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THE ACTION SPECTRUM, ABSORPTANCE AND QUANTUM YIELD OF PHOTOSYNTHESIS IN CROP PLANTS

K. J. McCREE

Institute of Life Science and Biology Department, Texas A and M University, College Station, Texas (U.S.A.)

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ABSTRACT

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The measurements were made to provide a basis for discussion of the definition of "photosynthetically active radiation". The action spectrum, absorptance and spectral quantum yield of CO_2 uptake were measured, for leaves of 22 species of crop plant, over the wavelength range 350 to 750 nm. The following factors were varied: species, variety, age of leaf, growth conditions (field or growth chamber), test conditions such as temperature, CO_2 concentration, flux of monochromatic radiation, flux of supplementary white radiation, orientation of leaf (adaxial or abaxial surface exposed). For all species and conditions the quantum yield curve had 2 broad maxima, centered at 620 and 440 nm, with a shoulder at 670 nm. The average height of the blue peak was 70% of that of the red peak. The shortwave cutoff wavelength and the height of the blue peak varied slightly with the growth conditions and with the direction of illumination, but for the practical purpose of defining "photosynthetically active radiation" the differences are probably insignificant. The action spectrum for photosynthesis in wheat, obtained by HOOVER in 1937, could be duplicated only with abnormally pale leaves.

INTRODUCTION

The aim of these measurements is to provide a factual basis for a standard definition of "photosynthetically active radiation". The need for a standard definition has been repeatedly emphasized (e.g., GABRIELSEN, 1940; RABINOWITCH, 1951, pp.837–844; McCREE, 1966), but so far, no one definition has been agreed upon. In applied photosynthesis research, the three most commonly used units of light and radiation measurement are: (*1*) the illumination in lux or footcandles (flux of lumens, the photometric unit based on the brightness response of the eye); (*2*) the irradiance in W/m^2 or gcal. cm^{-2} min^{-1} (flux of radiant power within a certain waveband, such as 0.2–3 μ, 0.4–0.7 μ, 0.38–0.72 μ); and (*3*) the flux of absorbed quanta in micro-Einsteins, cm^{-2} sec^{-1} within a certain waveband, usually 0.4–0.7 μ. These are measurements of three quite different characteristics of light, and there is no unique way to relate one with another.

Certain basic information about the spectral response of photosynthesis is required for a rational discussion of the relative merits of the various definitions

of photosynthetically active radiation. This could be in the form of an action spectrum, that is, the rate at which carbon dioxide is taken up (or oxygen evolved), divided by the rate at which energy is received by the leaf. A more basic parameter is the spectral quantum yield, which is the rate of photosynthesis per unit rate of absorption of quanta; this can be calculated from the action spectrum, the energy per quantum and the spectral absorptance of the leaf.

If the action spectrum were flat between the wavelengths 400 and 700 nm, the irradiance within this waveband would be a perfect measure of photosynthetically active radiation. If the spectral quantum yield were flat, the flux of absorbed quanta would be the perfect measure.

REVIEW OF THE LITERATURE

RABINOWITCH (1951, pp.1142–1168) and GABRIELSEN (1960) have reviewed the literature on spectral effects in photosynthesis and only a few key papers need to be mentioned here. Almost all of the quantum yield measurements center on the role of the carotenoids and other accessory pigments, and they have been made on algae, which provide a more interesting range of pigment systems for physiological research than higher plants (EMERSON and LEWIS, 1943; HAXO and BLINKS, 1950; TANADA, 1951; HAXO, 1960; BLINKS, 1964; KRINSKY, 1968).

Action spectra for photosynthesis in higher plants have been obtained for wheat (HOOVER, 1937), for radish and corn (BULLEY et al., 1969), and for bean (BALEGH and BIDDULPH, 1970). Some more limited measurements with three broadband colored filters were made on *Sinapis alba*, *Corylus maxima* and *Fraxinus excelsior* by GABRIELSEN (1940), and on wheat, pine and spruce by BURNS (1942).

The action spectra are quite diverse. The Hoover curve for wheat has two very pronounced peaks, one in the red and the other in the blue. Burns obtained roughly the same result for wheat, but not for pine and spruce, which showed much lower rates in the blue than in the red. The leaves tested by Gabrielsen, by Bulley et al. and by Balegh and Biddulph also gave a lower response in the blue. As Gabrielsen pointed out, differences of this type could be caused by differences in spectral absorptance between a dark green and a pale green leaf. The absorptance was not measured in these studies.

Spectral quantum yields have been measured for *Solidago virgaurea* L., *Mimulus cardinalis* and *Plantago lanceolata* (BJÖRKMAN, 1966, 1968; BJÖRKMAN et al., 1965). These three species of wild plant showed very similar responses. Quantum yield was relatively constant from 650 nm to the limit of measurement at 450 nm, a fact used by TANNER (1968) as a basis for his proposal that photosynthetically active radiation be measured with a quantum counter. There was a sharp fall at 700 nm, which could be modified by simultaneous irradiation with shorter wavelengths (Emerson enhancement). Some algal measurements (MCLEOD and KANWISHER, 1962; HALLDAL, 1964, 1967) indicate that photosynthesis can

occur in the ultraviolet down to about 300 nm, but the shortwave limit has not been determined for higher plants. One would expect that ultraviolet radiation would have more difficulty penetrating to the chloroplasts.

As a basis for a discussion of the definition of "photosynthetically active radiation", the published measurements have the following limitations:

(*1*) they do not extend to the shortwave limit of photosynthesis;

(*2*) they cover a very limited range of species (especially of crop plant);

(*3*) there are no data on the variability within species, within varieties, or within a single plant;

(*4*) there are no data on the variability with growth conditions or with test conditions; and

(*5*) there are no comparisons of the action spectra and the spectral quantum yield, as possible invariate plant parameters.

The measurements described in this paper were done to provide a more comprehensive set of data.

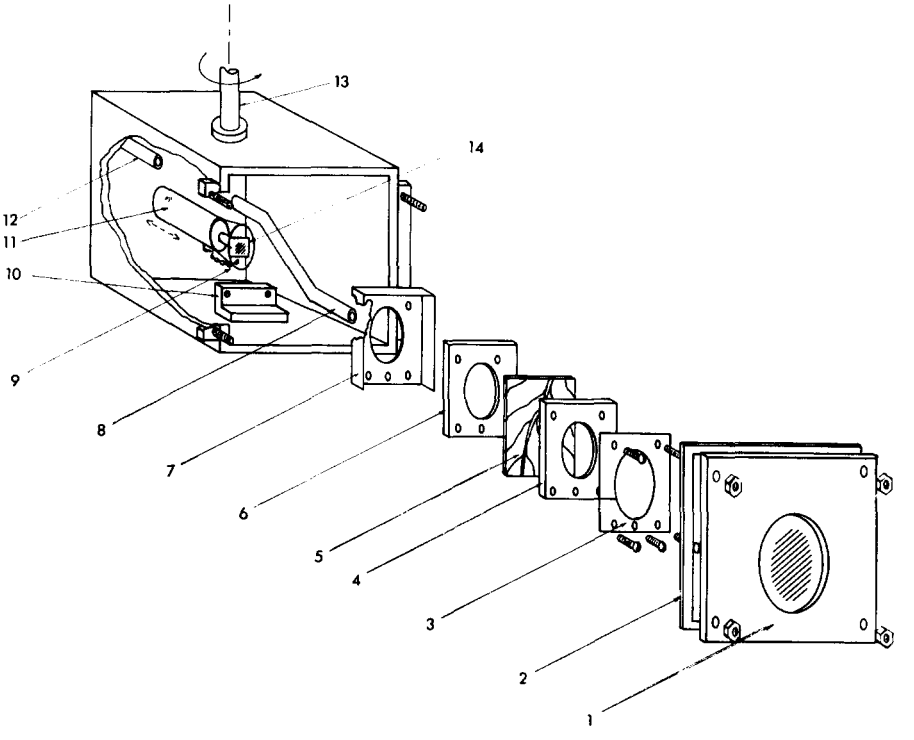

Fig.1. Assimilation chamber. *1* = front plate of chamber, with quartz window; *2* = gasket; *3* = front plate of leaf holder; *4* = wet cellulose sponge; *5* = leaf sample; *6* = wet cellulose sponge; *7* = back plate of leaf holder; *8* = air inlet; *9* = thermocouple for leaf temperature measurement; *10* = mounting block for leaf holder; *11* = adjustable holder for thermocouple and thermopile; *12* = air outlet; *13* = shaft of fan; *14* = thermopile for irradiance measurements.

