THE RADIATION ENVIRONMENT AND REGULATION
OF PHOTOSYNTHESIS IN *PENNISETUM TYPHOIDES*

A thesis
submitted for the degree
of
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STATEMENT

The work presented in this thesis is my own apart from some aspects of the radiation simulation study. Specific contributions made by others are referred to in the acknowledgments and text.

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Finally, special thanks are due to my wife, Colleen, for her patience and encouragement.
The absorption of radiant energy by plants and the utilization of this energy by the photosynthetic system involves processes that vary widely in their effectiveness and in their susceptibility to modification. In order to optimise plant production it is necessary that we identify and describe the processes which have the greatest influence on growth and development and, where possible, establish means of improving their performance.

The work reported in this thesis is concerned with several aspects of plant-environment interaction considered to be important in regulating crop growth. The topics discussed include a study of the relative importance of various environmental and physiological mechanisms regulating photosynthesis in attached leaves, a theoretical consideration of the effect of canopy architecture on the absorption of radiant energy, and a proposal for improving techniques for measuring photosynthetically active radiation.

A large amount of information on the photosynthetic system and the plant environment has accumulated in the form of theory, techniques, and descriptive data. It is felt that the most fruitful approach to be taken now is to attempt to focus this information on critical areas of plant environment interaction. This is considered to be the most efficient means of indicating the shortcomings in our knowledge and therefore the areas to which we should direct our attention. It is certainly the only means of reaching the ultimate goal of our research, the provision of recommendations for optimising plant production.
The studies reported here are based on this approach. The diversity of the topics discussed is an expression of the broad approach that is needed to describe the many facets of the plant-environment system. The degree to which the investigations are interrelated and interdependent is a measure of the stage that has been reached in working available information into a unifying framework.

In Chapters 1 and 2 the results of leaf chamber studies on single attached leaves of *Pennisetum typhoideae* (Burm.) S. & H. (bulrush millet) are presented and their implications are discussed. The experiments were conducted to establish the response of net photosynthesis to the temperature, radiation, and CO$_2$ environment and to identify which of the physical and biochemical processes played the most important part in determining this response.

The results contribute information that is, on one hand, specific to the plant material used providing data, for example, on maximum rates of net photosynthesis, light saturation flux densities, and leaf maturity effects. These data describe the photosynthetic capability of the leaves, and such information can be used in various types of growth models to predict the plant's performance under a variety of conditions. On the other hand, the results provide information which has wider implications in the study of the processes regulating net photosynthesis rates. They show, for example, the importance of the gas-phase resistances to CO$_2$ transport at high rates of CO$_2$ uptake, and the necessity for taking these resistances into account in whole-leaf studies of the photosynthetic system.
Chapters 3 and 4 present a mathematical model that was developed for the simulation of the penetration, propagation, and absorption of radiation in plant canopies. The objective of the work was to provide a comprehensive and realistic model and to establish the validity of the assumptions it incorporates by testing it against measurements made in plant canopies of known architecture.

The field tests provided evidence to show that we can predict upward and downward horizontal flux densities in regular canopies of known architecture. Further development is now required in the analysis of the spatial heterogeneity of radiant flux density so that the non-linear response of net photosynthesis to radiation can be taken into account and so that an assessment can be made of the effect of larger scale canopy heterogeneity on the applicability of one-dimensional radiation models of the type presented here.

An improved technique for the measurement of photosynthetically active radiation is proposed in Chapter 5. Instruments generally used in physiological studies are sensitive to a much wider waveband than that available to the photosynthetic system. This has led in the past to considerable problems in interpreting measurements made where the spectral quality of the radiation is unknown. The direct filtering of silicon photocells has provided instruments that are suitable for measuring photosynthetically active radiation under a range of conditions. These instruments were used extensively both in the leaf chamber, and in the field studies.

Each of the five chapters presented in this thesis is the manuscript of a paper which has been prepared for publication in essentially its present form.
MECHANISMS REGULATING PHOTOSYNTHESIS IN

PENNISETUM TYPHOIDES

SUMMARY

Leaf chamber studies were conducted on single attached leaves of *Pennisetum typhoides* (bulrush millet) to identify and describe the processes regulating photosynthesis.

Stomatal resistance to CO$_2$ diffusion was the largest and most variable of the resistances regulating net photosynthesis rates at optimum temperatures (35°C). It varied widely with radiation and constituted, at normal CO$_2$ concentrations, from 53% to over 80% of the total resistance. The variation with external CO$_2$ concentration was linear in the range 200-600 x 10$^{-9}$ g cm$^{-3}$. The residual resistance was relatively small, varying from 0.2-4.7 s cm$^{-1}$ with radiation and CO$_2$ concentration, and constituted from 10% to 42% of the total resistance.

