A rational approach to light measurements in plant ecology

K. J. McCree

Soil and Crop Sciences Department, Texas Agricultural Experiment Station, Texas A&M University, College Station, Texas 77843

The photometric system and its equivalent in the plant sciences

The art of making good light measurements seems to elude most plant scientists. As a matter of fact it eludes many physicists too. Perhaps we can all lay the blame on the lighting engineers, who first introduced candles, grease spots, lumens, nits and other such fanciful notions into what had been a relatively clean science (5, 7, 11).

Their reason for doing so, of course, was that they wanted to measure light as it was perceived by human beings in their normal daily life, not light as the physicists saw it. Since the biology of vision had not yet been worked out, the engineers were forced to adopt a purely empirical approach. They based their measuring system on the visual appearance of the light given out by a standard source (at first this was a candle, then a gas lamp, then an electric lamp, and finally a piece of platinum at its freezing point).

Visual matches can be very precise. As long as the apparent color of a test light source is exactly the same as that of the standard, the luminous intensities of two sources can be compared by a competent observer with an accuracy of ±1% or better. When the colors are different (as they usually are), a "match" of intensities can still be made, but the end point varies with the observer, and with the conditions of observation (7).

A physical detector such as a photocell will, of course, give much more reproducible results, but its readings have to be adjusted in some way to conform with the visual match, which is the ultimate standard. This is done by adjusting its spectral response, for equal incident radiant power fluxes, to match that of a Standard Photometric Observer, as defined by the International Bureau of Weights and Measures (B.I.P.M.) in 1933 (6). This standard response curve (the so-called **V** curve) was based on many visual matches made by trained observers, working under uniform conditions in standardizing laboratories. As published (Fig. l), it is a relative response curve, that is, it has a maximum value of 1.00. The absolute magnitude of the luminous intensity of a source, in candelas (lumens sr^{-1} m^{-2}), or of the illuminance at a surface, in lux (lumens m^{-2}), still has to be determined by comparison with a piece of freezing platinum (10). Eventually, one hopes, the B.I. P.M. will have the courage to set the maximum value of **V** in absolute units, thus finally abandoning the idea of a "standard candle" as a basic unit. At the present time, the generally-accepted value of this maximum is 680 lumens per watt of radiant power (6).

The photometric system of light measurement, then, is not a physical system, even though physical instruments are usually used. Neither is it a biological system - it takes no account of the complex mechanisms involved in the visual response of the human eye. It is a psychological system, based on the judgment of a hypothetical standard observer about the brightness of lights of different color.

Yet it works. It has allowed architects and lighting engineers to design suitable lighting environments for a great variety of practical tasks (5). Manufacturers have competed vigorously to produce lamps with greater luminous efficiencies, with the result that there has been a 10-fold increase in efficiency since the system was introduced 40 years ago.

What are the lessons in all this for plant scientists and engineers? The first and most obvious one, of

course, is that they should never use this system. Psychological units of light surely have no place in plant sciences. This has been repeatedly pointed out (1) at least since the time of Gabrielsen (2), but apparently with little success, to judge from the current issues of the plant science journals. Probably the main reasons for this are that the system is well established, that instruments are available off the shelf, and that most of the people to whom plant scientists turn for advice on light matters are lighting engineers.

The most important lesson, however, is that in order to make progress, the lighting engineers had to devise their own system of measurement. In essence, the problem they faced was one of communication rather than one of basic science. They realized that it was more important to reach a consensus on a workable system of measurement than it was to make sure that the system was based on the best possible science, either physical or biological.

No doubt partly for historical reasons, and partly because of the state of the art in the biological sciences at the time, the system as it finally evolved relied heavily on "behavioural" data, that is, data obtained by observing the response of an organism to a physical stimulus. After it had been established by repeated measurement, both in the laboratory and in the field, that the response was sufficiently reproducible for all practical purposes, the data were pooled to obtain a "standard" response, which was then universally adopted. The development of photometric instrumentation followed rapidly.

