologist has always been a method for estimating light intensity that would yield quantitative data proportional to the actual value of the light for photosynthesis. The modern photo-electric cells have provided a much nearer approach to this ideal and those of the rectifier type have the added advantages of convenience and portability. We owe much to the work of Dr. Atkins of Plymouth for his investigations on the physical aspects of the use of the various types of photo-electric cells.

In the data embodied in this paper two types of photo-electric recorders have been employed namely Cuprite cells and Selenium cells. Of several Cuprite cells tested one was found to be far superior than the others in respect to light of photosynthetic significance. As a diaphragm was always employed with these cuprite cells the reversal phenomenon, which Atkins has shewn to be due to a marginal effect, was minimised.

Each type of instrument, and indeed even different instruments of the same type, has its own characteristic departure from the ideal physical linear relation between light intensity and illumination as indicated by the application of the law of inverse squares.

The investigations of Wolkoff, Reinke, Pantanelli and others have shewn that at lower light intensities the rate of photo-

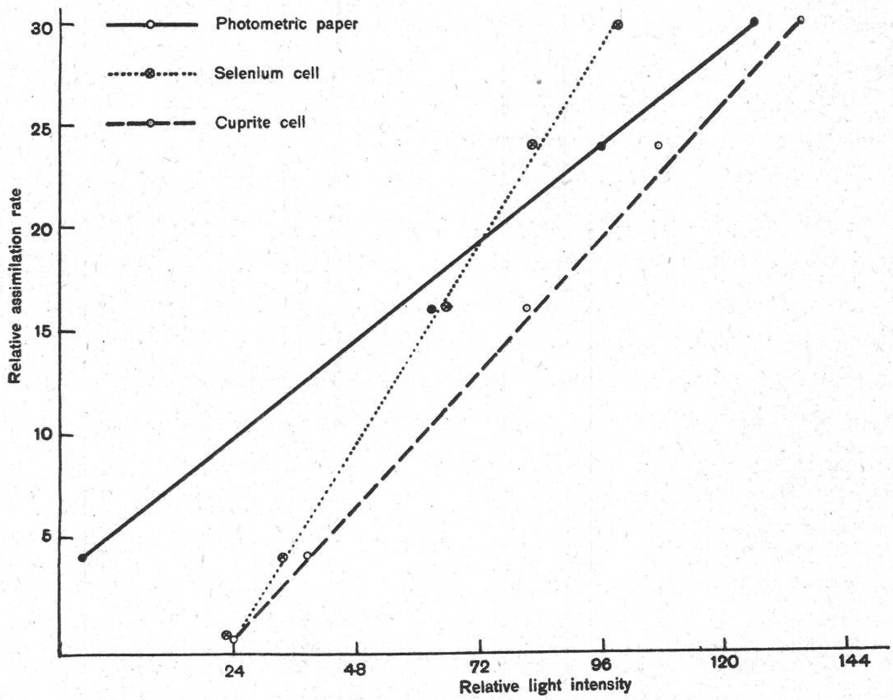

Fig. 1.
Correlation between assimilation rate of Elodea canadensis and light intensity as measured by three different methods.

synthesis is approximately proportional to the intensity of the light though at the higher intensities the departure is often marked and may be said to depend mainly as regards its magnitude upon the ecological status of the plant involved. The departure of the plant on the one hand from the ideal relation between photosynthetic activity and light intensity and on the other the departure of our recording instruments from a direct linear relation to the intensity of illumination, render it essential, if we are to assess the ecological significance of our estimations, that we should obtain some direct knowledge of the relation between intensity as recorded by our instruments and the actual rate of photosynthesis.

For this purpose both the Cuprite and Selenium cells employed were simultaneously used to estimate the light intensities at varying distances from an open window and under diverse conditions of natural illumination. Simultaneously with each light intensity determination the rate of assimilation was estimated by the bubble-counting method employing a variety of aquatic plants. In making these determinations I am indebted for help to my colleague Dr. P. Haas.

