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Effect of Light Quality on Stomatal Opening in Leaves of *Xanthium strumarium* L.[1]

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ABSTRACT

Flux response curves were determined at 16 wavelengths of light for the conductance for water vapor of the lower epidermis of detached leaves of *Xanthium strumarium* L. An action spectrum of stomatal opening resulted in which blue light (wavelengths between 430 and 460 nanometers) was nearly ten times more effective than red light (wavelengths between 630 and 680 nanometers) in producing a conductance of 15 centimoles per square meter per second. Stomata responded only slightly to green light. An action spectrum of stomatal responses to red light corresponded to that of CO_2 assimilation; the inhibitors of photosynthetic electron transport, cyanazine (2-chloro-4[1-cyano-1-methylethylamino]-6-ethylamino-*s*-triazine) and 3-(3,4-dichlorophenyl)-1,1-dimethylurea, eliminated the response to red light. This indicates that light absorption by chlorophyll is the cause of stomatal sensitivity to red light. Determination of flux response curves on leaves in the normal position (upper epidermis facing the light) or in the inverted position (lower epidermis facing the light) led to the conclusion that the photoreceptors for blue as well as for red light are located on or near the surfaces of the leaves; presumably they are in the guard cells themselves.

Until recently, light was thought to affect stomatal opening indirectly through the light dependence of CO_2 assimilation (9, 11). However, new analyses of stomatal responses to CO_2 and light led to the conclusion that, in most cases, stomata responded to changes in the intercellular CO_2 concentration only to a small extent; most of the response to light was "direct", *i.e.* not mediated by CO_2 (13, 14). Comparison of stomatal behavior in leaves of normal orientation (upper epidermis facing the source of light) with that in leaves in the inverted position (lower epidermis facing the light) led us to conclude that the photoreceptors for the direct response to light are located in each epidermis, presumably within the guard cells (13). Wong *et al.* (15) believe that an additional response to "another metabolite of photosynthesis" in the mesophyll, a metabolite other than CO_2, is involved in linking stomatal conductance to the photosynthetic activity of the mesophyll.

We used monochromatic light to obtain further information on the location of the photoreceptors involved. Action spectra of several stomatal activities have already been obtained with isolated epidermal strips (3, 5). All of them show a considerably stronger stimulation of stomatal opening and related processes by blue light than by red light; green light was virtually ineffective. If, in whole leaves, photosynthetic activity in the mesophyll is important in determining stomatal opening, we should expect a combination of the action spectra for stomatal opening in isolated epidermis and for photosynthesis to appear when we determine the spectral dependence of stomatal opening on light in whole leaves. No information is available on the spectral sensitivity of stomata in leaves exposed to quantum fluxes normally occurring in the field (full sunlight corresponds to approximately 2000 μE m^{-2} s^{-1}). We therefore extended the range of light treatments to quantum fluxes that approached the highest values of our earlier experiments with white light (13) and thereby caused saturation of the stomatal responses.

We continued to use plants of *Xanthium strumarium* for our experiments because we were able to obtain leaves with low stomatal sensitivity to CO_2; interference by CO_2-mediated responses was thereby minimized (8). We combined exposure to monochromatic light with our earlier approaches of using leaf inversion and inhibitors of photosynthetic electron transport for the attempted localization of the photoreceptors involved in the adjustment of stomatal aperture to light (13).

MATERIALS AND METHODS

Plants. Plants of *X. strumarium* L. (Chicago strain) were grown in a growth chamber with a daylength of 20 h; 24 C/20 C day/night; 75% RH. Light was provided by General Electric lamps H 400 DX 33-1 (mercury vapor) and LU 400 (high-temperature sodium vapor) (General Electric Co., Cleveland, OH). During each day the irradiance was increased in three steps to 230 w m^{-2} (as measured with an Eppley pyranometer (Eppley Laboratory Inc., Newport, RI) behind a Corning No. 4600 IR absorbing filter (Corning Glass Works, Corning, NY)) and then decreased. A 20- x 2.5-cm wick was placed in each pot containing a gravel-soil mixture, such that about 15 cm was in contact with the soil and 5 cm dipped into a gravel bed containing distilled H_2O.