Probably the branch of the applied plant sciences to which a similar approach would be most applicable is plant ecology. It is obviously important to know the amount of light available for plant growth in any plant ecological study, yet the ecologist will search in vain for an instrument which measures this in internationally recognized units. If he has studied the subject, he knows that the standard meteorological instruments respond to a much wider band of wavelengths than plants do, and that photometric instruments have an adjusted spectral response which is also quite unsuitable. Yet he is forced to use one or the other of these instruments, if he is to produce numbers which his colleagues will recognize in print.

How close are we, in 1973, to being able to provide the plant ecologist, and others like him, with acceptable light measuring equipment? I shall attempt to answer this question in the remainder of this commentary.

The spectral properties of light, and of plants

There are certain basic principles of the interaction of light and matter which simply cannot be ignored when light measurements are being discussed. The most important of these is that both the physical properties of the light and its biological effects depend strongly on wavelength. These basic spectral properties have to be taken into account in any proposed "simplification" of light measurements.

Measuring the spectral distribution of either the *radiant intensity* of a source (radiant power flux emitted from a point source, per unit solid angle and per unit wavelength interval, in W nm^{-1} $sr-^{-1}$), or the *radiance* (radiant intensity per unit area of a finite source), or the *irradiance* produced by a source at a surface (radiant power flux per unit surface area, per unit wavelength interval, in W m^{-2} nm sr^{-1}), is a task which should not be lightly undertaken. The limitations of the instruments and methods being used must always be established, by the methods laid out in the standard texts on spectrophotometry (3, 4, 11). Many amateurs do not realise that it is difficult to achieve an absolute accuracy of better than ±20%, outside of a standardizing laboratory. For many purposes, it may be better to rely on published data, or on data supplied by the lamp manufacturer, than to attempt these measurements with inadequate facilities and little experience. Measuring the spectral distribution of the available light for for its own sake is certainly an exercise in futility for the plant scientist .

The measurement of the spectral properties of plant material is also a relatively complicated physical measurement. Most commercial spectrophotometers are designed to handle chemical solutions, which do not scatter radiation nearly as much as do intact plant materials. In biological materials, the incoming beam of radiation is scattered as well as absorbed, and that fraction which is scattered in a given direction is often highly dependent on the wavelength and the angle of incidence. With an integrating sphere, one can determine the total fraction of the incident beam which is "reflected" (back-scattered), and that which is "transmitted" (forward-scattered), and hence calculate by difference the fraction which is "absorbed". This fraction, called the absorptance, is not to be confused with the absorbance, a term which the chemists use for the optical density, $\log_{10}$ (1/fraction transmitted). In a non-scattering, non-reflecting medium (which exists only in perfect chemistry), the optical density is proportional to the concentration of the absorbing medium

The optical properties of the sample are ignored in most photobiological research. Most "action spectra" consist of a curve relating the observed response to the incident spectral irradiance, this in spite of the fact that, at the photochemical level, no response can occur if the radiation is not absorbed, and further, that the photochemical action should be proportional to the absorbed flux of quanta, not energy. In photobiology, the incident energy flux (irradiance) is a prime example of an irrelevant physical parameter.

Of course photobiological experiments are not simply photochemical experiments. In most cases it would be extremely difficult to establish a direct relationship between the observed response and the flux of quanta absorbed by a single chemical. Nevertheless, since a photochemical basis is at least inferred, it would seem logical to measure quantum fluxes rather than radiant power fluxes, and to make some attempt to measure the fraction absorbed in the sample.