Net photosynthesis rates varied considerably with leaf maturity, particularly with respect to the stage of individual leaf development but also with order of leaf emergence. This variation was due largely to changes in stomatal resistance with maturity, although less significant changes in residual resistance also occurred. High net photosynthesis rates of up to 277 x 10$^{-9}$ g CO$_2$ cm$^{-2}$ s$^{-1}$ were recorded.

A. INTRODUCTION

Photosynthesis in plant leaves is dependent on a series of interacting physical and biochemical processes which together
determine the rate of the overall process. The potential rates of the individual processes vary widely and so, consequently, does their importance in the regulation of photosynthesis. Identification of the key regulatory processes, those with the slowest rates, aids the interpretation of growth response data and permits a more accurate assessment of the possibilities for increasing plant growth rates.

Rate-regulating processes may influence the supply of CO₂ to the site of photosynthesis in the chloroplasts, its photochemical incorporation, or its subsequent biochemical utilization. These processes can be identified and their nature explored by determining their differential response to various environmental parameters. This paper reports the results of such investigations in which the effect of radiation, temperature, and CO₂ on the rates of net photosynthesis in leaves of *Pennisetum typhoides* was determined with a view to identifying and describing the key processes regulating photosynthesis under normal growth conditions.

Considerable evidence has accumulated demonstrating that for a large number of species, the resistances to CO₂ transport play an important role in regulating photosynthesis. In addition, it is becoming recognized that studies of the photosynthetic system in intact leaves can be meaningfully interpreted only if the resistances to CO₂ transport are taken into account. Stomatal resistance is particularly important in this respect because of its variability (Bierhuizen and Slatyer, 1964; Lake, 1967; Meidner, 1969; Troughton, 1969; Troughton and Slatyer, 1969; Gifford, 1970). For these reasons, the experiments described here were designed to obtain the information necessary for estimating the relative magnitude of the resistances to CO₂ transport, and for interpretation of their role in regulating photosynthesis.
B. THEORY

The relationships between the rate of net photosynthesis and the rate-determining processes directly affecting it can be described using an analogue of Ohm's Law based on Fick's Law of diffusion. The form of the equations used by various workers has varied considerably, as has interpretation of the results produced. Difficulty has often arisen when interpretation of the analogue has been more literal than is justified, and when similar notation and terminology have been used to convey different ideas. For this reason the relationships used in this paper are discussed in some detail and, where necessary, different terminology employed.

The equations to be described can be used only to provide an overall description of net photosynthesis because, at this time, insufficient information is available to provide a more complete and detailed description of the many contributing processes.

The net flux of CO₂ into the leaf, F, is taken as the index of net photosynthesis and is given by:

\[ F = \frac{C_t - C_i}{r_a' + r_s' + r_r'} = C_t - C_w = \frac{C_w - C_i}{r_r'} \]  

(1)

The effects of the rate-regulating processes are described as resistances. It is possible to distinguish experimentally two components of the total resistance, \( r_r' \), affecting net photosynthesis: the boundary layer resistance, \( r_a' \), and stomatal resistance, \( r_s' \). The third component, the residual resistance, \( r_r' \), is found by difference. The gradients driving net photosynthesis are usually thought of as CO₂
concentration gradients. For example the gradient causing the transport of CO₂ in the gas phase across the boundary layer, then through the stomatal pores and sub-stomatal cavities to the surface of the mesophyll cell walls. This gradient is given by the difference in concentration between the external air, Cₜ', and the effective concentration at the mesophyll cell walls, Cₚ'. Providing the variability in the diffusion path length to the individual mesophyll cells is allowed for, this gradient has physical reality and can be defined experimentally.

The total "gradient" driving photosynthesis is more difficult to define. Many workers have taken the gradient as (Cₜ - Cₚ'), where Cₚ' is the "CO₂-concentration in the chloroplasts" (Gaastra, 1959). The assumption is made that, when F is primarily regulated by the rate of CO₂ supply to the chloroplasts, Cₚ' = 0. As no means is available for estimating Cₚ' under other conditions, the application of the model has usually been restricted to the CO₂-regulated case. The appropriate resistance was termed by Gaastra the "mesophyll resistance", rₘ', and described the rate-regulation imposed by the transport of CO₂ from the mesophyll cell walls to the sites of reduction.

A later development (Bierhuizen and Slatyer, 1964) was the definition of the gradient as (Cₚ' - Cᵢ), where the effective intracellular CO₂ concentration, Cᵢ, was taken as the CO₂ compensation point (termed Γ by Heath, 1959) and used to define the lower limit of the gradient. The associated resistance term used by Bierhuizen and Slatyer was the mesophyll resistance rₘ'. This parameter has also been called the intracellular resistance, rᵢ', by Osmond et al. (1969). Gifford (1970) used the term residual resistance, rₑ', to describe any component of rₑ' not accounted for by rₐ' and rₛ'.
Residual resistance has a wider meaning than $r'_m$ but it has the same value where the rate of supply of CO$_2$ to the sites of CO$_2$ reduction is effectively governing the rate of net photosynthesis (i.e., on the linear part of the CO$_2$ response curve). The approach taken by these authors contrasts with that of Gaastra (1959) in that it makes some allowance for the effect of respiratory CO$_2$ production on net CO$_2$ exchange.