TABLE I

LIST OF PLANTS USED

	Common name	*Species*	*Cultivar*
	Grain crops		
1	Corn	*Zea mays* L.	Texas hybrid 28A
2	Sorghum	*Sorghum bicolor* L. Moench	Hybrid RS 626
3	Wheat	*Triticum aestivum* L. em. Thell.	Tascosa
4	Oats	*Avena sativa* L.	Coronado
5	Barley	*Hordeum vulgare* L.	Era Goliad Cordova
6	Triticale	*Triticum durum* Desf. × *Secale cereale* L.	
7	Rice	*Oryza sativa* L.	Lacrosse
	Oilseed crops		
8	Sunflower	*Helianthus annuus* L.	HA 60
9	Soybean	*Glycine max* L.	Lee
10	Castorbean	*Ricinus communis* L.	Hale
11	Peanut	*Arachis hypogaea* L.	Starr
	Vegetable crops		
12	Lettuce	*Lactuca sativa*	Great Lakes Big Boston
13	Tomato	*Lycopersicon esculentum*	Floradel
14	Radish	*Raphanus sativus*	Globemaster
15	Cabbage	*Brassica oleracea* L.	Marion Market
16	Cucumber	*Cucumis sativus* L.	Ohio MR-17
17	Cantaloupe	*Cucumis melo* L.	Perlita
18	Squash	*Cucurbita pepo* L.	Early prolific straightneck Dixie hybrid yellow
	Miscellaneous		
19	Clover	*Trifolium repens* L.	New Zealand White C1852
20	Cotton	*Gossypium hirsutum* L.	Deltapine
21	Sugarbeet	*Beta vulgaris* L.	S 1
22	Pigweed	*Amaranthus edulis* Speg.	UCD 1966

PLANT MATERIALS

Table I lists the plants used.

During the fall and winter months, the plants were grown in a growth chamber in the following conditions: day temperature 25 ± 1 °C; night temperature 20 ± 1 °C; irradiance 100 ± 20 W m^{-2} (400–700 nm); light source, cool-white fluorescent plus incandescent lamps; daylength 16 h. The plants were grown in vermiculite and were supplied daily with nutrient of the following composition (concentrations in mg/l): $NH_4H_2PO_4$ 117; KNO_3 605; $Ca(NO_3)_2 \cdot 4H_2O$ 944;

$MgSO_4 \cdot 7H_2O$ 494; H_3BO_3 3.1, $MnCl_2 \cdot 4H_2O$ 2.0; $ZnSO_4 \cdot 7H_2O$ 0.23; $CuSO_4 \cdot 5H_2O$ 0.10; $Na_2MoO_4 \cdot 2H_2O$ 0.10; $FeSO_4 \cdot 7H_2O$ 25; Na_2-EDTA 33; KOH to pH 6–7.

During the spring and summer months, samples of selected species were also taken from plants growing on the university farm in College Station, Texas.

METHODS

The measurements were made with the apparatus shown in Fig.1 and 2.

Photosynthesis measurements (Fig.1)

A section of leaf approximately 25 mm square was cut with a razor blade and placed, within a few seconds, between two sheets of wet household cellulose sponge. The sandwich of leaf and sponge was then clamped between two sheets of aluminum and screwed into a block in the base of the assimilation chamber. The sponge dipped into a pool of water in the bottom of the chamber. The chamber was closed and the air supply was turned on. For the standard test, air from a cylinder of compressed air (breathing quality), containing 350 $\pm$ 20 μl per litre of CO_2, was humidified by passing it over a saturated solution of NaCl in boiled distilled water (75% r.h.). The flow rate was 200 $\pm$ 10 ml min^{-1}, measured with a Brooks Sho-Rate rotameter. The volume of the chamber was 125 ml. The air in the chamber was stirred with a fan rotating at 3,000 r.p.m. The temperature of the air was 28 $\pm$ 1 °C, and the temperature of the leaf, as measured with a thermocouple pressed to the back surface, was within 0.5 °C of the air temperature.

The effect of changing the temperature (11 °–38 °C) and CO_2 concentration (200–600 $\mu l\ l^{-1}$) was determined on selected samples.

The difference in CO_2 concentration between incoming and outgoing air was measured with a differential infra-red gas analyser (Beckman 315A). It was less than 10 $\mu l\ l^{-1}$, and was measured to $\pm$ 0.2 $\mu l\ l^{-1}$. Since both air streams were humidified, the water added by the leaf had little effect on the differential indicated by the analyser (less than 2% of the differential). The area of sponge exposed to the air was kept to a minimum to reduce exchange of CO_2 by the water in the sponge. As an additional precaution, boiled distilled water was used in the sponge, and both were kept over KOH when not in use.

The photosynthetic rates of leaf sections treated in this manner were surprisingly reproducible. After a period of up to one hour of adaptation in moderate illumination, during which the stomata were presumably opening, the rate of CO_2 uptake under constant test conditions remained steady ($\pm$ 5%) for several hours. (BARTOS et al., 1960; NATR, 1970). The only exception was when the leaf was under water stress at the time the sample was cut. We had no means of determining whether or not the absolute rates of photosynthesis would be identical in an intact leaf. We were primarily interested in comparing the relative response at

different wavelengths. This was quite reproducible from one sample to another. All the curves presented here are the averages of at least two curves from different samples.

Light source (Fig.2)

Monochromatic light was obtained from a Bausch and Lomb High Intensity Monochromator, fitted with a grating which covered the range 350–800 nm, a xenon arc light source, quartz optics, and variable slits. Higher orders of diffracted light were blocked with Corning CS 0–54 (350–575 nm) and CS 3–69 (600–750 nm) glass filters. A quartz cuvette containing water was placed before the entrance slit to reduce the radiant heat load on the grating. The wavelength calibration was checked with the mercury lines from a fluorescent lamp and found to be correct

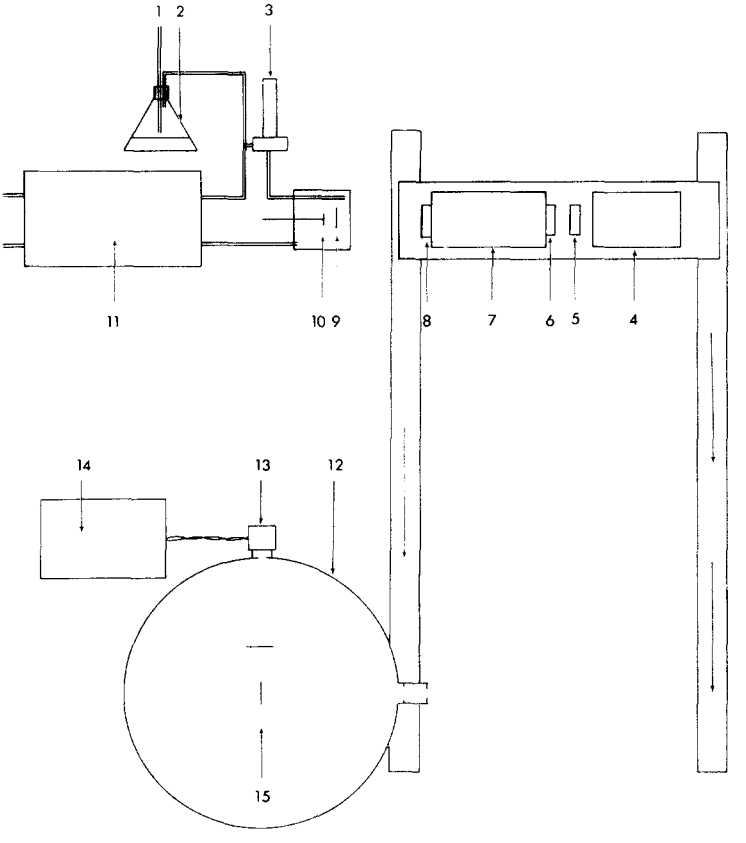

Fig.2. Schematic diagram of equipment. *1* = compressed air supply; *2* = humidifier; *3* = flowmeter; *4* = xenon light source; *5* = water filter; *6* = entrance slit; *7* = grating monochromator; *8* = exit slit; *9* = leaf sample in assimilation chamber; *10* = thermopile and thermocouple; *11* = CO_2 analyser; *12* = integrating sphere; *13* = photomultiplier; *14* = photometer; *15* = leaf sample in sphere for absorptance measurements.

within ± 3 nm. Stray light was checked with Corning CS 7–54, 3–69 and 3–73 filters and found to be less than 2%. The width of the entrance slit was set to 6 mm, and the width of the exit slit was varied, from 1.5 mm up to a maximum of 4 mm, which corresponds to a bandwidth of 25 nm, according to the manufacturer's specifications. The irradiance at the leaf was found to be proportional to the slit width, at all wavelengths.