As the graphs shew, there is for the medium intensities of light, in which the ecologist is usually the most interested, an almost linear relation between the light values as recorded by these methods and the

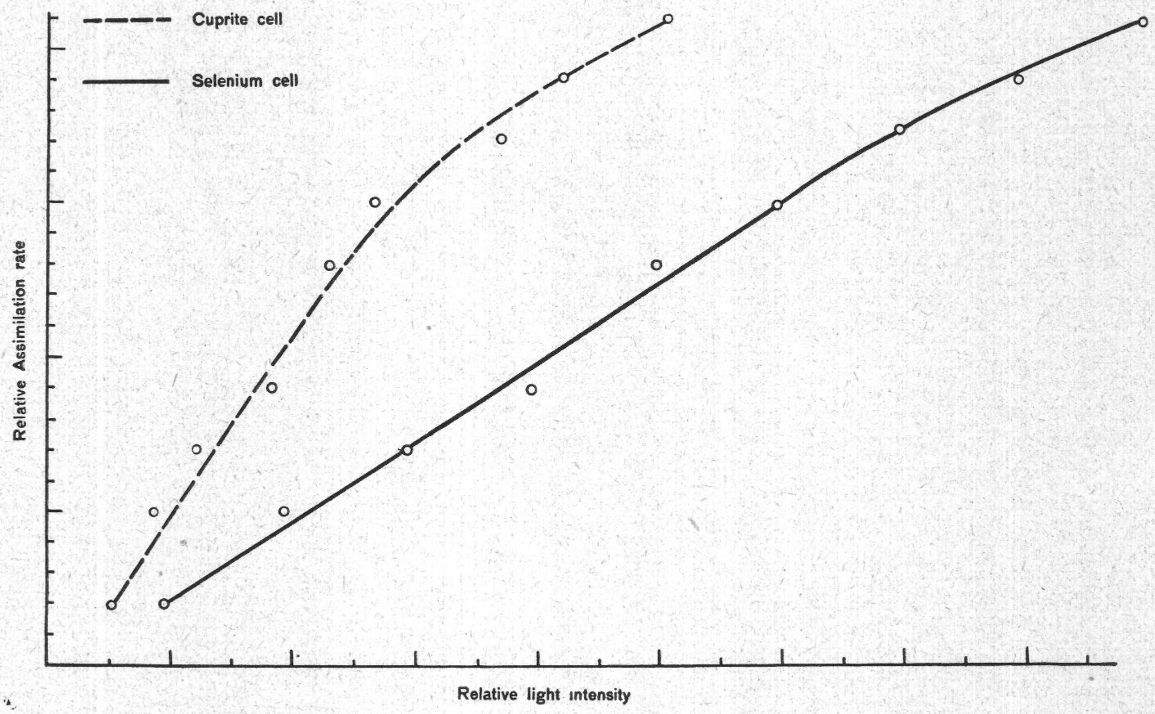

Fig. 2.

Relation between light intensity and assimilation rate of Elodea canadensis in artificial illumination.

rate of photosynthetic activity. Only at very high and very low values is there a marked departure from this relation. It may therefore be assumed that the readings obtained by these methods in the field furnish a reasonably close approximation to the proportionality in respect to photosynthetic efficiency. Even if apparatus were available that gave a linear relation to light intensity throughout the natural range of illumination the limiting character of other factors than light at the higher intensities, and the relation between photosynthesis and respiration at the lower, would render difficult the task of interpretation towards the extremes.

Since many of the earlier investigations, including my own observations in woodlands, were made with the use of photosensitive paper, it is a matter of no little interest to learn to what extent such determinations correspond with values obtained by the more reliable photoelectric methods. The data presented in Fig. 1 which is one of a number of determinations of this character shews the relative rates of photosynthesis of *Elodea canadensis* plotted against the relative light intensities as determined by (a) a Selenium Cell, (b) a Cuprite Cell, (d) Photometric paper. It should be noted that in this diagram no attempt has been made to equate the values obtained by the different methods. In the following Table I intensities by the three methods have

