

PHOTOSYNTHESIS IN RELATION TO LEAF ORIENTATION AND LIGHT INTERCEPTION

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Summary

This paper examines the photosynthetic response of single attached leaves (of four different species) to an increasing angle of incidence (θ) of incoming radiation. The intensity of light falling upon a leaf can be deduced from geometrical optics to be proportional to $\cos \theta$. The results reported here suggest that the photosynthetic activity of leaves exposed to a limiting light intensity follows a similar relationship. Explanations of this empirically determined relationship are discussed.

I. INTRODUCTION

The amount of light energy falling upon the foliage of a plant community is frequently the environmental factor that limits the growth rate of that community (Donald 1961). Two of the factors that influence the photosynthetic rate of individual leaves within the canopy, as Verhagen, Wilson, and Britten (1963) have pointed out, are (i) the disposition of leaves in relation to the incident light, and (ii) the optical properties of the leaves themselves. Both of these factors will influence the proportion of the incident light that is reflected, absorbed, and transmitted. The optical properties of four types of leaves have been studied experimentally by Tageeva and Brandt (1961) who indicated that for these studies recourse to the theoretical principles of geometrical optics is impossible. This is also true if the effect of angle of incidence (θ) of incoming radiation upon individual leaf photosynthetic rate is to be studied. However, Went (1958) suggested, on the basis of geometrical optics, that individual leaf photosynthetic rate would be proportional to $\cos \theta$;† and that this emphasized the advantage of large values of θ , such as frequently occur in vertically disposed foliage, when the incident light intensity was above that required to saturate the photosynthetic mechanism of a horizontally disposed leaf.

The importance of the angle of incidence of radiation falling on the leaf surfaces of a foliage has also been thoroughly examined, in a theoretical discussion, by Warren Wilson (1960).

The present paper describes experiments which examine the relationship between the angle of incidence of incoming radiation, θ , and the photosynthetic rate of individual attached leaves of four species. The light intensities used were non-saturating, and the four leaf types differed in morphology and thickness.

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† It should be noted that Went (1958, p. 233) defined angle of incidence (θ') as the angle between the incoming radiation and the leaf surface. Thus he deduced that the photosynthetic rate of a leaf would be proportional to $\sin \theta'$.

II. MATERIAL AND METHODS

The photosynthetic behaviour of single attached leaves was studied for four different species, viz. *Eucalyptus regnans* (mountain ash), *Beta vulgaris* (sugar-beet), *Triticum vulgare* (wheat, cv. Sabre), and *Glycine max* (soybean). Experimental plants were grown in pots of soil under glasshouse conditions.

Measurements of photosynthesis were conducted in a constant-temperature room (21°C) by measuring with an infrared gas analyser the amount of CO₂ absorbed by an illuminated leaf from a CO₂-buffered air stream recirculating at 15 litres/min. The adaxial leaf surface was illuminated with a high-pressure mercury vapour lamp (HPT 400 W). The lamp's emission of light was restricted by aluminium foil wrapping to a narrow zone 5 by 4 cm opposite the assimilation chamber. A water-bath, 2.5 cm deep and flushed continuously with filtered tap water, was fixed in place between the lamp and the assimilation chamber to reduce heat transmission. The Perspex assimilation chamber had internal dimensions 17.5 by 6.5 by 0.8 cm and the experimental leaf was suspended at the mid-plane of the chamber between two sets of six fine nichrome wires. These wires ran longitudinally, one set being suspended from the lid, and the other set raised above the base of the chamber. This arrangement enabled a replicable leaf position, and prevented the formation of dead space between the leaf surface and the wall of the assimilation chamber. In setting up the apparatus, the lamina was carefully positioned in the chamber, with its petiole running to the outside through a groove cut in the end wall. The petiole was then sealed into place with silicone "rubber" (Silcote 1104) and while this substance was still setting the lid of the chamber (with inner edges greased) was clamped in position, rendering the system gas tight, except for inlet and outlet tubing. The angle of incidence (θ) of incoming radiation could be varied from 0 to 90° by rotating the assimilation chamber about its longitudinal axis.