Gas Analysis. Air was passed through soda lime to remove all CO_2 and then humidified in a gas washing bottle. The CO_2 concentration of the air was adjusted by injecting 1 or 5% CO_2 (in air) into the air stream through capillaries of varying resistance. Passage of the air through a glass condenser set the dew point. The temperature of the condenser was maintained at 18 C by a constant temperature water bath and was measured with a thermocouple. The air stream was split and the air stream passing over the leaf was adjusted to 50 liters h^{-1} over each surface. The leaves were mounted between two waterjacketed aluminum chambers whose temperature was kept at 23 C by a constant temperature circulator. The petiole of the leaf dipped into a beaker containing either water or a solution to be fed to the leaf. In each chamber, a leaf area of 2.44 cm^2 was exposed to the air stream. A small copper-constantan thermocouple was pressed against the nonilluminated surface of the leaf. Those parts of the leaf not covered by the chambers were trimmed off (8). The molar fluxes of CO_2

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and H_2O for both upper and lower leaf surfaces were measured with four differential gas analyzers (URAS 2, Hartmann und Braun, Frankfurt, West Germany).

Assimilation and evaporation rates, conductance (stomata and boundary layer together), and intercellular CO_2 concentration were calculated by computer. The intercellular CO_2 concentration (c_i) was obtained using the following equation:

$$c_i = c_a - 1.6A/g$$

where c_a is the CO_2 concentration in the air passing over the leaf, A is the assimilation rate, and g is the conductance for water vapor of the stomata and the boundary layer. The factor 1.6 is the ratio of the diffusivities of water vapor and CO_2 in air. The units used for the gas exchange parameters are those of Farquhar *et al.* (2).

Light. Monochromatic light was produced by filtering white light (from air-cooled xenon arc lamps) through band pass filters ($\Delta\lambda$ about 150 nm) and water-cooled interference filters. The interference filters had a half-band width of 20 nm, except for the experiment reported in Figure 3 for which filters with a half-band width of 12 nm were used. The filters were tandem filters made by Schott, Mainz, West Germany, type DAL (20 nm half-band width) or DIL (12 nm half-band width). The irradiance was reduced with neutral density Plexiglas filters (no. 800 and 838, Röhm und Haas, Darmstadt, West Germany). Two 2.5 kw lamps were set up to shine into one box from which all other light was excluded. (An earlier version of the monochromator equipment is described in reference 7).

In the irradiation compartment, the leaf chamber was mounted on an optical bench and could be positioned under either lamp. With this setup, the wavelength of the light shining on the leaf could be changed in less than three s by sliding the chamber from one lamp to the other. A 6.5 kw lamp was available when high quantum fluxes were needed.

The leaf chamber was fitted with a beam splitter (a microscope slide fixed at a 45° angle to the light beam) which reflected about 10% of the light to two silicon cells. These silicon cells were calibrated by the following method: An intermediate pair of silicon cells was calibrated against an Eppley thermopile (model D-3), then put into the leaf chamber. The silicon cells of the beam splitter were then calibrated against the intermediate pair of silicon cells so that the signal from the beam splitter silicon cells could be converted directly into quantum flux inside the leaf chamber. This calibration was done for each wavelength of light used.

RESULTS

Action Spectra. In the experiments we reported before (13), stomata on the abaxial (lower) surface of leaves of *X. strumarium* proved to be much more sensitive to light than stomata on the adaxial surface. We therefore performed all measurements necessary for the assembly of an action spectrum of stomatal opening on inverted leaves with light impinging upon their lower surfaces. The conductance values we report are for the directly illuminated abaxial surfaces only, whereas assimilation rates are the sums of the rates of CO_2 exchange of both sides of the leaves.