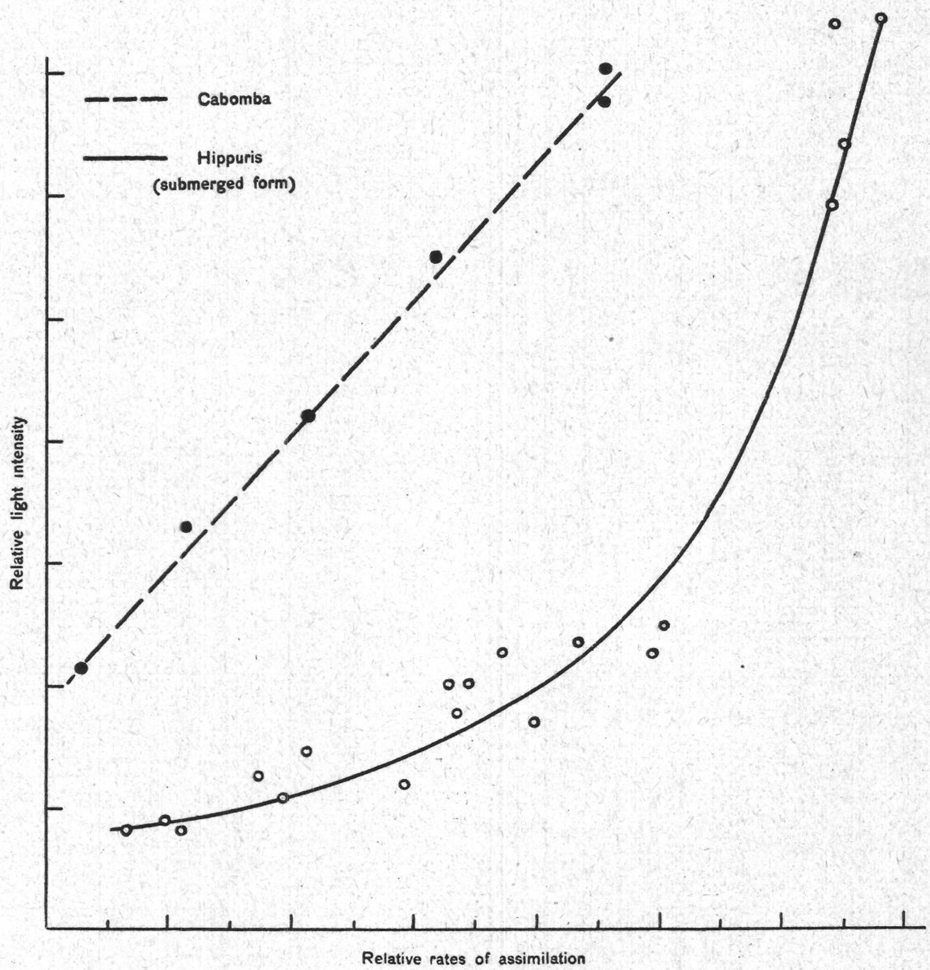

Fig. 3.

Curves illustrating value of light intensity determinations as measures of photosynthetic efficiency of light.

been equated to the same scale of units for light intensities ranging from about 1/30 th. of full sunlight to 1/6 full sunlight.

It is evident from the figures cited that the selected Cuprite cell and the Selenium cell give closely parallel values for the light intensity whilst though the photometric paper yields data that are somewhat divergent from those obtained by the other methods yet the approximation is sufficiently close to warrant our regarding the general conclusions based on photo-sensitive paper as in general terms valid though requiring modification in detail.

Estimations with photo-sensitive paper have the disadvantage that not only are the results mainly dependent upon the shorter wave lengths but accurate determinations demand considerable experience and skill in the matching of tone values. Still, despite these drawbacks, the method is useful for medium and low intensities when a high degree of accuracy is not essential. In low light intensities in wood-