The monochromator produced a spot of light about 22 mm in diameter, and this was masked down to 20 ± 1 mm. The irradiance at the leaf surface was measured with an Eppley air thermopile, 6 mm square, which could be moved forward to the position normally occupied by the leaf. The irradiance was uniform to ± 5%. The output of the thermopile was measured on a Hewlitt Packard DC Micro Volt Ammeter, Model 425A, calibrated to ± 2% with a Leeds and Northrup Millivolt Potentiometer, Model 8686.

Experimental design

The photosynthesis measurements were made as follows. The leaf was kept under an irradiance of 30 W m^{-2} at 650 nm until a steady reading of CO_2 differential was obtained. The irradiance was then reduced to zero in 5 steps, in order to determine the dependence of the gross photosynthetic rate (light reading–dark reading) on irradiance, at 650 nm. This relationship was always hyperbolic (RABINOWITCH, 1951, p.1043; MOSS, 1964). Consequently, the action and quantum yield could not legitimately be calculated by dividing the photosynthetic rate by the irradiance, no matter how low the irradiance. However, experiments showed that the effect of the non-linearity was independent of wavelength, if the measurements were made at a constant photosynthetic rate, rather than at constant irradiance. Details of these experiments will be presented later. The absolute value of the quantum yield obtained at a constant photosynthetic rate was less than the maximum, by 10–30%, depending on the shape of the irradiance response curve.

The following sequence was used: dark, 350, 375 . . . 725, 750 nm, dark, 750, 725 . . . 375, 350 nm, dark. At each wavelength, the width of the exit slit was adjusted until the photosynthetic rate was the same as at the previous wavelength. Where this was not possible (wavelengths 400 nm or less, and 700 nm or more) the slit was set to 4 mm. A steady reading was normally reached within 2 min, and the whole sequence could usually be completed in 90 min. If the reading obtained during the return half of the cycle was not within 10% of that obtained during the outgoing half, the whole set of results was rejected. With corn, and more particularly with sorghum, the readings at some wavelengths showed damped oscillations which took up to 15 min to die out (BJÖRKMAN et al., 1970) and it sometimes took several hours to obtain a good set of equilibrium readings.

Absorptance measurements (Fig.2)

When the photosynthesis measurements were complete, the leaf sample

was removed, clamped into a transparent acrylic holder and placed into the integrating sphere for absorptance measurements. The sphere was coated with several layers of Eastman White Reflectance Paint, which has a barium sulfate base. The radiance of the sphere wall, with and without the sample in place, was determined with a photomultiplier photometer (Gamma Scientific, Model 2020), and the spectral absorptance calculated from the difference in readings. The light source and monochromator used for the photosynthesis measurements were also used for the absorptance measurements. The bandwidth was constant at 20 nm.

Calculation of results

The following parameters were calculated for each wavelength:

absorptance $= (PM_o - PM_s)/PM_o$

where PM_o = photomultiplier reading without sample; and PM_s = photomultiplier reading with sample.

action $= k_1(C_L + C_D)/I$

where k_1 = constant to convert to micromoles/joule; C_L = CO_2 differential in light; C_D = CO_2 differential in dark (interpolated); and I = irradiance.

quantum yield $= k_2$(action)/(wavelength $\times$ absorptance)

where k_2 = constant to convert to moles/Einstein absorbed.

relative action, relative quantum yield = action, quantum yield normalized to a maximum of 1.00

RESULTS

Effect of test conditions

Irradiance. The relationship between photosynthetic rate (P) and irradiance (I) closely fitted a rectangular hyperbola of the form:

$$P = aI/(1+bI)$$

where a is the slope at zero I; and $1/b$ is the value of P at infinite I. This may be re-arranged to give:

$$P/I = a - bP$$

Thus for any given wavelength, a plot of quantum yield Q (which is proportional to P/I) against P should be a straight line, the intercept on the ordinate being the value of Q as P tends to zero, and the slope being a measure of the effect of increasing P on Q. If the slope is independent of wavelength, the shape of the spectral quantum yield curve measured at constant P will be the same as that at $P = 0$, where Q is a maximum. This was tested on several samples and found to be approximately true. The results for a cantaloupe leaf are shown in Table II and Fig.3. These results indicate that the effect of irradiance on the relative spectral quantum yield can be ignored, if the measurements are made at constant P.

TABLE II

CONSTANTS IN THE LINEAR EQUATIONS RELATING Q TO P, AT VARIOUS WAVELENGTHS, FOR A CANTALOUPE LEAF FROM THE GROWTH CHAMBER[1]

Wavelength (nm)	*Intercept Q_0 (10^{-2} moles/Eins.)*	*Slope dQ/dP (10^3sec m^2/Eins.)*	*Regression coeff. ($n = 6$)*
400	3.4	3.6	0.97
450	5.8	5.1	0.98
500	5.2	3.8	0.94
550	6.8	4.1	0.96
600	8.1	5.8	0.91
650	7.0	4.7	0.92
675	7.7	6.4	0.89
700	3.9	2.9	0.81

[1] P was varied over the range 1–6 micromoles $sec^{-1}m^{-2}$ (1.6–9.6 mg hr^{-1} dm^{-2}), by varying the irradiance from 3 to 27 W m^{-2} (16–150 micro-Einsteins sec^{-1} m^{-2}).

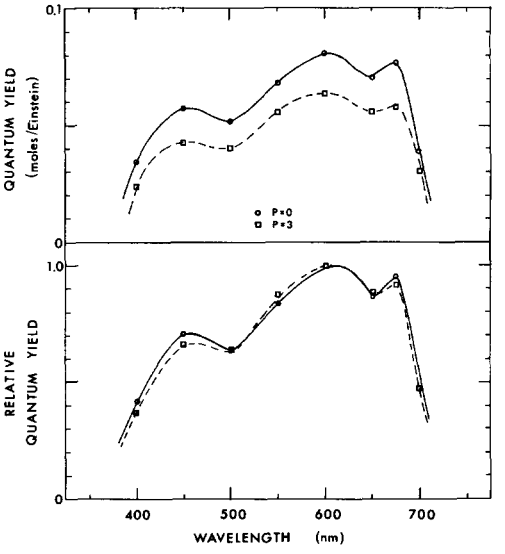

Fig.3. Effect of irradiance on spectral quantum yield; cantaloupe leaf from growth chamber. $P = 3$, irradiance adjusted at each wavelength for constant photosynthetic rate of 3 micromoles $sec^{-1}m^{-2}$ (4.8 mg h^{-1} dm^{-2}); $P = 0$, extrapolated values for zero P (Table II).

Temperature. The effect of ambient air temperature on the quantum yield was determined for samples of oat and corn leaves. For oat (Fig.4), the absolute quantum yield decreased slightly with increasing temperature, but the relative spectral yield remained constant. For corn, there was possibly a slight reduction in yield in the blue relative to the red, with decreasing temperature.