An action spectrum for stomatal opening was constructed using the steady-state method, *i.e.* a leaf was exposed to a quantum flux at a particular wavelength until the conductance no longer changed. In general, stomata adjusted to a new quantum flux within 30 min. Three sections could be distinguished in the quantum flux-response curves (Figs. 5, 6). At low levels of quantum flux stomata were hardly open, if at all. At intermediate levels stomatal conductance increased nearly linearly with the logarithm of quantum flux. At very high levels, saturation with respect to light occurred. In red light, stomatal responses to increasing quantum fluxes saturated at lower conductances than in blue light (Figs. 5, 6). A linear regression was performed for each wavelength for the points that fell in the linear response range (except at 711 nm, for which only two points could be used). Lines were obtained for stomatal responses to light of 16 wavelengths. The length of each line in Figure 1 indicates the range over which the stomatal response was linear with logarithmic changes in quantum flux. The slopes of the lines in blue light were greater than the slopes in red light. The average slope of all lines between 400 and 500 nm was 19.4 ± 3.7 cmol m^{-2} s^{-1} per decade change in quantum flux, whereas the average slope of all lines between 600 and 700 nm was 12.8 ± 0.8 cmol m^{-2} s^{-1} per decade. Using data from Figure 1, an action spectrum was assembled by plotting the inverse of the quantum flux required to produce a conductance of 15 cmol m^{-2} s^{-1}, *versus* wavelength (Fig. 2). This method deemphasizes the peak of activity in red light since the slopes of the flux-response curves are smaller in red light than in the blue. Another action spectrum was constructed (not shown) by extrapolating the regression lines of Figure 1 to the conductance value obtained in the dark for each individual leaf (not entered in Fig. 1) and plotting the inverse of the quantum flux thus obtained *versus* wavelength. In that case the red peak was 20% of the blue peak rather than close to 10% as in Figure 2.

Because the action spectrum obtained resembled closely the spectra for stomatal opening and ^{86}Rb accumulation, and in

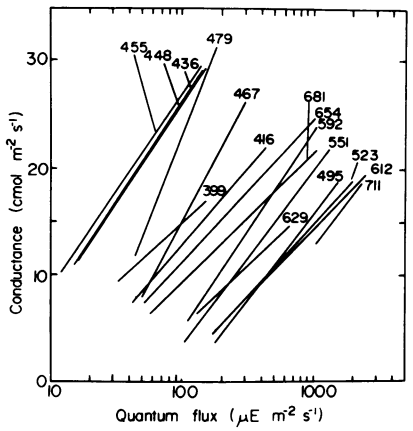

FIG. 1. Stomatal response in leaves of *X. strumarium* to quantum fluxes of light of 16 wavelengths (numbers indicate wavelength in nm). From measurements of the conductance for water vapor of the abaxial (lower) surface which was directly illuminated. The lines are linear regressions of the three or four points that fell on the linear response portion of the curve. The extent of each line indicates the range over which the stomata responded linearly to changes in the logarithm of the quantum flux. Each line was derived from data obtained from one leaf. Stomata did not respond to quantum fluxes up to 1000 μE m^{-2} s^{-1} at 749 and 731 nm, and up to 100 μE m^{-2} s^{-1} (limit of the light source) at 386 and 372 nm. All measurements were conducted at a CO_2 concentration of 320 μl l^{-1} in the atmosphere.

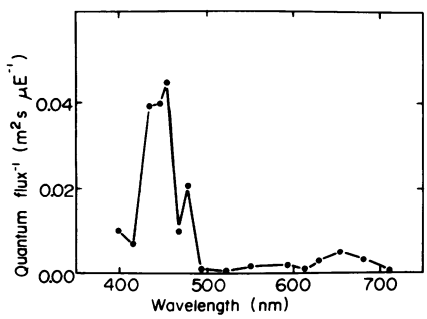

FIG. 2. Action spectrum of stomatal opening in the lower epidermis of leaves of *X. strumarium*. The measure of action is the inverse of the quantum flux required to produce a conductance of 15 cmol m^{-2} s^{-1}.

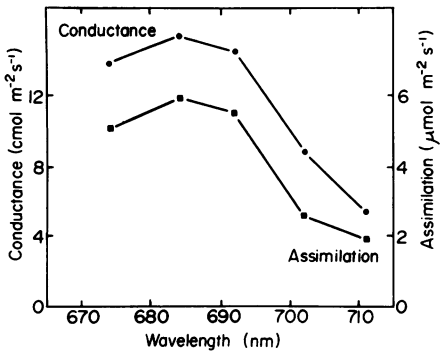

FIG. 3. Conductance for water vapor and assimilation rate in leaves of *X. strumarium* exposed to a quantum flux of 300 μE m^{-2} s^{-1} at various wavelengths of red light and an intercellular CO_2 concentration close to 250 μl l^{-1}. Averaged values are from four leaves. Conductance data are for the directly illuminated abaxial surface only, whereas the assimilation data are for both leaf surfaces. Assimilation (■) is plotted against the right scale and conductance (●) is plotted against the left scale. The average stomatal conductance in darkness was 4.6 cmol m^{-2} s^{-1}. The interference filters used had a half-band width of 12 nm and a one-tenth band width of 20 nm.