Unfortunately, determinations of $C_i$ can be made only for the case where $F=0$ as then $C_i = C_t$, a quantity that can be directly measured. This means that in equation (1) there normally exist two unknowns, $C_i$ and $r'_t$, and assumptions made about one of these will affect the numerical value of the other. In this paper, as in Bierhuizen and Slatyer (1964), $C_i$ refers to the CO$_2$ concentration at the effective carboxylation/decarboxylation surface. This parameter is termed $C_C$ by Gifford (1970). $r$ is used only for the special case defined by Heath (1959) where $F=0$.

A satisfactory numerical description of net photosynthesis is possible in spite of the above-mentioned problems, and restrictions lie not in the use of the solutions but in ascribing physical reality to them. Two possible approaches are described (Fig. 1): the first where the gradient is considered to change while the corresponding resistance remains constant; the second where the gradient is assumed to remain constant while the resistance changes.

On the effectively linear portion of the curve it is generally accepted that the supply of CO$_2$ to its site of reduction is the primary rate-regulating process. Under these conditions it is assumed that the effective CO$_2$ gradient is $(C_w - \Gamma)$. At higher values of $C_w$, departure of the response curve from linearity indicates that other
Fig. 1. - Diagrammatic representation of two alternative procedures for describing net photosynthesis.
processes are becoming important (e.g. supply of photosynthetically active radiation), and under these circumstances, where the rate of CO₂ supply exceeds its rate of reduction, accumulation of CO₂ will occur \( (C_i > \Gamma) \). If \( r'_m \) should remain constant \( C_i \) will increase from \( C_i(1) = \Gamma \) to the value \( C_i(2) \) shown in Fig. 1(a). This buildup will cause a decrease in the gradient from \( (C_w - C_i(1)) \) to \( (C_w - C_i(2)) \). The change in \( F \) is described, in this case, entirely by the change in \( C_i \), and consequently \( C_i(2) - C_i(1) \) is an expression of any factor affecting the rate of the carboxylation - decarboxylation processes, other than the supply of CO₂ to the mesophyll cell walls.

An alternative, and perhaps more convenient, method of describing the non-linear changes in \( F \) with \( C_w \) is to regard \( C_i \) as constant (and equal to \( \Gamma \)) and consider the change in \( F \) to be the result of resistance, further to that accounted for by \( r'_m \), being introduced to the system (Fig. 1b). Such additional "resistance" corresponds to the "excitation" and "carboxylation" resistances of Monteith (1963).

As separate identification of the various components can not be made they are referred to as one resistance, and distinguished from \( r'_m \), which has a more restricted meaning, by using the term "residual resistance", \( r'_r \), proposed by Gifford (1970). The term "residual" usefully conveys the idea of the remaining resistance required to describe \( F \) once the resistances that can be directly estimated (\( r'_a \) and \( r'_s \)) have been accounted for.

In summary, the second alternative of using a variable \( r'_r \) with a constant \( C_i = \Gamma \) (Fig. 1b) is regarded as the most convenient means of description although it is recognized that the first alternative, where the concentration gradient change accounts for changes in \( F \), is perhaps easier to visualise in physical terms (Fig. 1a). In
both cases the numerical result is the same and the different formulations are equally useful to describe the real physico-chemical system.

Estimation of $r'$ from the relationship

$$r' = \frac{C_w - C_i}{F}$$

was based on values of the CO$_2$ concentration at the mesophyll cell walls, $C_w$, derived from the relationship

$$C_w = C_t - F(r'_a + r'_s)$$

The stomatal and boundary layer resistances were estimated in the usual manner from water vapour fluxes and concentration differentials (Gaastra, 1959). However, conversion of the resistances determined for water vapour transport, $r_a$ and $r_s$, to those applicable to CO$_2$, $r'_a$ and $r'_s$, was made using a different value for the coefficient, $R$, based on the ratio of the diffusivities for water vapour, $D_{H_2O}$, and CO$_2$, $D_{CO_2}$, in air.