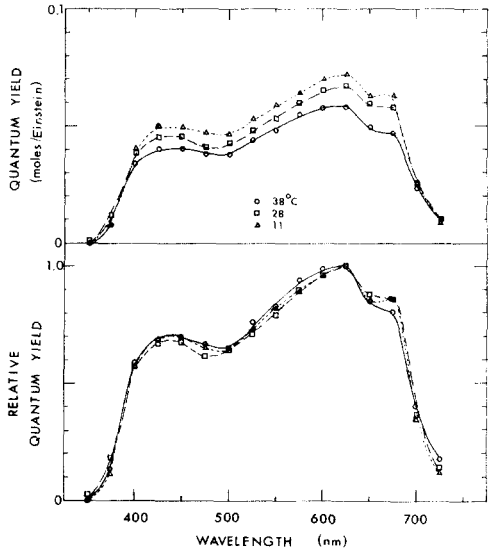

Fig.4. Effect of ambient air temperature on spectral quantum yield; oat leaf from growth chamber.

CO_2 concentration. The effect of ambient CO_2 concentration was tested with sugar beet (Fig.5). The absolute quantum yield increased with increasing CO_2 concentration, but the relative spectral yield remained constant.

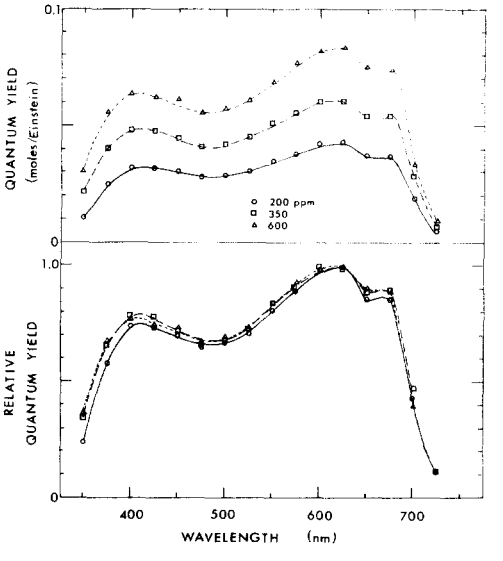

Fig.5. Effect of ambient CO_2 concentration on spectral quantum yield; sugar beet leaf from growth chamber.

Added white light. It has been shown many times (MYERS, 1963; BJÖRKMAN, 1968) that the photosynthetic rate in the combined radiation of two wavelengths is not equal to the sum of the two separate photosynthetic rates. This is known as the Emerson enhancement effect, and it is greatest at the far red end of the spectrum, where the two photosystems in the chloroplast apparently have unequal sensitivities (FORK and AMESZ, 1969).

Because the effects of different wavelengths are not additive, it is not possible to calculate the photosynthetic efficacies of white light sources from any action spectrum or spectral quantum yield curve. In addition, since the degree of enhancement depends on the species and the test conditions (for example, an excess of the shorter wavelength is required), it is difficult to estimate the size of the error.

The most practical test would be to calculate the photosynthetic rate in white light, from the action spectrum and the spectral distribution of the light, and to compare the calculated rate with the observed rate. Tests of this nature are under way, and will be reported elsewhere.

In the meantime, we can report the results of a different experiment which should indicate the possible size of the Emerson enhancement error. White light from the xenon arc was piped around the monochromator to the sample with an acrylic plastic light pipe. The spectrum of this light is shown in Fig.6. It is

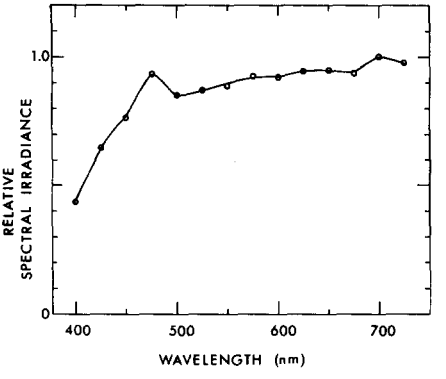

Fig.6. Spectrum of the white light added to monochromatic light for the enhancement test.

probably sufficiently broad to keep both chloroplast photosystems in operation. To this white light was added a small amount of monochromatic light of different wavelengths. The increment in photosynthetic yield was compared with the yield in monochromatic light alone (Fig.7).

The absolute quantum yield of the monochromatic light decreased when the white light was added, because of the non-linearity of photosynthetic response, but the relative spectral response remained constant, indicating that under these conditions, Emerson enhancement was negligible. The same result was obtained with corn and sorghum leaves.

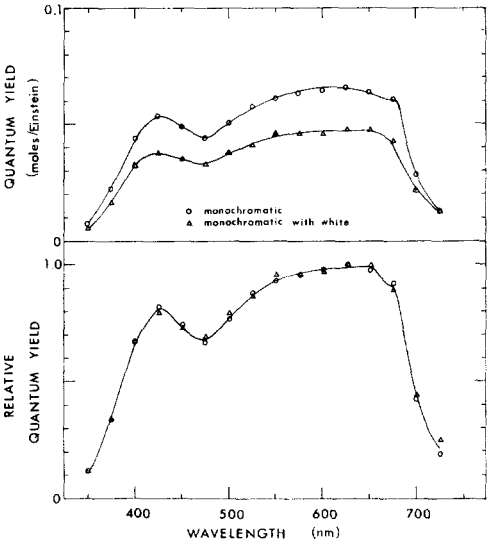

Fig.7. Effect of added white light on spectral quantum yield; oat leaf from growth chamber. P in monochromatic light = 2.4 micromoles $sec^{-1}m^{-2}$; P in white light = 5.3 micromoles $sec^{-1}m^{-2}$.

Effect of leaf variables

Orientation. Under natural conditions, both sides of the leaf receive light. MOSS (1964) found that in white light, the photosynthetic responses of the two sides

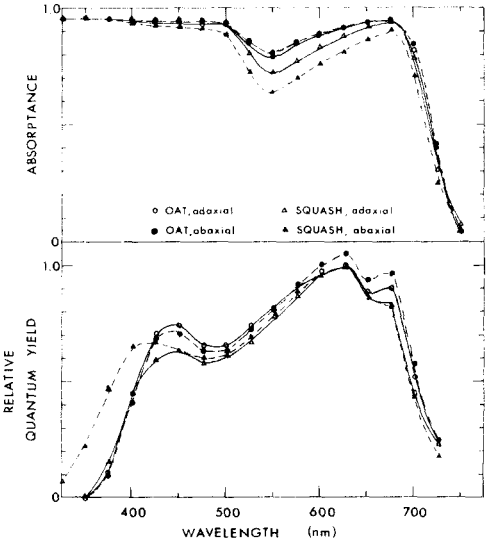

Fig.8. Effect of orientation of leaf to light beam, for a typical monocot (oat) and a typical dicot (squash); field samples.

were equal for the monocotyledons corn and sugar cane, but unequal for the dicotyledons sunflower and tobacco. We have found the same to be true for the spectral response (Fig.8).

In the monocots (oat is used as an example), the spectral absorptance was the same for both surfaces, but in the dicots (such as squash) the lower (abaxial) surface had a smaller absorptance, mainly because of its greater reflectance. Consequently, the photosynthetic rate of the leaf was less when the lower surface was illuminated. However, the yield per quantum absorbed was generally the same for both directions of illumination, except at the ultraviolet end of the spectrum, where the yield was greater for light directed to the lower surface.

The most likely explanation is that the ultraviolet radiation penetrated to the chloroplasts more easily through the lower surface (METZNER, 1930; SEYBOLD and WEISSWEILER, 1942; CALDWELL, 1968). The difference is interesting, but not of great practical importance, since:
(*1*) the leaves of dicots are displayed more or less horizontally; and (*2*) few light sources produce a large proportion of their radiation in this part of the spectrum. Only the results for the upper (adaxial) surface are presented in the following sections.