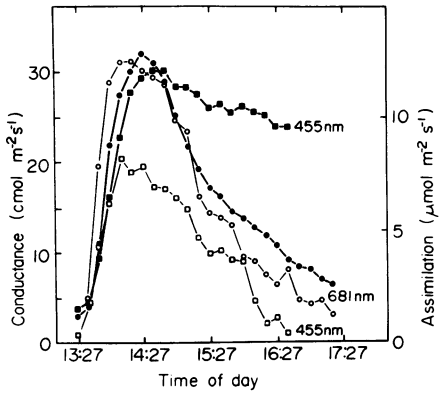

FIG. 4. Time courses of conductance for water vapor and assimilation of *X. strumarium* leaves supplied with 5×10^{-5} M cyanazine and placed in red or blue light (abaxial surface illuminated). Assimilation rates (○, □, right scale) and conductance (●, ■, left scale) rose initially in response to light (650 μE m^{-2} s^{-1} at both wavelengths). The CO_2 concentration in the air was 320 μl l^{-1}. The conductance values are those of the directly illuminated abaxial surface only; the assimilation rates are the sums of CO_2 exchanges through both surfaces.

particular the action spectrum of malate accumulation in isolated epidermis of *Vicia faba* (3, 5), we made no attempt to verify, by repetition of our experiments, details of the spectrum we had obtained.

Many investigators assume that Chl is involved in stomatal responses to light. While Chl cannot be the only pigment involved, it could be the pigment responsible for the activity of red light in causing stomatal opening. We tested this possibility by measuring the steady state conductance of leaves in a quantum flux of 300 μE m^{-2} s^{-1} at each of 5 wavelengths at the long wavelength end of the Chl absorption spectrum where interference by accessory pigments should be minimal. (Narrow band width filters were used for this purpose.) For two leaves the wavelength of the illuminating light was increased during the experiment from the shortest to the longest, and for two additional leaves the wavelength was decreased, from the longest to the shortest. The intercellular CO_2 concentration was kept at 253 ± 8 μl l^{-1} by adjustment of the ambient CO_2 concentration for all wavelengths except 711 nm. At 711 nm, the intercellular CO_2 concentration was 282 μl l^{-1}. For each leaf the shape of the curve relating conductance to wavelength was the same, although the absolute conductance values varied from leaf to leaf at each wavelength. (In each of the four leaves the conductance at 690 nm oscillated with a period of about 25 min and decreasing amplitude). The averaged results from four leaves are shown in Figure 3. The pattern of stomatal responses to changes in the wavelength of red light was virtually identical with that of the simultaneous responses of net assimilation.

Inhibition of Photosynthesis. In whole leaves stomatal responses to red light disappeared after application of the inhibitors of photosynthetic electron transport, DCMU, and cyanazine[4]. Figure 4 shows the result of one of three similar experiments. In blue light (λ = 455 nm) both conductance and assimilation increased rapidly until sufficient inhibitor had accumulated in the leaf to reduce the rate of photosynthesis. Conductance fell slightly. This may have been a CO_2 effect inasmuch as the intercellular CO_2 concentration rose by 30 μl l^{-1} as CO_2 assimilation declined. In red light (λ = 681 nm) assimilation rate and conductance both fell as the inhibitor of photosynthesis began to act. Table I contains

Table I. *Effect of DCMU on CO_2 Assimilation and Conductance for Water Vapor in Blue and Red Light*

The dose was calculated by integrating the stripchart record of water loss for the 6 h duration of the experiment and multiplying the result by the concentration of DCMU in the irrigation water (50 μM). The dose was taken up by a leaf trimmed to an area of about 20 cm^2, of which 2.4 cm^2 were exposed to the light.