The spectral properties of plants cannot be ignored even when dealing with non-photobiological effects such as heating. For example, in the field, the energy balance of a leaf is strongly influenced by its spectral absorptance. In most leaves, the absorption is largely confined to the 300-700 nm region, in which the pigments absorb strongly. Infrared solar radiation is mostly scattered by leaves (1). Other parts of the plant, such as developing buds, flowers and fruits, may not be so lucky, but their problems have received little attention. In this area of research the spectral irradiance (in energy units) is quite relevant. However, to be of value, the measurements must span the entire solar spectrum (300 to 3,000 nm), and this poses some technical problems.

Photosynthetically active radiation

As an example of the application of these principles to the practical measurement of light in plant ecology, I shall consider the measurement of "photosynthetically active radiation" (PAR). As those working in photosynthesis will know, there have been several attempts to define PAR in the past, but no consensus has yet been reached. I believe we now have the facts on which to base a rational decision on this important topic (8, 9).

As every schoolboy knows, chlorophyll is the magic substance which makes green plants grow. He should also know, but often isn't told, that it gets a great deal of help from various other colored substances, especially the yellow ones. The result (reverting to scientific jargon) is that the action spectrum for photosynthesis. (CO_2 uptake) is a fairly flat curve over practically all of the visible spectrum (400 to 700 nm) (Fig. 1). This is especially obvious when it is plotted, as it should be, as the action par unit of quantum flux absorbed. Also, there is very little difference between one green plant and another, which is not surprising, since they all contain the same photochemical apparatus. What differences there are can probably be explained by the screening properties of inactive pigments, which

lie either in the epidermis or in the mesophyll itself.

Although the photosynthetic efficiency of an absorbed quantum of blue light is actually slightly less than that of one of red light, the practical importance of this is greatly reduced by the fact that plants are never grown in monochromatic light, but always in light which contains some quanta at both wavelengths. Also, healthy green plants absorb so strongly throughout the visible spectrum that the distinction between absorbed and incident quanta is of no practical importance.

Thus we are left with the conclusion that what we may call the **P** curve, by analogy with the **V** curve for the human eye, is close enough to a rectangle bounded by the wavelengths 400 to 700 nm, for all practical purposes, when it is expressed on the basis of equal incident quantum fluxes. This very useful result is a consequence of the photochemical nature of the primary acts of photosynthesis, along with the highly efficient energy transfer among the various pigments. It means that we can define and measure photosynthetically active radiation as the incident quantum flux in the waveband 400 to 700 nm, without involving any experimental plant response curves (except to define the wavelength limits).

A **P** curve based on equal radiant power fluxes would not be close to a rectangle, since, by the laws of physics, the quantum content of a given radiant power flux at 400 nm must be 4/7ths of that at 700 nm. Thus it would not be equally satisfactory to define PAR as the radiant power flux in the waveband 400 - 700 nm. This definition would also fail to convey the essential idea that we are dealing with a photochemical effect. The most logical use for radiant power flux measurements is in connection with energy balance studies.

Of course, the PAR flux is not the only light flux which affects plant growth. In some experiments it may also be necessary to measure "photomorphogenically active radiation" (PMAR?), for example. Since photomorphogenic responses are also basically photochemical in nature, a quantum flux measurement would probably be in order here too, with different wavelength limits. This can be decided only after a proper study of the relevant action spectra.

Conclusions

(1) In basic photobiological research, the spectral properties of both the irradiating source and the target should always be determined. These are difficult measurements, which should not be attempted without some competent technical help.

(2) In the applied plant sciences such as plant ecology and agronomy, there is a need for a simple system for measuring the light which is active in plant growth, analogous to the photometric system for measuring the light which is useful to humans in their daily life. The best likely candidate is "photosynthetically active radiation" (PAR).

(3) The PAR system should be based, as was the photometric system, on a single, generalized spectral response curve, which has been shown by experiment to represent the response of an "average plant" with sufficient accuracy for all practical purposes.

(4) All the available data indicate that the photosynthetic response curves of healthy green leaves to equal incident quantum fluxes are quite close to being rectangles bounded by the wavelengths 400 and 700 nm. Therefore, the quantum flux within this waveband should represent PAR, with sufficient accuracy for all practical purposes.