The proportion of the incident light transmitted through the Perspex lid (3 mm thick) of the assimilation chamber was calculated from an empirical determination of the percentage transmission through the lid (approximately 98%), and by reference to the reflective properties of Perspex (I.C.I. specifications, undated). The intensity of illumination at the leaf surface, due to the proportion of light transmitted through the Perspex, was calculated from the cosine relationship (Lambert's Law). The relationship between the intensity of illumination on the Perspex and leaf surfaces, for various values of θ , is given in Figure 1.

During measurements of photosynthesis, the CO₂ concentration of the air in the assimilation chamber was maintained between certain levels by adjusting the input of CO₂-buffered air into the recirculating system. When, for example, conditions promoted high rates of photosynthesis, the rate of input was increased to prevent excessive CO₂ depletion, and, conversely, when assimilation rates fell due to reduced light intensity or lowered θ , the input rate was decreased so that the supply of CO₂-buffered air would not elevate the CO₂ concentration in the recirculating system above the prescribed level. During photosynthesis measurements, the mean CO₂ concentration in the assimilation chamber was maintained at 330 (± 20) p.p.m. except in the experiments on *E. regnans* where it was kept at 420 (± 5) p.p.m.

Differences in the CO_2 concentration of the air entering compared with that of the air leaving the assimilation chamber were reduced to less than 5 p.p.m. by the fast rate of recirculation. The leaf's photosynthetic rate usually took about 10 min to stabilize after an alteration in experimental conditions, and CO_2 assimilation was measured continuously for a further 10–15 min.

Leaf temperature on the undersurface (away from the light) was measured with a thermocouple probe (from an Ellab type T.E. 3 electric thermometer) which entered the assimilation chamber through a stoppered aperture. Leaf temperature during assimilation measurements never rose above 25°C . Light intensity was

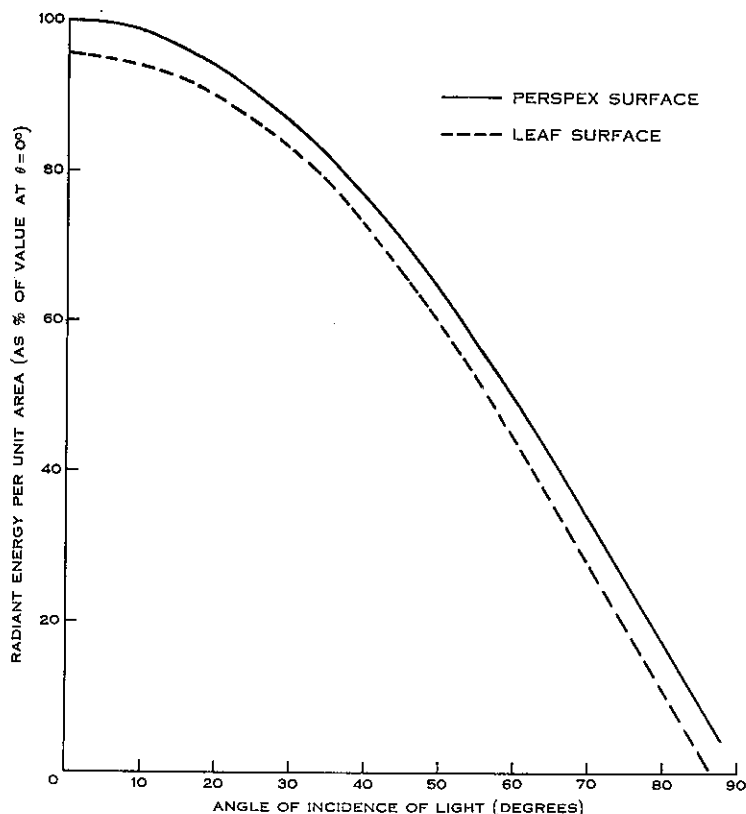


Fig. 1.—Relative magnitudes of the radiant energy per unit area incident upon the leaf surface and the lid of the assimilation chamber at different angles of incidence.

measured within the assimilation chamber, at a position normally occupied by the leaf, with a selenium photocell (uncorrected to the wavelength response curve of the human eye) from a Weston lightmeter, model 756. Light intensity readings in foot-candles were transformed to energy units using the conversion factor from Gaastra (1959) for the appropriate light source and photocell.