Light, λ	Quantum Flux	Conductance	Assimilation Rate	Dose
nm	*$\mu E\ m^{-2}\ s^{-1}$*	*$cmol\ m^{-2}\ s^{-1}$*	*$\mu mol\ m^{-2}\ s^{-1}$*	*nmol*
Blue 455	650	33.2	0.21	36.5
Blue 455	65	33.6	0.33	36.3
Red 684	650	7.8	1.99	23.0
Blue[a] 455	650	16.8	1.97	

[a] Same leaf as used for 684 nm. This line shows that when stomata in red light are closed by DCMU, they can still respond to blue light.

data from a similar experiment, this time with DCMU as inhibitor. Because almost 10 times more quanta of red light than of blue were required to produce a conductance of 15 cmol m^{-2} s^{-1} (Fig. 2), the experiment included one treatment in which the quantum flux of blue light was one-tenth that of the red light. After 6 h of irradiation, the two leaves in blue light (first two lines) had large conductances, while the leaf in red light had attained only a low conductance value. Because stomata became narrow in red light but remained open in blue light, the amount of DCMU taken up during the course of the experiment (as judged by the water lost by the leaves) was 50% higher in the blue light treatments than in the red light treatment. After stomata had closed in red light, in response to DCMU, they still were able to respond to blue light though not as strongly as during the first opening movement (fourth line in Table I).

Leaf Inversion. Stomata open in red light (Figs. 1, 2); the action spectrum in the red region of the spectrum coincided with that of the assimilation of CO_2 (Fig. 3). In red light stomata were sensitive to inhibitors of photosynthetic electron flow (Fig. 4, Table I). These observations are consistent with the suggestion that photosynthesis in the mesophyll controls stomatal conductance (15). For a test of this hypothesis, we determined conductances in normally oriented and in inverted leaves that were exposed to blue or to red light (Fig. 5). When illuminated directly stomata began to open at much lower quantum fluxes than when they

[4] Cyanazine, 2-chloro-4-(1-cyano-1-methylethylamino)-6-ethylamino-*s*-triazine, is the active ingredient of the herbicide Bladex by Shell Chemical Company.

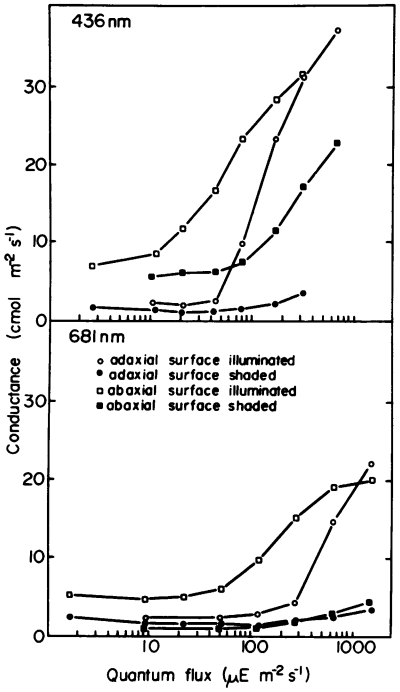

FIG. 5. Stomatal responses to monochromatic blue or red light in the normal or inverted orientation of leaves of *X. strumarium*. The leaf blades were positioned so that light was shining on the adaxial (upper) surface (abaxial surface shaded by the mesophyll) or on the abaxial (lower) surface (adaxial surface shaded). The filters had half-band widths of 20 nm. The average transmittance of the leaves was 1.7% in blue light and 3.9% in red light. (Separate leaves were used for each color and leaf position. The flux-response curve for an epidermis in the shaded position does therefore not appear as an exact displacement of the curve for the illuminated position.)

were shaded by the mesophyll. This was observed in blue light as well as in red light. At any one particular quantum flux, stomata directly exposed to the impinging light also were open wider than those of the shaded surface of the leaves.

Effect of CO_2. Some investigators, notably Brogårdh (1), believe that stomatal responses to red light are mediated by changes in the concentration of CO_2, whereas responses to blue light are caused by light absorption in the guard cells. To test the modification of stomatal responses to red or blue light by CO_2, flux response curves were determined at a high and at a low level of CO_2 in the air. The results shown in Figure 6 indicate that CO_2 affected stomatal responses to red and to blue light in a similar manner. In light of both qualities, conductances were lower if the CO_2 concentration in the air was above the normal CO_2 concentration in the atmosphere than when the CO_2 concentration was approaching 100 $\mu l\ l^{-1}$. In red light as well as in blue light, a high level of CO_2 lowered the maximum conductance reached by the stomata. It also appears that stomata of *X. strumarium* were able to respond to red light without mediation by the intercellular concentration of CO_2.