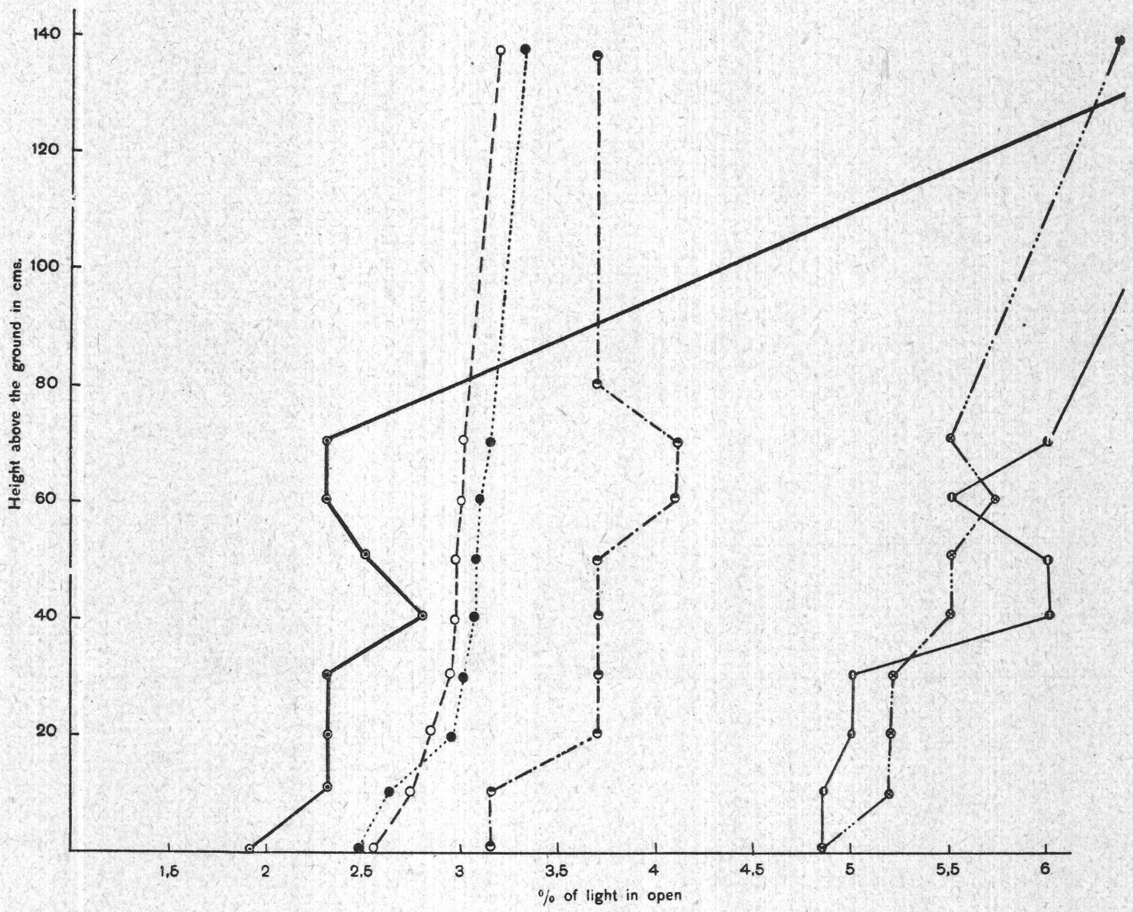

Fig. 4.

Light intensity gradients in Fagetum, Shade Phase, at 6 different locations (Light intensity in open = 14,400 Int. Lux.)

Table I.

Comparative values obtained by different methods of estimation for light intensities.

Intensity by Selenium Cell (S)	Intensity by Cuprite Cell (C)	Intensity by Photometric paper (P)	(S—C)	(S—P)
44	38	40	+ 6 (13,6 %)	+ 4 (9 %)
70	83	45	—13 (19 %)	+25 (35 %)
110	120	117	—10 (9 %)	— 7 (6 %)
283	250	248	+33 (12 %)	+35 (12 %)
356	375	352	—19 (5 %)	+ 4 (1,4 %)
409	395	476	+14 (3 %)	—67 (16 %)
450	462	523	—12 (2,6 %)	—73 (16 %)
500	504	583	— 4 (0,8 %)	—83 (16 %)

lands where the time required for darkening is very prolonged the result is an integration of the intensities over a period which cannot be obtained with anything like the same facility by means of photo-electric determinations. On the other hand the practicability of almost simultaneous estimations by the photo-electric method, inside and outside a woodland is perhaps of even greater importance than the