(5) Again by analogy with the history of the photometric system, the next step should be further practical testing of this proposition, using instruments already available, followed by attempts to reach an international consensus, and finally by official adoption by an international agency with power of enforcement.

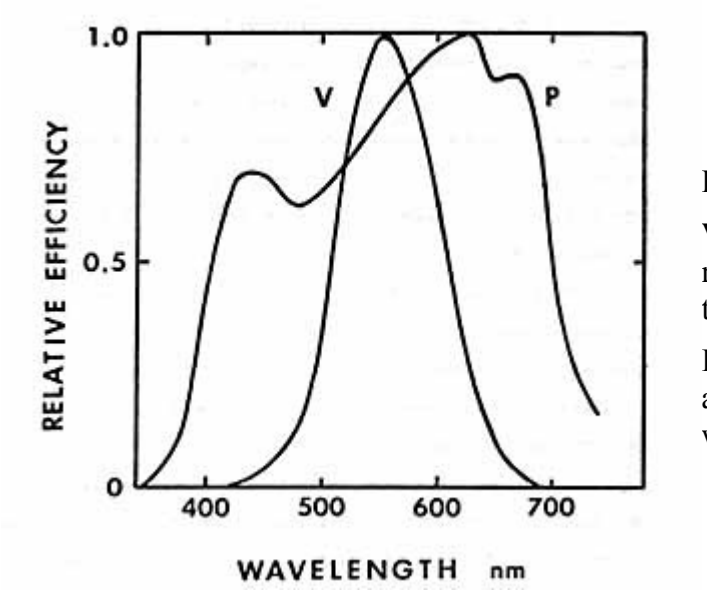

Figure l

V: relative luminous efficiency of equal incident radiant fluxes as a function of wavelength, for the C. I. E. Standard Photometric Observer (6).

P: relative photosynthetic efficiency of equal absorbed quantum fluxes, as a function of wavelength, for an average green leaf (8).

References

(1) BICKFORD, E. D., AND DUNN, S. Lighting for plant growth. Kent State Univ. Press, (1972) 221 pages.

(2) GABRIELSEN, E.K. Einfluss der Lichtfaktoren auf die Kohlensaüreassimilation der Laubblätter. Dansk Bot. Arkiv 10 (1940) 1-177.

(3) GIBSON, K. S. Spectrophotometry. U. S. Nat. Bur. Stand. Circular No. 484 (1949).

(4) HENDERSON, S. T and HALLSTEAD, N. B. The spectrophotometry of light sources. Br. J. Appl Phys. 3 (1952) 255-259.

(5) ILLUMINATING ENGINEERING SOCIETY HANDBOOK (4th Edition). J. E. Kaufman, Ed., Illum. Eng. Soc. N. Y. (1966).

(6) INTERNATIONAL LIGHTING VOCABULARY (3rd Edition). Commission Internationale de l'Eclairage, Paris (1970) 359 pages.

(7) LE GRAND, Y. Light, colour and vision. Wiley, N. Y. (1957) 512 pages.

(8) MCCREE, K. J. The action spectrum, absorptance and quantum yield of photosynthesis in crop plants. Agric. Meteorol. 9 (1972) 191-216.

(9) MCCREE, K. J. Test of current definitions of photosynthetically active radiation against leaf photosynthesis data. Agric. Meteorol. 10 (1972) 443-453.

(10)U. S. NAT. BUR. STAND. SPECIAL PUBL. 330. The International System of Units (SI) (1972 Edition) 45 pages.

(11)WALSH, J. W. T. Photometry. Constable, London (1953) 544 pages.

From : CURRENT ADVANCES IN PLANT SCIENCE, Vol. 3 No. 4 pages 39-43. 1973
COMMENTARIES IN PLANT SCIENCE No. 5, October 1973.