DISCUSSION

The action spectrum of stomatal opening in leaves of *X. strumarium* (Fig. 2) resembles the spectra obtained by Hsiao *et al.* (3), and by Ogawa *et al.* (5), for stomatal opening in leaf discs and epidermal strips of *V. faba*, and of the accumulation of ^{86}Rb and malate in epidermal samples of the same species. Blue light stimulates stomatal opening 10 to 20 times more than red light (depending on the measure used). Even at saturating fluxes with red quanta, stomatal conductances remain one-third below those attainable in blue light (Figs. 5, 6). Green light is much less

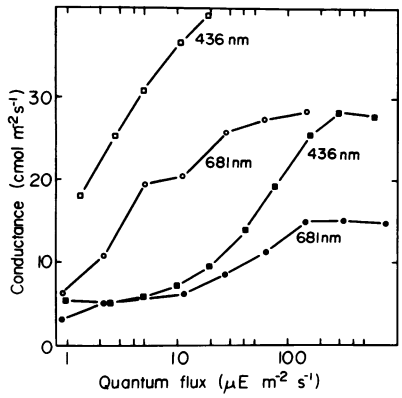

FIG. 6. Effect of CO_2 on stomatal responses to red or blue light in leaves of *X. strumarium*. The conductances given are those of the directly illuminated abaxial surface. (○, □): low ambient CO_2 concentration (110 $\mu l\ l^{-1}$ for blue, 130 $\mu l\ l^{-1}$ for red). (●, ■): high ambient CO_2 concentration (510 $\mu l\ l^{-1}$ for blue, 580 $\mu l\ l^{-1}$ for red).

effective in causing stomata to open than light of other wavelengths. The greater slopes of the flux-response curves in blue light than in red light are evidence for the involvement of two pigments in the stomatal response to light.

Ogawa *et al.*, on the strength of their experiments involving simultaneous irradiation with light of two wavelengths, suggested that two pigments participate in the stimulation of malate formation in epidermal tissue. In all likelihood, one of the receptor molecules is Chl; the other is possibly a flavin (5). Participation of two light responses in the stimulation of stomatal opening was also suggested by Brogårdh (1); he observed large overshoots in the transpiration rates of oat seedlings when blue light was given, but only gradual increases when the plants were illuminated with red light.

Our evidence supports the suggestion that stomatal opening in red light involves the photosynthetic apparatus. First, in whole leaves of *X. strumarium*, the red region of the action spectrum of stomatal opening was identical with that of the assimilation of CO_2. Secondly, in leaves exposed to red light, stomata closed when inhibitors of photosynthetic electron transport like cyanazine or DCMU were applied; but conductance remained high when the experiment was performed in blue light (Fig. 4, Table I). Because the photosynthetic apparatus is not the only system that confers light sensitivity to the stomata, we have to expect variability among the effects inhibitors of photosynthesis have on stomatal behavior (see 9 for a review). For instance, it is easy to see why DCMU causes stomatal closure when the experimental material is exposed to an incandescent lamp which emits predominantly red light (4).

Where are the photoreceptors located? The close resemblance of the red regions of the action spectra of conductance and assimilation (Fig. 3), as well as the observed effects of inhibitors of photosynthesis, are consistent with the suggestion of Wong *et al.* (15) that stomata respond to a metabolite of photosynthesis in the mesophyll. In whole leaves the response of guard cells to red light could indeed have been mediated by light absorption in the photosynthetic tissue. But after referring to Figure 5 and comparing stomatal behavior in leaves in the normal position (light impinging upon the upper epidermis), with that in inverted leaves (light impinging upon the lower epidermis), we come to a different conclusion. The conductance of an epidermis was considerably higher when it faced the light than when it was turned away. This difference in opening occurred in the adaxial epidermis as well as in the abaxial epidermis, and in blue light as well as in red light. Therefore, the receptors for blue light and for red light appear to be located in each epidermis. If radiation absorbed in the meso-

phyll does contribute to stomatal opening then the layer of absorption must be very close to the epidermis. We have no evidence for such a situation. Rather, we know that the action spectra for stomatal opening in leaf discs and in whole leaves (reference 3 and this study) agree with the action spectra of various stomatal processes that were obtained on isolated epidermal samples (3, 5). We see no reason to postulate a contribution from the photosynthetic activity of the mesophyll to stomatal opening in the light other than that through the depletion of CO_2 of the intercellular spaces (13).