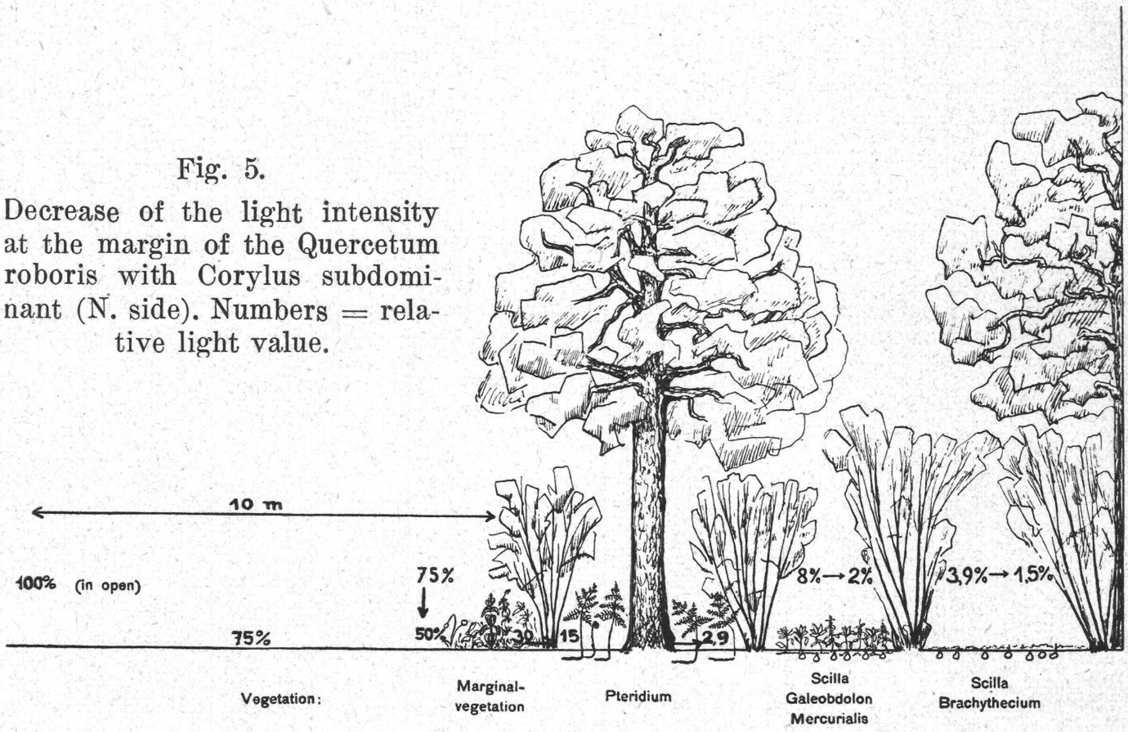

Fig. 5.
Decrease of the light intensity at the margin of the Quercetum roboris with Corylus subdominant (N. side). Numbers = relative light value.

increased sensitivity since, owing to the necessarily variable character of natural illumination, it is most convenient to express the habitat illuminations as percentages of the maximum in the open. The ease with which large numbers of readings can be obtained in a comparatively short time at numerous spots enables one to estimate average values that are probably of much greater significance than integrations from only a few situations.

The curves presented in Figures 3 and 4 shew that an approximately linear relation holds between light intensity as estimated by these methods and assimilation in various species, though there is a notable departure at the higher intensities as might be expected when using as experimental material the submerged form of *Hippuris* which came from a habitat of very low illumination. It is of course true that the submerged aquatics employed are all more or less shade plants but it is perhaps significant that the tropical *Cabomba* shewed a linear relation up to moderately high intensities. It is therefore not improbable that so far as the medium intensities are concerned the data obtained by these methods do approximate to the photosynthetic efficiency values of the light for woodland species.