Growth conditions. Similar differences in the ultraviolet were found when plants grown in the field were compared with those grown in the growth chamber (Fig.9). In every case, the field-grown material had a smaller ultraviolet response. At the same time, the dry weight per unit area of leaf was greater (Fig.10), again indicating that the loss of response was due to the ultraviolet radiation having to pass through

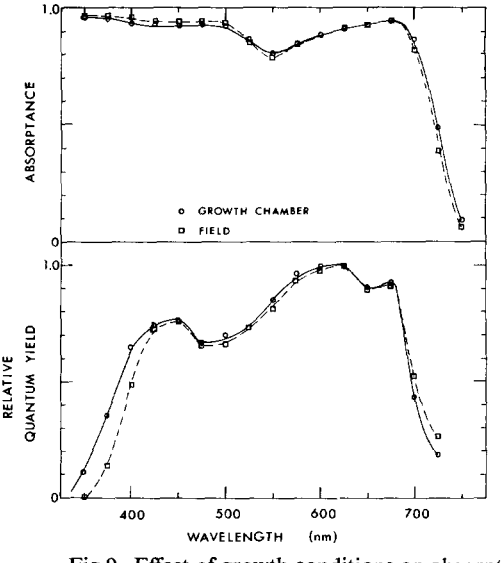

Fig.9. Effect of growth conditions on absorptance and spectral quantum yield; oat leaves.

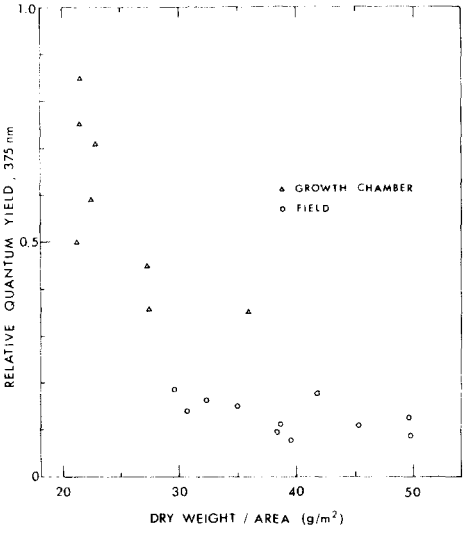

Fig.10. Relationship of quantum yield in the ultraviolet to dry weight per unit area, for field and growth chamber samples of various species.

more material to reach the chloroplasts. The absorptance of the whole leaf was always so high in this region that it was barely possible to detect differences in absorptance due to growth conditions.

Age. The effect of leaf age was tested on a field-grown corn plant. The plant was growing rapidly in the vegetative phase, was 2 m high and had 17 leaves, 5 of

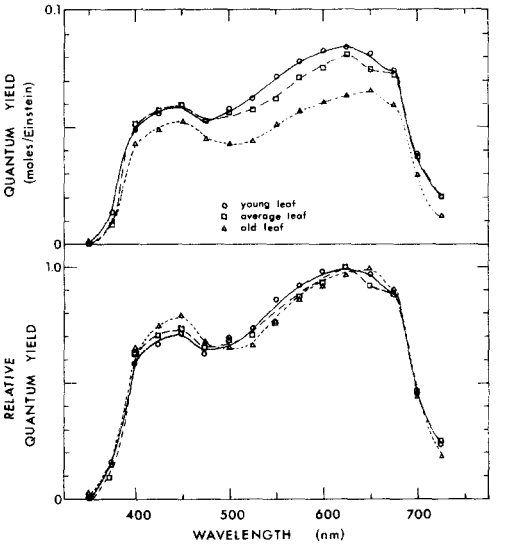

Fig.11. Effect of leaf age on spectral quantum yield; corn plant, field.

which were sampled. The youngest leaves showed the highest absolute quantum yields (Fig.11), but the relative spectral quantum yield was very similar for all leaves. A limited number of tests was also made on other species, grown in the growth chamber, with the same result.

Variety. No significant varietal effects were detected in tests made with three varieties of barley and two varieties of squash (Fig.12).

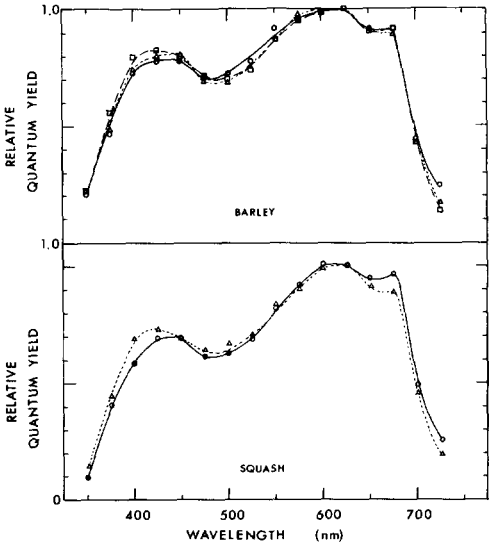

Fig.12. Spectral quantum yield for three varieties of barley (Era, Goliad and Cordova) and two varieties of squash (Early prolific straightneck and Dixie hybrid yellow). Growth chamber samples.

Species. The results for the 21 species tested are tabulated in Tables III–VIII. The superimposed relative quantum yield curves in Fig.13 illustrate the range of curve shapes encountered. The growth chamber plants have been separated from the field plants, because of the systematic differences described above.

In the growth chamber plants, the shortwave cutoff wavelength varied considerably. Since those species which produced thinner and more succulent leaves, such as lettuce, radish and clover had a greater ultraviolet response than those which produced a more robust leaf, such as sunflower, castorbean and peanut, it is reasonable to ascribe these differences to differences in leaf anatomy, rather than to differences in photochemistry.

The field plants cover a more limited range of species, since not all of those listed are grown in this area. Nevertheless, it does appear that the shortwave cutoff wavelength was more constant, as well as longer, for the field-grown plants.

As mentioned earlier, the plants which have the C_4-dicarboxylic acid

TABLE III

RELATIVE QUANTUM YIELD OF GROWTH CHAMBER PLANT SPECIES (Nr. 1–22 from Table I)

nm	*1*	*2*	*3*	*4*	*5*	*6*	*8*	*9*	*10*	*11*	*12*	*13*	*14*	*15*	*16*	*17*	*18*	*19*	*21*	*22*	*Mean*
350	0.08	0.21	0.20	0.11	0.20	0.17	0.01	0.10	0.12	0.02	0.15	0.14	0.42	0.12	0.05	0.08	0.15	0.23	0.29	0.28	0.16
375	0.42	0.56	0.39	0.35	0.47	0.49	0.11	0.27	0.21	0.22	0.53	0.47	0.81	0.50	0.22	0.26	0.45	0.76	0.57	0.84	0.45
400	0.69	0.75	0.60	0.65	0.73	0.69	0.37	0.55	0.39	0.57	0.75	0.59	0.79	0.70	0.54	0.50	0.70	0.90	0.72	0.95	0.66
425	0.77	0.86	0.78	0.75	0.78	0.77	0.68	0.72	0.60	0.73	0.78	0.66	0.77	0.79	0.67	0.70	0.73	0.87	0.75	0.85	0.76
450	0.75	0.72	0.79	0.77	0.78	0.77	0.78	0.77	0.66	0.72	0.75	0.72	0.73	0.76	0.69	0.67	0.70	0.80	0.70	0.83	0.75
475	0.72	0.65	0.72	0.67	0.71	0.71	0.65	0.67	0.58	0.65	0.66	0.66	0.70	0.67	0.65	0.63	0.65	0.70	0.62	0.76	0.68
500	0.77	0.76	0.71	0.70	0.73	0.69	0.67	0.67	0.64	0.68	0.72	0.68	0.72	0.69	0.68	0.67	0.67	0.73	0.66	0.73	0.71
525	0.75	0.79	0.71	0.74	0.78	0.71	0.71	0.77	0.69	0.70	0.76	0.73	0.73	0.71	0.75	0.75	0.70	0.74	0.71	0.68	0.74
550	0.83	0.84	0.89	0.85	0.92	0.88	0.80	0.86	0.85	0.84	0.86	0.85	0.87	0.86	0.83	0.83	0.83	0.90	0.85	0.86	0.87
575	0.97	0.85	0.97	0.96	0.95	0.97	0.91	0.94	0.92	0.94	0.94	0.93	0.93	0.93	0.94	0.99	0.89	1.00	0.91	0.92	0.95
600	0.98	0.93	1.00	1.00	1.00	1.00	0.97	0.98	1.00	1.00	1.00	0.98	1.00	1.00	1.00	1.00	0.98	1.00	0.95	1.00	1.00
625	1.00	0.98	0.96	0.99	1.00	0.97	1.00	1.00	0.98	1.00	0.99	1.00	0.99	0.98	0.98	0.97	1.00	0.98	1.00	0.99	1.00
650	0.93	1.00	0.91	0.91	0.92	0.94	0.90	0.90	0.92	0.94	0.94	0.92	0.98	0.89	0.94	0.94	0.91	0.91	0.87	0.97	0.94
675	0.91	0.85	0.95	0.93	0.92	0.87	0.95	0.98	0.93	0.95	0.96	0.88	0.93	0.91	0.89	0.93	0.89	0.86	0.87	0.90	0.92
700	0.44	0.47	0.44	0.44	0.44	0.44	0.41	0.44	0.42	0.44	0.46	0.42	0.46	0.47	0.42	0.39	0.44	0.43	0.44	0.45	0.44
725	0.21	0.10	0.15	0.19	0.25	0.17	0.21	0.19	0.23	0.19	0.29	0.19	0.24	0.20	0.19	0.18	0.19	0.25	0.12	0.18	0.20