The diffusion coefficients used by different workers have varied widely (Gaastra, 1959, $R = 1.71$; Slatyer and Jarvis, 1966, 1.68; and Gale and Poljakof Mayber, 1968, 1.56). In many cases the source of the coefficients and the temperature to which they are applicable were not given. Close agreement was found among the values supplied by the International Critical Tables (1929) and more recent work in the field of diffusion (Montgomery, 1947, Lee and Wilke, 1954; Fuller, Schettler, and Giddings, 1966). Consequently, these values have been used here ($D_{H_2O} = 0.220 \text{ cm}^2 \text{ s}^{-1}$, $D_{CO_2} = 0.138 \text{ cm}^2 \text{ s}^{-1}$, both at 0°C, and $R = 1.594$, independent of temperature). It has been questioned
whether the diffusion coefficients determined in free air apply to diffusion through small apertures. However, Milthorpe and Penman (1967) found that any such error is negligible in the computation of R.

In converting \( r_a \) to \( r'_a \), \( R \) was raised to the \( 2/3 \) power (giving \( R = 1.37 \)) to account for the non-diffusive portion of the boundary layer transfer (Cowan, 1968; Gale and Poljakoff Mayber, 1968).

C. METHODS

A leaf chamber was used to provide accurate environmental control over single attached leaves. A metered air flow was sampled before and after passage through the leaf chamber, and measurements were made of water vapour concentration by using differential psychrometers (Slatyer and Bierhuizen, 1964), and \( \text{CO}_2 \) concentration by using a URAS2 infrared gas analyser calibrated with Wösthoff gas-mixing pumps. Leaf and air temperatures were measured with 42 s.w.g. copper-constantan thermocouples. Those measuring leaf temperature were held by tension of the wire against the underside of the leaf.

The light source used was an AC xenon arc (Wotan XBF 2500) fitted with a reflector which gave even light distribution over the leaf (± 2.5% over most of the leaf, ± 5.0% maximum in the leaf chamber). Small silicon photovoltaic cells (active area 0.3 x 0.4 cm) fitted with glass filters (Schott and General, BG38 and GG19) were used to determine the flux of photosynthetically active radiation (PAR) incident on the leaf (McPherson, 1969; Chapter 5). These instruments were calibrated in terms of photon flux density (0.4 - 0.7 \( \mu \) waveband) expressed as Einsteins cm\(^{-2} \) s\(^{-1} \) (one Einstein is defined as Avogadro's number of photons). These units are more appropriate than energy units as photosynthesis is essentially a quantum-dependent reaction. For the xenon lamp used, conversion to energy units can be made from
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E \times 10^{-9} \text{ cm}^{-2} \text{ s}^{-1} / 4.6 = \text{ mw cm}^{-2} (0.4 - 0.7 \mu \text{ waveband}). \text{ Full sunlight} = 200 \times 10^{-9} \text{ E cm}^{-2} \text{ s}^{-1}.

The perspex leaf-chamber was of similar construction to that described by Jarvis and Slatyer (1966) but rectangular in shape, and with one chamber enclosing a leaf area of approximately 100 cm². The actual enclosed leaf area was measured by planimeter from the leaf silhouette obtained on a sheet of self-developing photographic paper (Kodak, Studio Proof F) placed under the ready-positioned leaf and exposed. All flux measurements related to leaf area are based on this projected area. An even airflow over the leaf surface was provided by two inlet and two outlet manifolds running parallel to the main axis of the leaf. The velocity due to the normal throughflow was supplemented by pumping air through an external recycling loop.

_Pennisetum typhoides_ (Burm.) S. & H. cv. Katherine Pearl plants (Commonwealth Plant Introduction No. 11378; Division of Plant Industry, CSIRO, 1967), were grown in aerated modified Hoaglands solution in a glasshouse with air temperatures approximately 30°C day and 15°C night. The photoperiod was maintained at over 12½ hours to ensure floral initiation did not occur. A review of some aspects of the morphological development, physiology, and agronomy of this species is given by Norman and Begg (1968).

D. RESULTS

1. Leaf temperature

Net photosynthesis was, as expected, rather insensitive to leaf temperature and a broad temperature optimum was established for single leaves in the range 35-40°C. All subsequent experiments were conducted with leaf temperatures maintained at approximately 35°C.
2. Carbon dioxide concentration

Net photosynthesis showed a linear response to external CO₂ concentrations in the range 200-600 × 10⁻⁹ g cm⁻³ (Fig. 2). However, the rate of change was influenced by the incident flux density of PAR, indicating that some radiation-dependent factor was mediating in the effect of Cₜ on F. Stomatal resistance estimates were obtained from water vapour measurements made during the same experiments and the response pattern with variation of Cₜ and PAR was seen to be similar, but inversely proportional to that of F (Fig. 3).

The obvious implication that stomatal resistance played an important role in regulating net photosynthesis was investigated by comparing the change in the total resistance to net photosynthesis with the change of stomatal resistance for the range of external CO₂ concentration and PAR considered (Fig. 4). The boundary layer resistance was held at a low and constant value throughout (rₐ = 0.5 s cm⁻¹) as indicated by the horizontal broken line. The diagonal broken line has unit slope and indicates the contribution of the boundary layer and stomatal resistances (calculated from water vapour measurements) to the total resistance to net photosynthesis (calculated from CO₂ measurements by rearranging the left-hand side of equation 1). The vertical distance between this line and the data points represents the residual resistance.