As a rough approximation we may assume that sun plants can benefit appreciably by increasing intensities of light up to one third or even a half of that in the open in bright sunlight whilst shade plants will probably benefit by intensities up to from 10 % to 20 %. Light

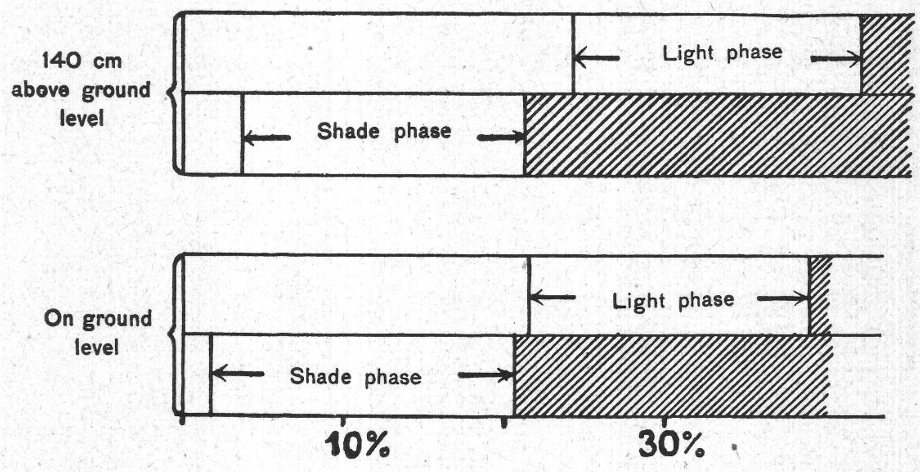

Fig. 6.
Relative light intensity in Fagetum.

intensities over 50 % will have therefore little differential effect upon species of the woodland margin except in so far as high intensities may be more deleterious to the chlorophyll of one species than another. For the extreme shade flora increase of light above 10 % of that in the open will probably not materially increase the rate of assimilation.

In comparing the light intensities during the "light phase" and "shade phase" of a woodland it is important to remember that the average outside value during the period when the trees and shrubs are devoid of foliage ("light phase") is for the deciduous forest zone about 0.6 of that during the "shade phase" so that an increase of light intensity up to from 17 % to 30 % of that in the open may have a significant influence on the rate of assimilation of the shade species during the "light phase" whilst intensities up to from 50 % to 80 % may augment the photosynthesis of sun species during the same period.

As, however, the above approximations are only broad generalisations and the light intensity in full sunlight changes appreciably throughout the "light phase" it is probably best to present the illumination in woodland habitats in terms of the extent to which the potential illumination is reduced. In other words as a percentage of the intensity in the open, remembering that the absolute intensity which such a percentage represents varies with the season.

It must also be remembered that the CO_2concentration in a woodland atmosphere may be appreciably higher than in the open thus rendering the utilisation of a higher intensity of light possible than could be profitably employed by the plant in a normal atmosphere. On the other hand during the light phase the low temperature may often reduce the maximum illumination that can be profitably utilised though as