At the end of each experiment, the leaf was detached from the plant, lamina and petiole were weighed separately, and the lamina was printed on dyeline paper

for area measurement by cutting out and subsequently weighing the print. The chlorophyll content of the leaf was then determined by macerating the leaf in 80% acetone and measuring the optical density of a clear extract at 6630 and 6450 Å (in a Unicam spectrophotometer) after the method of MacKinney (1941).

III. RESULTS

(a) Structure of the Leaves used for these Experiments

Some of the physical characteristics of the experimental leaves are given in Table 1. Plate 1, Figures 1-4, illustrates the anatomy of each type of leaf as seen in

TABLE 1
PHYSICAL CHARACTERISTICS OF EXPERIMENTAL LEAVES

Species	Laminar Area (sq cm)	Laminar Fresh Weight (g)	Ratio of Area to Weight (sq cm/g)	Chlorophyll Content (mg/sq dm)
<i>E. regnans</i>	29.7	0.560	53.0	3.91
<i>B. vulgaris</i>	40.2	0.945	42.6	4.77
<i>T. vulgare</i>	12.6	0.176	71.4	4.69
<i>G. max</i>	50.6	0.531	95.3	1.64

cross-section. These four leaf types represent a considerable range of leaf thickness and chlorophyll content. The leaf of *E. regnans* (Plate 1, Fig. 1) is isobilateral. Visually, the leaf surfaces of *E. regnans* and *B. vulgaris* appeared shiny, whilst those of *T. vulgare* and *G. max* were dull.

TABLE 2
PHOTOSYNTHETIC RATE OF INDIVIDUAL LEAVES OF FOUR SPECIES
Rate measured at a light intensity of 20×10^4 ergs/sec/sq cm

Species	CO ₂ Concentration during Assimilation (p.p.m.)	Photosynthetic Rate		
		(mg CO ₂ /hr/leaf)	(mg CO ₂ /hr/sq dm)	(mg CO ₂ /hr/mg chlorophyll)
<i>E. regnans</i>	420 ± 5	8.54	28.75	7.35
<i>B. vulgaris</i>	330 ± 20	9.25	23.00	4.82
<i>T. vulgare</i>	330 ± 20	2.17	17.25	3.69
<i>G. max</i>	330 ± 20	5.82	11.50	7.01

(b) *Variation of Photosynthetic Rate with Light Intensity, when Light Falls Normally on the Leaf Surface*

The response curves relating leaf photosynthetic rate and light intensity for each of the four types of leaf are given in Figure 2(a). The maximum photosynthetic rates for each leaf, and the expressions of this on a leaf area and chlorophyll basis, are given in Table 2.

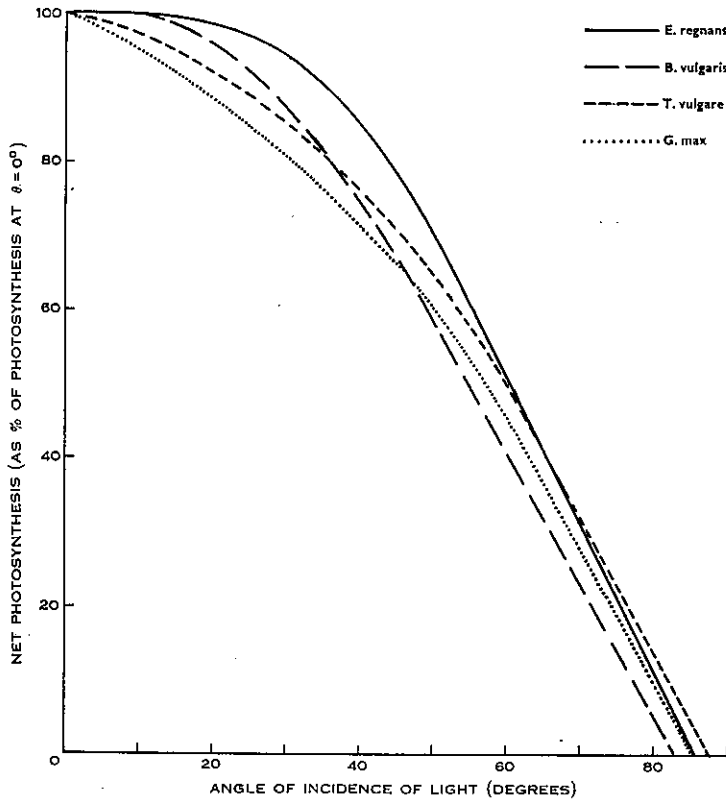


Fig. 3.—Relative net photosynthesis for single attached leaves of four species in relation to the incident angle of incoming light.