TABLE IV

RELATIVE QUANTUM YIELD OF FIELD PLANT SPECIES

nm	*1*	*3*	*4*	*6*	*7*	*8*	*18*	*20*	*Mean*
350	0.01	0.01	0.00	0.00	0.02	0.04	0.00	0.04	0.02
375	0.10	0.09	0.14	0.08	0.14	0.14	0.15	0.09	0.12
400	0.61	0.37	0.50	0.36	0.40	0.41	0.47	0.31	0.42
425	0.71	0.66	0.73	0.72	0.74	0.68	0.59	0.65	0.68
450	0.75	0.68	0.76	0.76	0.71	0.74	0.63	0.64	0.70
475	0.66	0.64	0.65	0.68	0.63	0.71	0.58	0.54	0.63
500	0.69	0.68	0.66	0.65	0.64	0.68	0.62	0.58	0.65
525	0.70	0.77	0.73	0.75	0.77	0.73	0.68	0.68	0.72
550	0.78	0.88	0.81	0.83	0.85	0.85	0.79	0.78	0.82
575	0.89	0.94	0.93	0.93	0.92	0.94	0.87	0.85	0.91
600	0.94	0.98	0.97	0.97	1.00	0.97	0.97	0.96	0.97
625	1.00	1.00	1.00	1.00	0.99	1.00	1.00	1.00	1.00
650	0.95	0.89	0.90	0.91	0.94	0.89	0.86	0.90	0.90
675	0.91	0.88	0.91	0.92	0.91	0.91	0.84	0.94	0.90
700	0.46	0.51	0.53	0.53	0.47	0.43	0.43	0.47	0.48
725	0.25	0.27	0.27	0.23	0.23	0.16	0.23	0.19	0.23

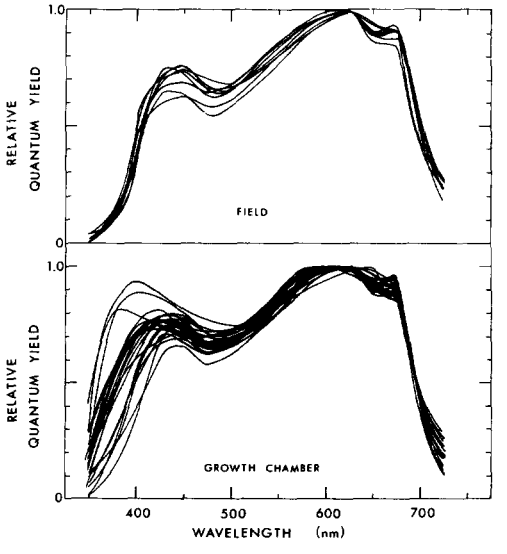

Fig.13. Spectral quantum yields, all samples. Individual results are tabulated in Tables III and IV.

TABLE V

RELATIVE ACTION OF GROWTH CHAMBER PLANT SPECIES (Nr. 1–22)

nm	*1*	*2*	*3*	*4*	*5*	*6*	*8*	*9*	*10*	*11*	*12*	*13*	*14*	*15*	*16*	*17*	*18*	*19*	*21*	*22*	*Mean*
350	0.05	0.12	0.11	0.06	0.12	0.10	0.01	0.05	0.07	0.01	0.08	0.08	0.24	0.07	0.03	0.04	0.09	0.14	0.17	0.16	0.09
375	0.26	0.34	0.24	0.21	0.29	0.31	0.07	0.16	0.13	0.13	0.31	0.30	0.48	0.30	0.14	0.15	0.28	0.49	0.36	0.52	0.28
400	0.45	0.48	0.38	0.41	0.46	0.46	0.24	0.34	0.25	0.36	0.46	0.39	0.50	0.44	0.36	0.32	0.47	0.61	0.48	0.62	0.43
425	0.54	0.58	0.51	0.50	0.53	0.53	0.46	0.47	0.41	0.49	0.51	0.45	0.52	0.53	0.48	0.47	0.52	0.63	0.54	0.60	0.52
450	0.55	0.52	0.55	0.54	0.56	0.57	0.56	0.53	0.47	0.51	0.52	0.54	0.53	0.54	0.52	0.48	0.53	0.62	0.53	0.62	0.54
475	0.56	0.49	0.53	0.50	0.54	0.55	0.49	0.48	0.43	0.48	0.48	0.52	0.53	0.50	0.51	0.47	0.51	0.57	0.50	0.59	0.51
500	0.61	0.58	0.55	0.55	0.57	0.57	0.52	0.50	0.51	0.53	0.53	0.56	0.56	0.55	0.56	0.52	0.55	0.62	0.55	0.59	0.56
525	0.54	0.56	0.52	0.57	0.58	0.56	0.52	0.57	0.53	0.53	0.47	0.58	0.52	0.55	0.59	0.56	0.51	0.56	0.53	0.50	0.55
550	0.55	0.57	0.62	0.65	0.66	0.68	0.56	0.63	0.64	0.61	0.48	0.65	0.58	0.64	0.64	0.61	0.46	0.65	0.60	0.58	0.61
575	0.75	0.66	0.75	0.80	0.76	0.82	0.72	0.75	0.76	0.74	0.62	0.79	0.70	0.76	0.79	0.80	0.70	0.80	0.74	0.70	0.75
600	0.84	0.80	0.86	0.91	0.88	0.93	0.85	0.85	0.90	0.87	0.77	0.92	0.85	0.90	0.93	0.89	0.86	0.91	0.86	0.86	0.88
625	0.94	0.91	0.89	0.96	0.95	0.97	0.94	0.92	0.94	0.93	0.84	1.00	0.92	0.95	0.98	0.92	0.96	0.97	0.98	0.94	0.95
650	0.95	1.00	0.90	0.93	0.95	1.00	0.91	0.88	0.94	0.93	0.88	0.98	0.98	0.92	1.00	0.94	0.94	0.98	0.92	0.99	0.96
675	1.00	0.91	1.00	1.00	1.00	0.97	1.00	1.00	1.00	1.00	1.00	0.99	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
700	0.41	0.37	0.42	0.45	0.42	0.47	0.38	0.42	0.41	0.42	0.37	0.42	0.41	0.46	0.42	0.38	0.42	0.43	0.44	0.45	0.42
725	0.08	0.05	0.08	0.11	0.11	0.10	0.08	0.10	0.11	0.09	0.08	0.08	0.08	0.09	0.08	0.08	0.07	0.09	0.06	0.08	0.09
750	0.04	0.02	0.00	0.02	0.04	0.03	0.04	0.02	0.01	0.02	0.02	0.02	0.02	0.01	0.03	0.01	0.02	0.01	0.00	0.03	0.02