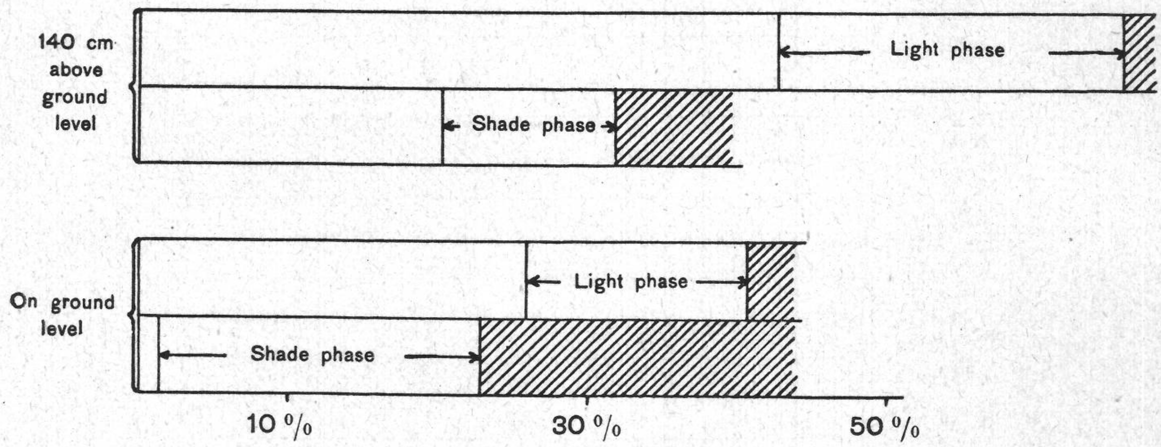

Fig. 7.
Relative light intensities in Quercetum roboris. L. P. = Light phase, S. P. = Shade phase.

F i r b a s has shewn the dark humus layer may absorb sufficient heat from direct sunshine to raise the woodland air temperature above that in the open.

In the accompanying diagrams (Figs. 5 and 6) the light intensities for four types of woodland community are presented for both the "light phase" and "shade phase" of each. The determinations on which the diagrams are based were made with photo-electric cells in the same spots during each phase. The woodland types were all adjacent to one another so that it was possible to obtain data from each on the same day under comparable lighting conditions.

The first point to emphasise is the nature of the illumination gradient as one passes upwards from the ground level. The gradients at six locations in a Fagetum are illustrated in Fig. 4. In all the locations selected there is, as might be anticipated, a general trend towards an increasing intensity from below upwards but the presence of gaps in the continuity of the foliar canopy results in irregularities. The two more regular gradients are typical of the general condition and it will be seen that the intensity becomes increased by about 1/5 at 25 cms. For a number of locations in a Fagetum during the shade phase the average increase at 20 cms. was about 7 % in excess of that at the ground level. But in areas where the ground flora was appreciably developed the increase with height was usually greater.

It is then evident that the height at which a species normally develops its foliage is not merely important in determining the degree to which it will shade, or be shaded by, others, but is of direct significance in affecting the rate of assimilation even in the absence of competition. The more irregular curves are typital of the conditions nearer the woodland margin and near light gaps where oblique illumination

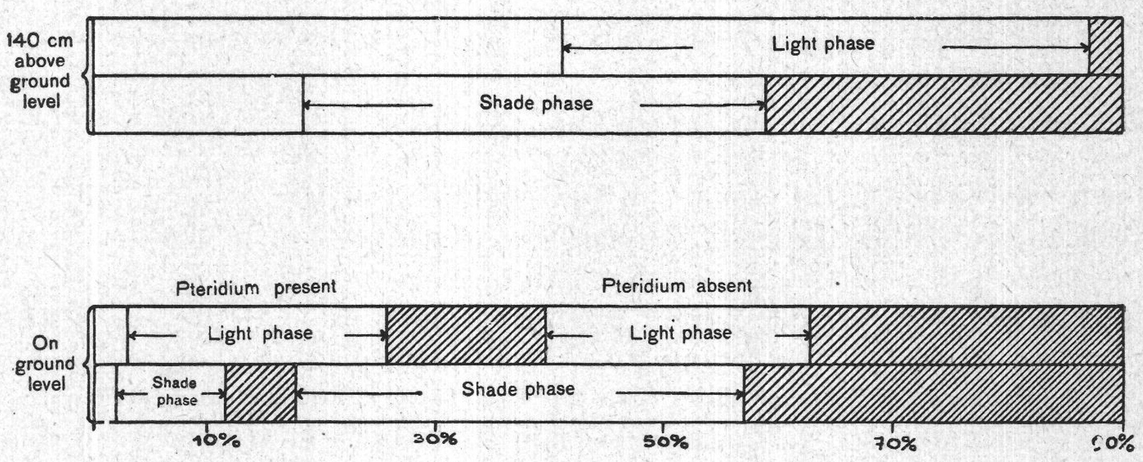

Fig. 8.

Relative light intensities in Betuletum. L. P. = Light phase. S. P. = Shade phase.

plays an appreciable role. The diagram in Fig. 5 illustrates the horizontal gradient of intensity at the woodland margin as exemplified on the northern edge where it tends to be most pronounced.