Light-saturated rates of photosynthesis were attained only with the leaves of *B. vulgaris* and *G. max*. The maximum rate for the leaf of *B. vulgaris* (23 mg CO₂/hr/sq dm) was similar to that obtained by Gaastra (1959) for sugar-beet, and was markedly higher than the value for soybean and wheat leaves (Table 2). However, when photosynthetic rate was expressed on a chlorophyll basis, the leaf of *G. max* (which had the least chlorophyll per unit leaf area—Table 1) was approximately twice as efficient as the wheat leaf. The photosynthetic activity of *E. regnans*, expressed on either a leaf area or chlorophyll basis, was greater than that of the other three leaves. This superiority may be due to an inherently more efficient structure, or to the fact that the photosynthesis of this leaf was measured in a gas stream of greater CO₂ concentration (420 p.p.m.) than was used for the other three leaves (330 p.p.m.).

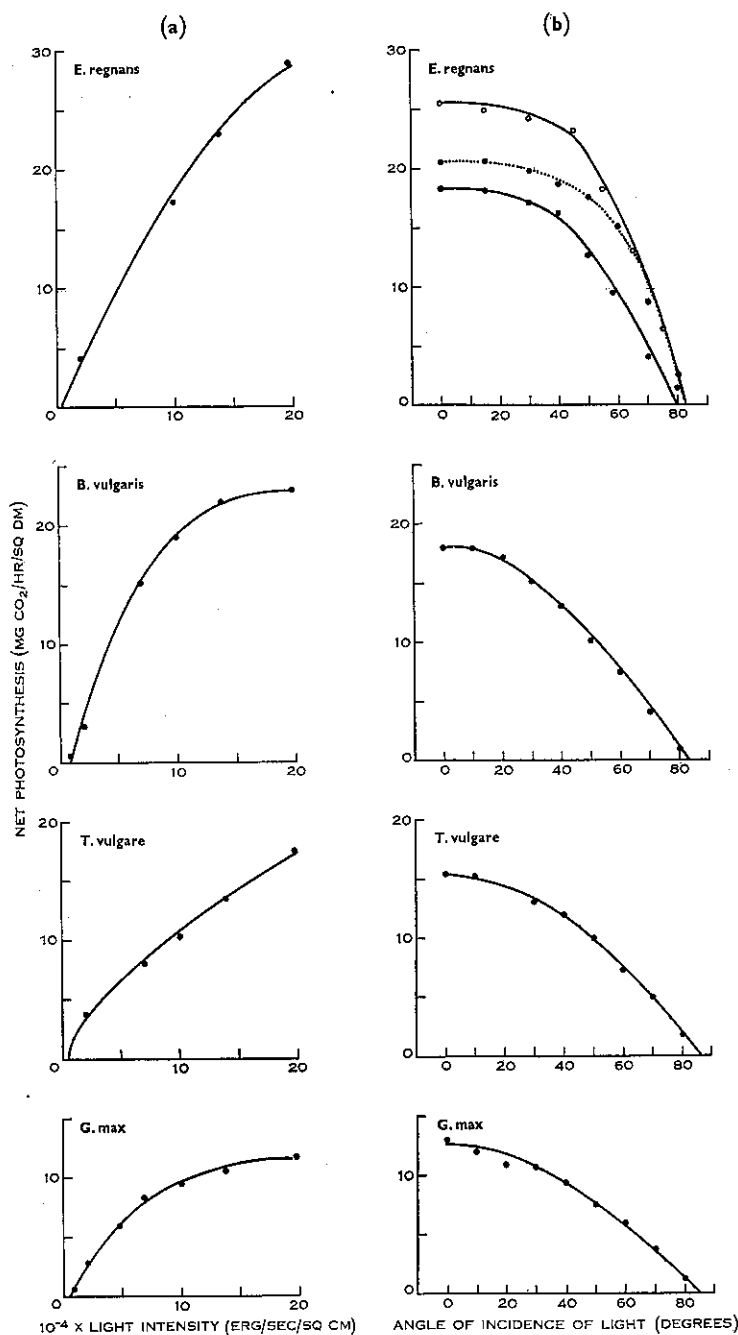


Fig. 2.—Net photosynthesis for single attached leaves of four species in relation to light intensity and the incident angle of incoming light.