It can be seen that the residual resistance made a relatively small and constant contribution to ∑r′ (rₐ′ ranging from 0.2 - 1.1 s cm⁻¹, with an average value of 0.6 s cm⁻¹). In contrast however, stomatal resistance values were larger, and varied over a wider range (1.4 - 4.6 s cm⁻¹). Stomatal resistance, then, exerted the greatest single influence on the rate of net photosynthesis and accounted for
Fig. 2. - The response of F to the external CO\textsubscript{2} concentration, C\textsubscript{t}, and incident PAR.
Fig. 3. - The response of stomatal resistance, $r_s'$, to CO$_2$ concentration, expressed as a function of the external CO$_2$ concentration, $C_t$, and PAR.
Fig. 4. - The contribution of stomatal resistance, $r_s'$, to the total resistance to net-photosynthesis, $r_t'$, in leaves of varying maturity, and for a range of external CO$_2$ concentrations and PAR ($C_t = 200-600 \times 10^{-9}$ g cm$^{-3}$, PAR = 41-120 $\times 10^{-9}$ E cm$^{-2}$ s$^{-1}$).
63-82% of $\bar{E}r'$. It also showed the largest changes with $C_t$ and PAR and so accounted for most of the change in net photosynthesis.

Considerable difficulty was experienced in achieving reliable results for external $CO_2$ concentrations from 0-200 x $10^{-9}$ g cm$^{-3}$ because of an unusual physiological response that occurred in this range. The symptoms involved visible tissue damage and irregular $CO_2$ exchange rates with a net release of $CO_2$ by the illuminated leaf of up to 440 x $10^{-9}$ g cm$^{-2}$ s$^{-1}$ (McPherson, in press; Chapter 2). The use of extremely high humidity air eliminated the effect but under these conditions accurate estimates of stomatal resistance using water vapour measurements could not be made accurately. It was possible, however, to establish that the "$CO_2$ compensation point", $\Gamma$, was zero and this value has been used in equation (1) to establish the values of $\bar{E}r'$ above.

Further experiments are being conducted employing high humidity air flow through the leaf to establish values of $C_w$ independently of $r^*_a$ and $r^*_s$ estimates (Lake and Slatyer, 1970). These should provide further information on the low minimum values of $r^*_r$ which indicate an unusually high efficiency for the processes involved in the transport of $CO_2$ through the mesophyll tissue and in its photochemical incorporation and subsequent utilization. The more direct determination of $C_w$ should also provide a check on possible errors in the estimates based on $r^*_a$ and $r^*_s$. Such errors could markedly affect values calculated for $r^*_r$.

3. Photosynthetically active radiation and maturity

The response of $F$ to PAR was determined for leaves of varying maturity. These experiments were conducted with leaf temperatures
regulated to approximately 35°C, normal ambient CO₂ concentrations \( (C_e = 600 \times 10^{-9} \text{ g cm}^{-3}) \), and a range of PAR flux densities incident on the leaf from zero to twice full sunlight.

Two aspects of maturity were considered. Firstly, the effect of order of emergence of leaves and secondly, the stage of individual leaves in their own maturity cycle. The maturity class for any given leaf at a given time was specified in two ways: one specifying emergence order and numbered in sequence up the stem from the first true leaf to develop; the other specifying the stage of any individual leaf in its maturity cycle as indicated by the time, in days, from full emergence. Appearance of the ligule was taken as indicating full emergence of a leaf and it was confirmed during the course of the experiments that lamina elongation had ceased at that stage.

The light response curves for two leaves from each of two plants are presented in Fig. 5 a-d, each graph showing the response for an individual leaf sampled at approximately weekly intervals. "Light saturation" at normal external CO₂ concentrations occurred at high incident PAR flux densities, equivalent to approximately full sunlight. Net photosynthesis under these conditions reached unusually high values of up to \( 277 \times 10^{-9} \text{ g cm}^{-2} \text{ s}^{-1} \). Respiration rates measured in the dark averaged \( -22 \times 10^{-9} \text{ g cm}^{-2} \text{ s}^{-1} \) which represents approximately 8% of maximum net photosynthesis rates.

Large effects of individual leaf maturity were evident. As the percentage differences in \( F \) were similar at all levels of PAR the change of net photosynthesis with maturity could be conveniently represented by the change in "light saturated" rates, \( F_{\text{max}} \) (Fig. 6). All four leaves studied showed an increase of \( F_{\text{max}} \) to a maximum, then a subsequent decline towards leaf senescence. No significant trend of respiration rates measured in the dark could be detected.
Fig. 5. - The response of F to incident PAR for four leaves, (a) - (d), two from each of two plants. The leaf number indicates the order of emergence. Each leaf was sampled at approximately weekly intervals to determine changes with individual leaf maturity ($C_t = 600 \times 10^{-9} \text{ g cm}^{-3}$).
The order of leaf emergence was also found to be significant, affecting the value of $F_{\text{max}}$, and the stage in the leaf maturity cycle that the maximum $F_{\text{max}}$ was reached.