TABLE VI

RELATIVE ACTION OF FIELD PLANT SPECIES

nm	*1*	*3*	*4*	*6*	*7*	*8*	*18*	*20*	*Mean*
350	0.01	0.01	0.00	0.00	0.01	0.02	0.00	0.02	0.01
375	0.06	0.05	0.09	0.05	0.09	0.09	0.10	0.05	0.07
400	0.40	0.25	0.32	0.24	0.26	0.27	0.32	0.20	0.28
425	0.49	0.47	0.50	0.50	0.51	0.48	0.44	0.44	0.48
450	0.55	0.51	0.55	0.55	0.52	0.55	0.49	0.44	0.52
475	0.51	0.51	0.50	0.52	0.49	0.55	0.48	0.41	0.49
500	0.55	0.55	0.53	0.51	0.52	0.55	0.53	0.46	0.53
525	0.53	0.59	0.56	0.54	0.58	0.57	0.52	0.51	0.55
550	0.58	0.67	0.60	0.57	0.60	0.65	0.57	0.57	0.60
575	0.73	0.80	0.78	0.73	0.72	0.79	0.70	0.69	0.74
600	0.85	0.90	0.88	0.84	0.87	0.88	0.88	0.85	0.87
625	0.97	1.00	0.98	0.94	0.94	0.97	1.00	0.95	0.97
650	0.98	0.95	0.93	0.93	0.95	0.92	0.93	0.91	0.94
675	1.00	1.00	1.00	1.00	1.00	1.00	0.98	1.00	1.00
700	0.46	0.50	0.52	0.47	0.46	0.43	0.43	0.46	0.47
725	0.13	0.12	0.13	0.09	0.11	0.08	0.09	0.09	0.10
750	0.03	0.03	0.03	0.02	0.04	0.02	0.02	0.02	0.03

pathway (corn, sorghum, *Amaranthus edulis*) showed a wavelength-dependent oscillation of photosynthetic rate, but when equilibrium values were used, the spectral quantum yield was not abnormal for these plants.

THE AVERAGE PLANT

The arithmetic mean for all species was calculated for the three variables relative quantum yield, relative action, and absorptance (Fig.14, Tables III–VIII). Again, field specimens were separated from growth chamber specimens. Until we know what caused these differences, it is difficult to decide which of the two sets of plants should be called "average", but the field plants are the more likely candidates.

The absolute value of the maximum quantum yield varied from 0.054 to 0.076 moles per Einstein, with a mean of 0.065. The extrapolated value at zero irradiance would be 0.07–0.08 moles per Einstein.

The same basic shape of curve was encountered in all species of green plant tested. The spectral quantum yield was always composed of three curves, with peaks at 440, 620 and 670 nm, $\pm$ 10 nm. We have not attempted to identify these components with particular chloroplast pigments. As RABINOWITCH (1951, pp.1162–1163) pointed out, this is much more difficult with leaves than with algae,

TABLE VII

ABSORPTANCE OF GROWTH CHAMBER PLANT SPECIES (Nr. 1–22)

nm	*1*	*2*	*3*	*4*	*5*	*6*	*8*	*9*	*10*	*11*	*12*	*13*	*14*	*15*	*16*	*17*	*18*	*19*	*21*	*22*	*Mean*
350	0.94	0.94	0.96	0.95	0.95	0.96	0.94	0.95	0.95	0.97	0.94	0.95	0.94	0.88	0.96	0.95	0.95	0.96	0.92	0.95	0.95
375	0.94	0.93	0.96	0.95	0.94	0.95	0.94	0.95	0.95	0.97	0.92	0.95	0.92	0.87	0.96	0.95	0.94	0.94	0.91	0.92	0.94
400	0.93	0.92	0.93	0.93	0.92	0.93	0.93	0.94	0.95	0.95	0.90	0.94	0.91	0.86	0.95	0.94	0.94	0.93	0.90	0.92	0.93
425	0.93	0.92	0.91	0.92	0.92	0.92	0.93	0.94	0.95	0.94	0.91	0.94	0.92	0.86	0.95	0.94	0.95	0.93	0.92	0.94	0.92
450	0.93	0.92	0.91	0.92	0.92	0.92	0.92	0.94	0.94	0.93	0.91	0.94	0.92	0.87	0.94	0.94	0.95	0.94	0.91	0.94	0.92
475	0.92	0.91	0.91	0.92	0.92	0.92	0.92	0.93	0.94	0.93	0.90	0.94	0.92	0.87	0.94	0.94	0.94	0.94	0.91	0.93	0.92
500	0.91	0.89	0.90	0.92	0.91	0.92	0.91	0.93	0.94	0.92	0.87	0.94	0.90	0.87	0.93	0.93	0.92	0.92	0.89	0.91	0.91
525	0.77	0.77	0.81	0.86	0.81	0.85	0.81	0.87	0.87	0.85	0.69	0.85	0.77	0.79	0.85	0.85	0.78	0.79	0.77	0.80	0.81
550	0.69	0.71	0.75	0.81	0.75	0.79	0.75	0.82	0.81	0.78	0.60	0.79	0.70	0.74	0.79	0.79	0.70	0.71	0.70	0.70	0.74
575	0.76	0.77	0.79	0.84	0.80	0.82	0.80	0.86	0.86	0.81	0.68	0.83	0.75	0.78	0.83	0.84	0.77	0.76	0.75	0.76	0.79
600	0.81	0.82	0.84	0.88	0.85	0.87	0.84	0.89	0.90	0.86	0.75	0.88	0.81	0.82	0.88	0.87	0.82	0.83	0.81	0.82	0.84
625	0.86	0.86	0.87	0.91	0.88	0.90	0.87	0.91	0.92	0.89	0.80	0.90	0.85	0.85	0.90	0.90	0.86	0.87	0.85	0.86	0.88
650	0.89	0.89	0.90	0.93	0.91	0.92	0.90	0.92	0.94	0.91	0.86	0.93	0.88	0.87	0.92	0.93	0.90	0.90	0.89	0.89	0.90
675	0.93	0.91	0.92	0.94	0.93	0.93	0.92	0.94	0.95	0.93	0.91	0.95	0.92	0.88	0.94	0.94	0.94	0.94	0.92	0.94	0.93
700	0.77	0.74	0.80	0.86	0.78	0.84	0.76	0.85	0.85	0.81	0.69	0.80	0.72	0.77	0.80	0.82	0.77	0.78	0.76	0.80	0.79
725	0.33	0.35	0.39	0.49	0.36	0.47	0.29	0.43	0.39	0.38	0.23	0.32	0.26	0.34	0.32	0.39	0.29	0.27	0.34	0.36	0.36
750	0.05	0.07	0.07	0.09	0.01	0.11	0.05	0.08	0.07	0.10	0.06	0.04	0.05	0.07	0.05	0.07	0.06	0.04	0.09	0.07	0.07

TABLE VIII

ABSORPTANCE OF FIELD PLANT SPECIES

nm	*1*	*3*	*4*	*6*	*7*	*8*	*18*	*20*	*Mean*
350	0.95	0.97	0.96	0.96	0.97	0.96	0.95	0.95	0.96
375	0.95	0.97	0.96	0.96	0.97	0.96	0.95	0.95	0.96
400	0.95	0.96	0.95	0.95	0.96	0.95	0.95	0.95	0.95
425	0.95	0.93	0.93	0.93	0.95	0.95	0.95	0.95	0.94
450	0.94	0.93	0.93	0.92	0.94	0.94	0.95	0.94	0.94
475	0.94	0.93	0.93	0.92	0.94	0.94	0.94	0.94	0.94
500	0.93	0.92	0.93	0.91	0.93	0.93	0.93	0.93	0.93
525	0.85	0.83	0.84	0.79	0.82	0.85	0.80	0.84	0.83
550	0.78	0.78	0.79	0.72	0.75	0.79	0.72	0.78	0.76
575	0.83	0.83	0.84	0.78	0.80	0.83	0.77	0.83	0.81
600	0.87	0.87	0.88	0.83	0.85	0.86	0.83	0.87	0.86
625	0.90	0.90	0.91	0.87	0.88	0.89	0.87	0.89	0.89
650	0.92	0.93	0.93	0.90	0.91	0.91	0.91	0.91	0.91
675	0.94	0.94	0.95	0.93	0.94	0.93	0.94	0.93	0.94
700	0.83	0.79	0.82	0.74	0.82	0.81	0.78	0.83	0.80
725	0.42	0.34	0.39	0.30	0.36	0.37	0.30	0.38	0.36
750	0.07	0.05	0.06	0.06	0.09	0.08	0.07	0.10	0.07

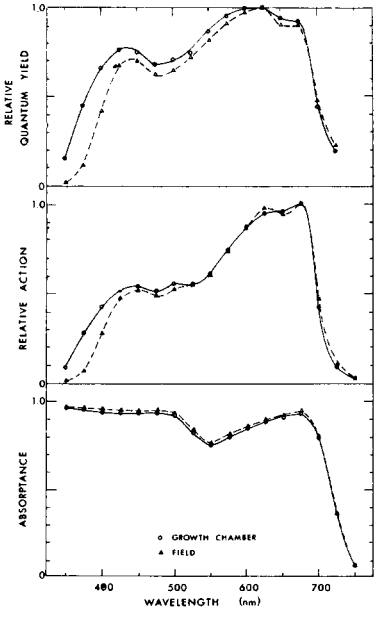

Fig.14. Mean, all samples (tabulated in Tables III–VIII).

because of the high optical density and because of absorption by non-chloroplastic material.