(c) *Relationship between Net Photosynthetic Rate and the Angle of Incidence of the Light Falling upon the Leaf Surface*

In measuring the effect of alterations in θ on leaf photosynthesis it is necessary to use a light intensity below saturation level, when $\theta = 0^\circ$, so that there will be no delay in the response of photosynthetic rate to increasing θ while a limiting light intensity is being approached. For this reason a constant light intensity of 10×10^4 ergs/sec/sq cm was chosen by reference to the photosynthetic response curves already obtained [Fig. 2(a)]. This intensity, when $\theta = 0^\circ$, is below the saturation level for all four types of leaf. For one leaf, that of *E. regnans*, the response of photosynthesis to alteration of θ was measured at two additional constant light intensities, namely: 14×10^4 and 20×10^4 ergs/sec/sq cm. Response curves of similar shape were obtained for all three light intensities.

The results for all four leaves are plotted in Figure 2(b). The relationship between the *relative* rate of net photosynthesis (100% when $\theta = 0^\circ$) and θ , for each of the four leaves, is given in Figure 3. These curves were constructed by replotting the data from Figure 2(b).

IV. DISCUSSION

For the purposes of discussion, a simple model of the fate of unidirectional incident energy (E_i) falling upon a leaf at an angle of incidence θ is given in Figure 4.

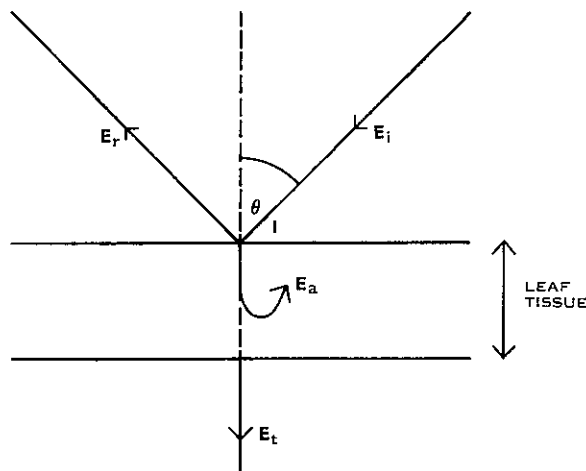


Fig. 4.—A simple model of the fate of radiant energy falling upon the surface of a leaf at an angle of incidence $= \theta$.

E_r is the reflected radiation and E_a and E_t the radiation absorbed by and transmitted through the leaf, respectively. The intensity of radiation at the leaf surface, I , is equal to $E_i \cos \theta$.

The radiant energy absorbed by the leaf (E_a) can be further apportioned as follows:

$$E_a = E_{rad.} + E_{H_2O} + E_p,$$

where $E_{rad.}$ is the energy which heats the leaf and is re-radiated, E_{H_2O} the energy used to vaporize water, and E_p the energy used in photosynthesis.

The experimental findings of this paper are summarized in Figure 5 where the relative mean photosynthetic rate for the four leaves and also the calculated intensity of illumination at the leaf surface (I), are plotted against $\cos \theta$.

As may be expected, I is linearly related to $\cos \theta$; however, this is also true of the mean photosynthetic rate for values of θ ranging from 0 to 80°. Thus, $E_a \propto I \propto E_i \cos \theta$, and since E_i has been kept constant, E_a is therefore proportional to $\cos \theta$. At first sight it appears unlikely that this simple, empirically determined, relationship would hold over a wide range of values for θ , on account of Fresnel's law of reflection for unpolarized light from a plane surface. This law demonstrates that for a plane surface, as θ increases from 45 to 80°, so E_r increases from approximately 4 to 40%; and if E_r increases, then the proportional value for E_a , and hence E_p , must decrease.