In considering the cause of the changes in the rate of net photosynthesis with both PAR and $C_{\text{ai}}$, it was first of all evident that the rate of the decrease in the rate of photosynthesis down to low PAR values for any one leaf (Fig. 2 a-d) was increased as the leaf reached the mature state and the rate of photosynthesis was reduced to the "light saturated" rates of 15 to 20% for different leaf maturity classes, had a significant effect. The wider range of the individual leaves and order of leaf emergence and the role in regulating the rate of net photosynthesis.

The behaviour of stomatal resistance estimated during these experiments indicated that it might again account for many of the observed changes in net photosynthesis. A curvilinear decrease in stomatal resistance, especially full sunlight and use rate and extent of change varied with leaf maturity. Representative results for leaf illustrate, in Fig. 5, the more important features observed in all four leaves (cf. Fig. 3a). The secondary layer resistance was maintained at the low and constant value of $r' = 0.3$ s cm$^{-1}$. The behaviour in response to PAR, of both stomatal resistance and residual resistance varied with individual leaf maturity but the changes were of differing.
The order of leaf emergence was also found to be significant, affecting the value of $F_{\text{max}}$, and the stage in the leaf maturity cycle that the maximum $F_{\text{max}}$ was reached.

In considering the cause of the changes in the rate of net photosynthesis with both PAR and maturity it was first of all evident that the family of light response curves for any one leaf (Fig. 5 a-d) deviated near the origin and remained curvilinear down to low PAR levels. This suggested that the rate-restricting process causing differences among the "light saturated" rates of net photosynthesis for different maturity classes, had a significant effect over a wide range of PAR. It also showed that even at low flux densities, equivalent to 10% of full sunlight, factors other than the supply of radiant energy played an important role in regulating the rate of net photosynthesis.

The behaviour of stomatal resistance estimated during these experiments indicated that it might again account for many of the observed changes in net photosynthesis. A curvilinear decrease in stomatal resistance accompanied increasing PAR up to approximately full sunlight and the rate and extent of change varied with leaf maturity. Representative results are shown in Fig. 7 for the 12th leaf to emerge (cf. Fig. 5d).

The relative importance of stomatal resistance and the other two resistances regulating photosynthesis was assessed, as before, by comparing their relative magnitude and variability. Results for leaf 11 illustrate, in Fig. 8, the more important features observed in all four leaves (cf. Fig. 5c). The boundary layer resistance was maintained at the low and constant value of $r'_a = 0.5$ s cm$^{-1}$. The behaviour in response to PAR, of both stomatal resistance and residual resistance varied with individual leaf maturity but the changes were of differing
Fig. 7. - Stomatal resistance, $r_s'$, as a function of incident PAR showing changes with maturity in the 12th leaf to emerge (c.f. fig. 6d).
Fig. 8. - The contribution of stomatal resistance, \( r'_s \), to the total resistance to net photosynthesis, \( \Sigma r \), in a leaf at different stages in its maturity cycle and for a range of PAR 20-400 \( \times 10^{-9} \) E cm\(^{-2}\) s\(^{-1}\) (\( C_t = 600 \times 10^{-9} \) g cm\(^{-3}\)).
magnitude and time course. In all cases examined, over a range in PAR from 10-200% of full sunlight \((20-400 \times 10^{-9} \text{ E cm}^{-2} \text{ s}^{-1})\), stomatal resistance exerted the greatest single influence on the rate of net photosynthesis contributing from 53% to over 80% of \(\Delta r'\). The residual resistance made a smaller contribution which, as would be expected, increased with decreasing PAR. It is evident that, as in the first series of experiments, the minimum values of \(r'_r\) are unusually small indicating high efficiency in the system \(r'_r\) describes. There were significant changes, with the stage of individual leaf maturity, in the magnitude of \(r'_r\) and its sensitivity to PAR. However, it was not possible to identify the component of \(r'_r\) that might have been responsible.