The action spectrum shows the same three peaks, with an additional dip at 550 nm due to the dip in absorptance at this wavelength. Because absorptance and action varied independently with species, the standard deviation at 550 nm was slightly greater for action than for quantum yield (7% of the mean, compared with 4%). At 450 nm, the standard deviations were about equal (7% of the mean).

The absorptance was invariably high throughout the ultraviolet and visible parts of the spectrum, with a dip in the green. The absorptance in the dip varied between 0.60–0.82, with a mean of 0.76.

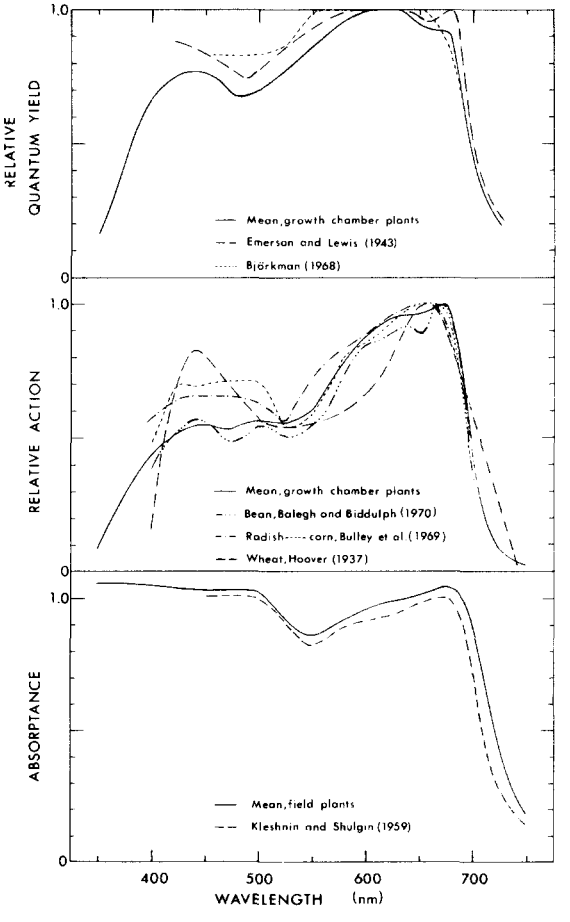

Fig.15. Comparison of mean quantum yield, action and absorptance with other published curves. (The Balegh and Biddulph curve has been recalculated for equal incident energy.)

COMPARISON WITH OTHER PUBLISHED CURVES (Fig.15)

The mean spectral quantum yield for growth chamber plants is slightly lower at the shortwave end than the curves published by BJÖRKMAN (1968) for three species of higher plant and by EMERSON and LEWIS (1943) for *Chlorella pyrenoidosa*. The double red peak appears in the Emerson and Lewis curve but not in the Björkman curve.

The mean action spectrum for growth chamber plants is similar in shape to those published by BULLEY et al. (1969) for radish and corn, and by BALEGH and BIDDULPH (1970) for bean. The HOOVER (1937) curve for wheat seems to be somewhat different in shape from any of these curves.

The mean absorptance is close to that published by KLESHNIN and SHULGIN (1959) as the average for 80 species of higher plant.

In all cases except one, the differences between our results and those previously published are within the limits of differences due to species or growth conditions. The exception is the Hoover action spectrum for wheat.

We have attempted to duplicate this action spectrum, with wheat plants grown under conditions similar to those used by Hoover. The two main differences between these conditions and those in our growth chamber were: (*1*) the light was less and of different color (1,500 footcandles, incandescent light passed through a heat-absorbing filter); and (*2*) the nutrient contained less nitrate (4 mm).

The leaves of the plants were decidedly pale by comparison with those of our growth-chamber plants. They were the color of a pale-green lettuce leaf. Their spectral absorptance (Fig.16) shows this. Their action spectrum was close to that published by Hoover, and quite different from that of our other wheat plants. The quantum yield was also abnormal.

It appears that the Hoover curve was obtained with abnormal plants. GABRIELSEN (1940) reached the same conclusion on circumstantial evidence. BURNS' (1942) measurements on wheat also indicate that very pale leaves would have to be used if Hoover's results were to be duplicated.

DISCUSSION

The same basic shape of curve was encountered in all of the plants and for all of the conditions tested. The response in the ultraviolet and blue up to about 500 nm varied somewhat with species, growth conditions and direction of illumination, probably because of variable absorption by non-chloroplastic material.

Neither the mean action spectrum nor the mean quantum yield can be said to be flat throughout the visible region. Therefore neither the irradiance nor the flux of absorbed quanta will be a perfect measure of "photosynthetically active radiation". Both will systematically overestimate the effectiveness of blue light relative to red, the irradiance overestimating more than the absorbed quantum flux.

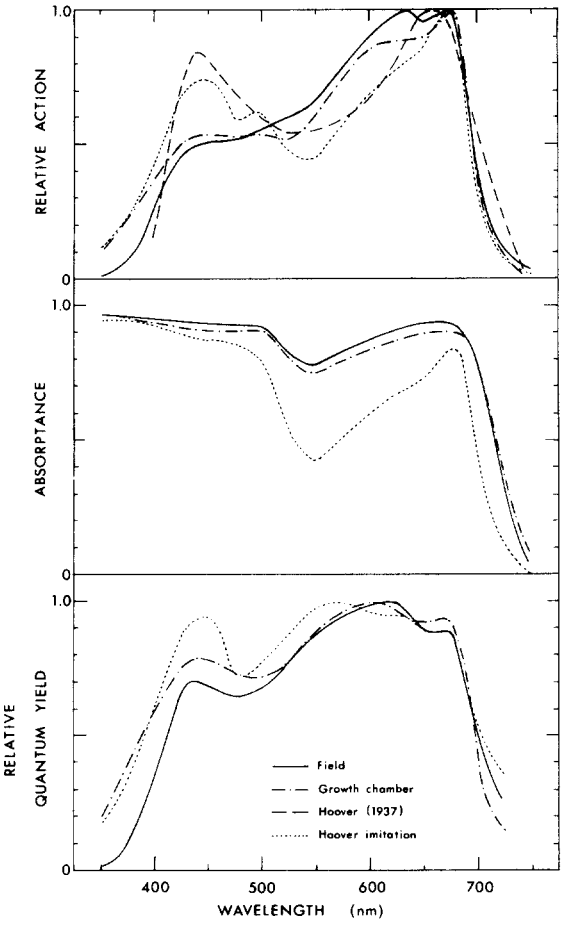

Fig.16. Comparison of Hoover's action spectrum curve for wheat with curves for growth chamber and field samples of wheat, and for very pale green wheat grown under conditions similar to those used by HOOVER.

The size of the error depends on the spectral quality of the light source. It also depends on the *quantity* of light; in the limit, the photosynthetic rate must be independent of light level. The error can be calculated for various combinations of light and plant response. GAASTRA (1968) made some calculations, based on the assumption that the spectral quantum yield curve was flat from 400 to 705 nm, which indicated that the irradiance would not be greatly in error, at least for the various types of light likely to be encountered in the field. We have made some more calculations using the data presented here, and the results will be reported in a separate paper.

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