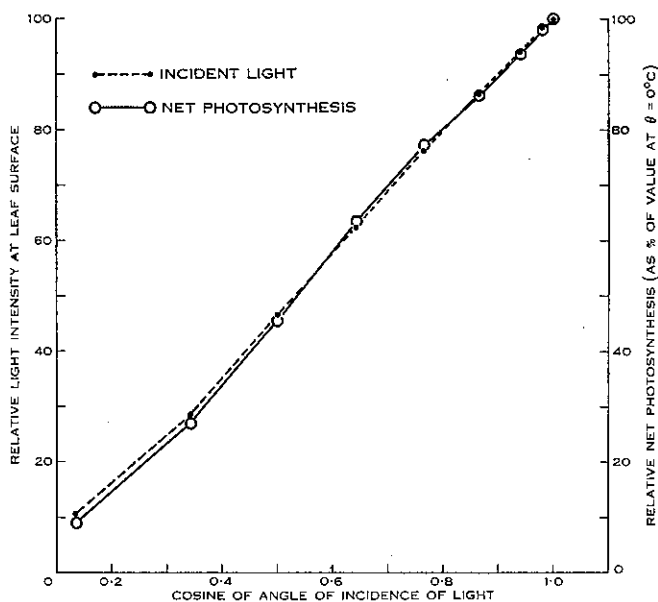


Fig. 5.—Net photosynthesis (mean for four leaves), and light intensity at the leaf surface, in relation to the cosine of the angle of incidence of incoming radiation.

However, the adaxial surface of leaves is not planar and from electron micrographs of carbon replicas (Plate 1, Figs. 5-7), appears exceedingly rough. Therefore Fresnel's law cannot be validly extended to the present considerations of leaf photosynthesis in relation to θ . That this is so receives further experimental support from Tagueva and Brandt (1961) whose measurements of the coefficient of absorption of white light for three different leaves are given in Table 3 (taken from their Figures 3, 4, and 5).

From this table it is evident that E_a does not diminish as might be expected if E_r increased according to Fresnel's law. In fact, as θ increases from 0 to 70°, E_r increases from 7 to only 10% with the *Hibiscus* leaf, and from 13 to 22% with the *Lactuca* leaf (Tagueva and Brandt 1961). Hence, for the leaves used in the experiments

reported in the present paper, it seems reasonable to assume that E_a remains approximately constant as θ is increased. If E_a does remain constant, then within the limits of experimental error, it is to be expected that: $E_p \propto E_a \propto I \propto E_i \cos \theta$, as is found empirically in Figure 5. Furthermore, the amount of light entering the leaf decreases as $\cos \theta$ increases and Gaastra (1958) has shown that the efficiency of light utilization in photosynthesis increases as the intensity of illumination on the leaf decreases. Thus the slight decrease in E_a which may occur when θ exceeds 60°

TABLE 3
COEFFICIENT OF ABSORPTION OF WHITE LIGHT BY THE LEAVES OF
HIBISCUS ROSA SINENSIS, LACTUCA SATIVA, AND COLEUS SP.
Results from Tagueva and Brandt 1961

Angle of Incidence (degrees)	Coefficient of Absorption (as % of incident light)		
	<i>H. rosa sinensis</i>	<i>L. sativa</i>	<i>Coleus</i> sp.
0	89	68	97
30	89	68	97
60	88	67	95
70	86	66	94

(Table 3) is perhaps offset by the absorbed light being used more efficiently in photosynthesis. In addition, a re-orientation of the chloroplasts with respect to the direction of incoming radiation could result in a more complete absorption of light with increasing angles of θ .

Thus, the photosynthetic rate of a leaf is proportional to the cosine of the angle of incidence of directional illumination apparently for at least two reasons: (1) the reflective surface of the leaf does not obey Fresnel's law, and (2) the increase in photosynthetic efficiency which occurs at low light intensities. This proportionality was hypothetically proposed by Went (1958) who also considered the possible adaptive advantage of leaf arrangements in which θ is large.