E. DISCUSSION

The photosynthetic response of \(P. \text{ typhoides}\) leaves of varying maturity to a range of PAR and \(\text{CO}_2\) concentrations at optimum temperatures demonstrated that stomatal resistance was the largest of those regulating photosynthesis. It was also the most variable of the resistances and accounted for the large majority of the observed variation in net photosynthesis, including the changes associated with leaf maturity. Consequently, any attempt to increase the rate of net photosynthesis per unit leaf area in these plants is most likely to be successful if attention is focused on minimizing stomatal resistance. Two associated factors would have to be taken into account, however. Firstly, in field canopies the gain to be achieved by decreasing stomatal resistance would be less than might be expected, as the leaf boundary layer resistance would be considerably greater than the low values achieved experimentally. Any additional resistance to the transport of \(\text{CO}_2\) into and through the canopy would further decrease
the percentage contribution of stomatal resistance and thereby its importance in the system. Secondly, it should be noted that any decrease in stomatal resistance would be accompanied by an increase in opportunity for water loss from the leaf.

The findings presented in this paper re-emphasize the importance, in whole leaf studies of photosynthesis, of determining the contribution of the resistances to CO$_2$ transport, particularly those that vary. This applies whether the studies are intended to establish levels of photosynthetic capability or to elucidate the fundamental processes themselves. It is possible, for example, that some of the genotypic differences in photosynthetic rates that have been described (Hesketh, 1963; Izhar and Wallace, 1967; Björkman, 1968; Waering, Khalifa and Treharne, 1968; and Wilson and Cooper, 1969) may have been caused by differences in the resistances to CO$_2$ transport rather than by the mechanisms proposed. In the absence of the necessary measurements this doubt remains. Kinetic relationships of the type used for theoretical considerations by Rabinowitch (1951) have at times been used to explain the photosynthetic response of entire leaves (Hesketh and Musgrave, 1962; Goldsworthy, 1968). It is clear, however, that many of the processes that could be validly described in this way can be masked by changes in the resistances to CO$_2$ transport unless these are taken into account.

Finally, it is interesting to note that in this species, which has possibly the highest reported rates of net photosynthesis per unit leaf area and of dry matter accumulation per unit area of crop (Begg, 1965), the most important limitations to photosynthesis are not found chiefly in the capacity of the biochemical system but in the physical processes involved in the supply of CO$_2$ to the sites of photosynthesis.
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PHYSIOLOGICAL DAMAGE IN LEAVES OF *PENNISETUM TYPHOIDES* AT LOW CO₂ CONCENTRATIONS

**SUMMARY**

Unusual physiological damage was detected in leaves of *Pennisetum typhoides* (bulrush millet) at CO₂ concentrations less than 50% of normal ambient.

The symptoms were anomalous depression of net CO₂ uptake by the leaves, and visible cell damage in small patches over the section of leaf blade given the low CO₂ treatment. In severe cases net CO₂ release by the leaf up to 150% of maximum uptake rates occurred in the light.

The severity of damage was approximately proportional to the reduction in CO₂ concentration and the duration of the low CO₂ conditions. The degree and rate of symptom development were, in general, inversely proportional to humidity, and when the ambient air was saturated with water vapour no damage occurred. There appeared to be no effect of radiation flux density on the occurrence of leaf damage.

**A. EXPERIMENTAL CONDITIONS**

The plant material used in most of the experiments was *Pennisetum typhoides* (Burm.) S. & H. cv. Katherine Pearl (Commonwealth Plant Introduction Number 11378; Division of Plant Industry, CSIRO, 1967). The cultivar Ingrid Pearl (C.P.I. No. 28818) was also used.
but the results were the same as for Katherine Pearl. The plants were grown in aerated modified Hoaglands solution in a glasshouse with air temperatures approximately 30°C day and 15°C night.

The experiments were conducted in a perspex leaf chamber similar to that described by Jarvis and Slatyer (1966) but rectangular in shape, with a single chamber enclosing a leaf area of approximately 100 cm$^2$. Provision was made for rigorous control and measurement of photosynthetically active radiation (PAR), temperature, and CO$_2$ and water vapour concentrations and fluxes (McPherson and Slatyer, in press; Chapter 1). All experiments were conducted at leaf temperatures optimum for net photosynthesis (35°C). The CO$_2$ concentration of the air was regulated by passing it through an absorbing column of indicating soda lime, or by bubbling it through a solution of 40% KOH. In both cases sensitive tests were made to ensure that no alkali was being carried through with the air stream, and a millipore filter (pore size 0.8 µ) was inserted in the air line as an additional precaution.

B. SYMPTOMS

The symptoms associated with low CO$_2$ concentrations, with a wide range of radiation flux density and air humidity, were abnormal CO$_2$ exchange rates and visible cell damage in patches on the leaf.