In isolated epidermis the photoreceptors for blue and red light must be situated in the guard cells themselves. Hsiao *et al.* (3) destroyed the ordinary epidermal cells by rolling and Ogawa *et al.* (5) by sonication. The action spectra for the accumulation of ^{86}Rb (3) as well as those for the accumulation of malate (5) prove that the metabolism of guard cells can be stimulated by blue and by red light; Zeiger and Hepler (16) showed that even isolated guard cell protoplasts begin to swell when they are exposed to light. We know that photosynthetic reduction of CO_2 does not occur in guard cells (6, 10, 12). If experimental evidence points to a participation of photosynthetic electron transport in the guard cells' responses to light, then this participation could occur through the provision of NADPH for the reduction of oxaloacetate to malate. We also have to consider the possibility that in guard cells the photosynthetic production of reducing equivalents is unimportant for the cells' supply of energy, but in combination with a response of the blue-light absorbing photoreceptor, is important for determining quantity and spectral composition of the light available to the leaf. (A one-pigment photoreceptor system is color-blind.)

Wong *et al.* (15) brought out the striking ability of plants to adjust their stomatal conductance in proportion to the needs of their photosynthetic apparatus for CO_2. The result of this adjustment is a nearly constant intercellular CO_2 concentration. We were surprised to learn that feedback (particularly of CO_2) contributes only partially to the apparent homeostasis of the intercellular level of CO_2 (13, 14). Much of the excellent correlation between conductance and photosynthesis is to be ascribed to the evolution of a concerted direct response of guard cells to light (13, 14), which in turn can be modified by the level of CO_2 in the air (Fig. 6). Light quality enters as a further modifying factor. When leaves of *X. strumarium* possessing stomata of low sensitivity to CO_2 were exposed to equal quantum fluxes of white, blue, and red light (Table II), white light of a spectral composition resembling that of sunlight caused conductances similar to those that occur in blue light. Conductances attained in the presence of an inhibitor of photosynthesis were of a magnitude equal to those reached when photosynthesis proceeded uninhibited; there is no indication of a dependence of conductance on photosynthesis in the mesophyll. Red light, when given alone, is insufficient to produce maximal stomatal conductance. We confirm the finding presented in Table IV of our previous publication (13) where we showed that, at a quantum flux of 740 $\mu E\ m^{-2}\ s^{-1}$, conductance was greater in blue light than in red light even though intercellular CO_2 concentration was higher and assimilation was lower.

Note added in proof: W. H. Outlaw, Jr., B. C. Mayne, V. E. Zenger, and J. Manchester (Plant Physiol. 67: 12–16) as well as E. Zeiger, P. Armond, and A. Melis (Plant Physiol. 67: 17–20) published evidence for the presence of a complete photosynthetic electron transport chain in guard-cell chloroplasts.

Table II. *Conductances for Water Vapor of Leaves of Xanthium strumarium Exposed to White or Monochromatic Light of Equal Quantum Fluxes*

Conductances are the sums of the conductances of the upper and lower epidermis. White light: light of a xenon arc lamp filtered through a Corning Glass No. 4600. Conversion factor is 4.5 $\mu E\ s^{-1}\ w^{-1}$ (13).

Light Treatment	Photosynthesis Inhibited	Ambient CO_2 Concentration	Conductance at a Quantum Flux of 180	450	700 ($\mu E\ m^{-2}\ s^{-1}$)	Source
		$\mu l\ l^{-1}$	*cmol* $m^{-2}\ s^{-1}$			
White[a]	no	320	35	39	47	Ref 13, Fig. 7
White	yes	250	27	50	60	Ref 13, Fig. 5
Blue, λ = 436 nm	no	320	35	54	60	This paper, Fig. 5
Red, λ = 681 nm	no	320	5	13	19	This paper, Fig. 5

[a] Data for leaf temperature 22 C; vapor pressure deficit 8 ml l^{-1}.

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