V. ACKNOWLEDGMENTS

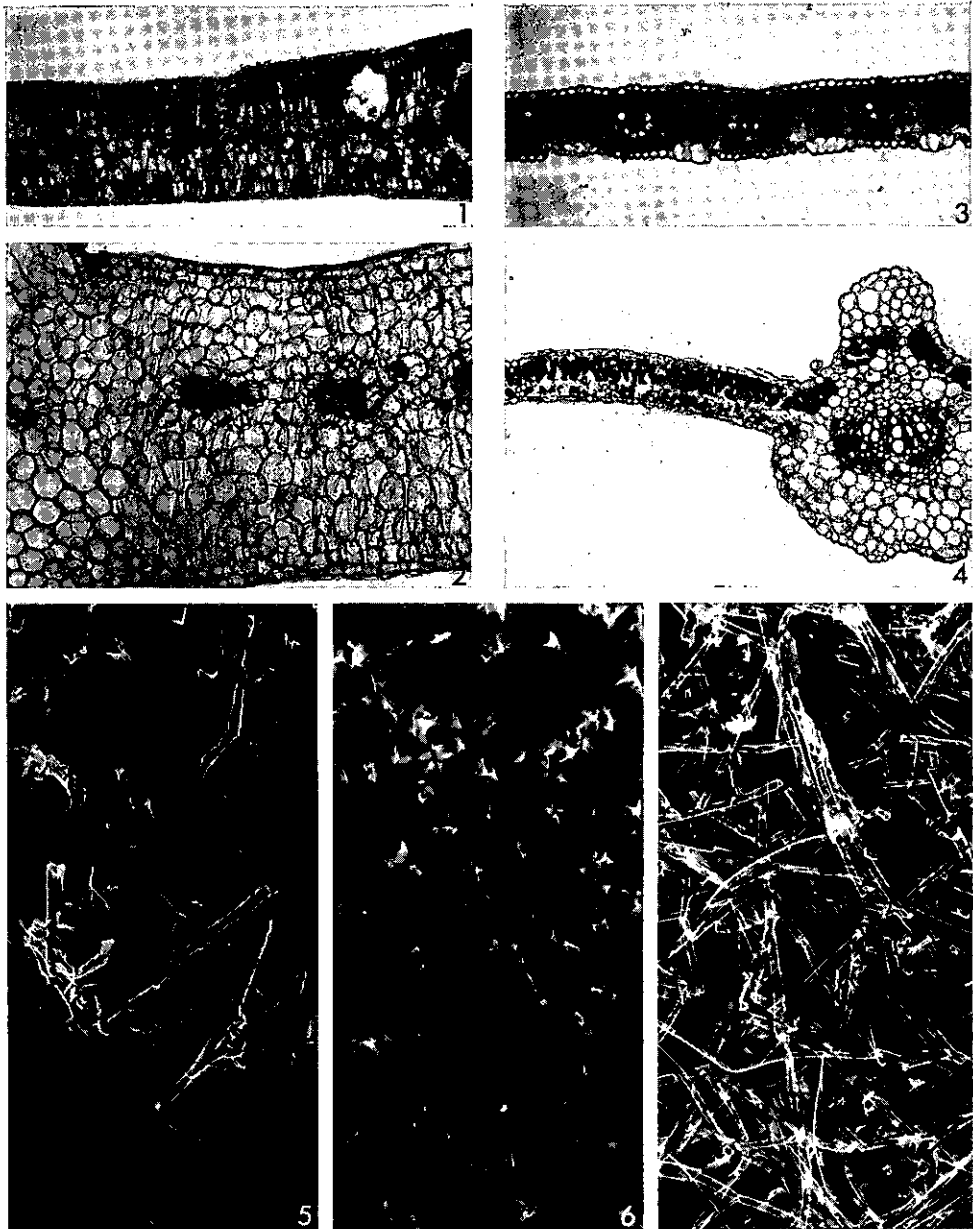
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Figs. 1-4.—Photomicrographs of transverse sections of laminar portions from the four different leaf types used in the experiments. $\times 50$. 1, *E. regnans*; 2, *B. vulgaris*; 3, *T. vulgare*; 4, *G. max*.

Figs. 5-7.—Electron micrographs of carbon replicas of the adaxial leaf surface ($\times 6250$) of *E. regnans* (5), *B. vulgaris* (6), and *T. vulgare* (7).