In Figs. 6 and 7 the light values in the two phases are represented both for the ground level and for a height of 140 cms. above the woodland floor. It is clear that the gradients vary in the different types. The least marked is that of the Fagetum in the "shade phase" just considered. In all types the gradient is most marked in the light phase so that differences in height of species may be expected to play a more important role in regard to winter-green and prevernal vegetation than in summer-green types.

In the Betuletum the intensity even in the shade phase is seen to be, over a considerable part of the range presented, adequate for marginal and sun species. But here the presence of *Pteridium* imposes a low light intensity, through the persistent fronds, even during the light phase so that whereas a dense vegetation may occupy areas where the *Pteridium* is absent, in its presence only markedly shade species can persist beneath the fronds. Actually the frequent poverty of ground flora in the Betuletum is conditioned by edaphic rather than climatic factors as is shewn by the rich herbaceous vegetation that may occur in woods of this type resulting from colonisation of heavy soils by Betula, prior to the arrival of the trees casting deeper shade.

The Quercetum Roboris selected for examination was an area with a comparatively poor ground flora but even so it is noteworthy that the light intensity during the light phase at the ground level is higher than in the Fagetum. At a height of 140 cms. the lowest intensities recorded in the Quercetum were in excess of the highest at the same level in the Fagetum. This suggests that increased stature is of greater advantage in the Quercetum than in the Fagetum.

The data furnished would further appear to confirm the conclusion previously based on determinations made with photometric paper, that an important factor in determining the rich vernal and prevernal herbaceous flora of the Quercetum as compared with the Fagetum is the more favourable light climate in the "light phase".

In assessing the light climate in woodlands it is necessary to recognise the important role that sun-flecks may play in rendering a particular spot suitable for a given species. Although the sun-flecks are due to gaps in the canopy this does not mean that they represent, even temporarily, an intensity comparable to that in the open. With the object of gaining some idea as to their importance a number of determinations were made of the light intensity in sun-flecks in the interior of woodlands as compared with the surrounding shade. Days were selected when the sky was cloudless and the intensity in the open was about 14,400 lux.

Table II.

Intensities in sun flecks values in Lux.

	Shade	Sun-flecks
Oak scrub		
Nepeta dom.	194	776—1164
Mercurialis	129	1290—1612
Nepeta dom.	323—388	1612—2907
Hedera	79—108	432
Bare of Ground Flora .	194—258	582 (Sun-flecks very few)
Fagetum		
Sanicula dom.	194—452	520—2600
Mercurialis dom. . . .	127—200	520— 975

These determinations shew that the intensity in the sun-flecks attained to values ranging from 3 % to 20 % of that in the open as compared with light values of 0,5 % to 3,1 % in the surrounding shadow. Such values only apply to sunny conditions and the movement and short duration of a sun-fleck upon a particular leaf, consequent upon the changing angle of the incident light, considerably diminish their assimilatory value. Nevertheless the fact that areas bare of ground flora are not infrequently characterised by a paucity of sun-flecks, as in the example cited, although the shadow intensity around may be no lower than, or even higher than, in adjacent areas with frequent flecks and sparse ground vegetation, suggests that the increased illumination which the transitory sun-flecks provide may play an appreciable part in rendering the light-climate tolerable where the intensity is near the "compensation point".

It should be noted that the vegetation that occupies areas where the light intensity is low usually consists of evergreen or winter-green species that probably rely on the higher light intensity during the beginning and still more towards the end of the "light phase" to carry on their chief assimilatory activity. During the "shade phase" these species may perhaps be working at or below the compensation point.

The foregoing considerations with respect to the light climate in woodlands have not only shewn the fundamental quantitative differences in illumination which are encountered in the light phases and shade phases respectively of one and the same community and the striking differences of light conditions between different woodland communities, but also they demonstrate the significance of such biological features as the periods of assimilatory activity, the height of assimilating surfaces, and the importance of the spatial structure of the canopy as affecting the frequency and duration of sun-flecks.