As ambient CO$_2$ concentrations were reduced the net CO$_2$ uptake decreased, at first in a regular manner. This regular decrease (solid line, Fig. 1) was consistent with the change in net photosynthesis brought about by the net effect of the reduced supply of CO$_2$ to the leaf surface and the increasing stomatal
Fig. 1. - Measured net CO$_2$ uptake as a function of the ambient CO$_2$ concentration. The sequence in which the measurements were made is indicated by arrows. PAR = 106 E cm$^{-2}$ s$^{-1}$, approximately 50% of full sunlight.
aperture (McPherson and Slatyer, in press; Chapter 1). However, when CO$_2$ concentrations approximately 50% of normal ambient were reached, an irregular depression of CO$_2$ uptake frequently occurred, and this could not be explained in the same way (broken line, Fig. 1). The depression was usually greatest at the lowest CO$_2$ concentrations, and at times respiration rates as high as $-430 \times 10^{-9}$ g cm$^{-2}$ s$^{-1}$ were reached. When normal ambient CO$_2$ concentrations were restored within a few minutes, the initial gas exchange rates were approached, or effectively regained where no visible leaf damage had been sustained. After longer periods of low CO$_2$ concentration, however, recovery from depression in CO$_2$ exchange rates was considerably less.

The visible changes in the leaf occurred only on the portion of the leaf receiving the low CO$_2$ treatment and usually appeared first near the distal end of the enclosed area, particularly at the leaf edges. The first evidence of change was a lightening in the colour of small elongated areas (say 0.05 x 0.10 cm) which lay parallel to the vascular bundles. Under continuing low CO$_2$ concentrations, the area affected increased longitudinally, and to a lesser extent, laterally. Eventually the affected tissue showed signs of collapse, and bleaching of the pigments occurred. Improved conditions halted the spread of visible changes. In most cases the changes were irreversible, but sometimes areas that had just begun to discolour regained normal appearance.

Oxygen-free nitrogen induced visible symptoms similar to those in low CO$_2$ air, but as would be expected, the net exchange of CO$_2$ did not become negative.

Susceptibility to low CO$_2$ concentrations varied between groups of plants grown at different times but from the same seed.
source and under apparently similar conditions. However, when leaves were susceptible the occurrence of abnormal CO$_2$ exchange rates and visible leaf damage were intimately related. On every occasion where leaf damage was observed some depression of net photosynthesis also occurred. In general, the degree of depression was proportional to the extent of the visible damage. On the other hand, abnormal CO$_2$ exchange was not always accompanied by visible changes in the leaf. A notable example was a leaf which was detached by excising the base of the lamina under water prior to its placement in the leaf chamber. CO$_2$-free air was used for several hours, but in spite of the high rate of net CO$_2$ release ($430 \times 10^{-9}$ g cm$^{-2}$ s$^{-1}$) no leaf damage was visible.

The time between the decrease in CO$_2$ concentration and the appearance of gas exchange anomalies or of visible leaf damage varied. It was most rapid, however, with large step reductions in concentration, and under these conditions both symptoms could occur within five minutes.

C. DISCUSSION

The possibility that leaf damage was related to radiation effects was considered, but it was rejected on the following evidence. The xenon arc source used for most measurements was enclosed in a glass water jacket and its emission in both the ultraviolet and the near infra-red was comparatively low. No relationship could be detected between radiation flux density and the rate or degree of symptom development. Symptoms were observed at PAR levels as low as $12 \times 10^{-9}$ Einstein cm$^{-2}$ s$^{-1}$ (approximately 6% of full sunlight). A mercury vapour lamp, filtered to reduce ultraviolet radiation, also produced the effect.
Evidence obtained regarding the possible importance of water relations was, at first sight, contradictory. On one hand there were several indications that the phenomenon was the outcome of an unusual form of water stress. The discoloured areas appeared first on parts of the leaf furthest removed from the major water supply routes. That is at the edges of the distal end of the lamina area enclosed in the leaf chamber. They were seldom observed, even under severe conditions, in the tissue bordering the midrib, and the density was always lowest at the proximal end. In addition, the change of colour was to a blue-grey typical of leaves water stressed in the field. Leaf-air water vapour concentration differentials in excess of the $20 \times 10^{-6} \text{ g cm}^{-3}$ normally used (air relative humidity 50%) appeared to accelerate the deleterious effects of low CO$_2$ concentrations.

In contrast to this evidence, low CO$_2$ symptoms appeared even with measured transpiration considerably below rates that could be sustained indefinitely at normal CO$_2$ concentrations without adverse effects. By increasing the water vapour content of the air it was possible to decrease transpiration rates at the same time as the CO$_2$ concentrations were reduced. However, leaf damage occurred even under these conditions.

These apparently conflicting results could be reconciled if localised water stress was occurring. Under the stimulus of low CO$_2$ concentration the stomata may have opened to the extent that, in some areas, the demand for water exceeded the supply. It is possible that this could affect the tissue sufficiently to cause local cell damage and, in turn, high respiration rates. Under such conditions the measured transpiration rates, which apply to a comparatively large area, would not necessarily be affected
significantly. The area affected by visible damage increased over an extended period and seldom reached 10% of the enclosed leaf area.

The strongest evidence in support of the water-stress hypothesis was that no low CO$_2$ effect could be detected when leaf-air vapour concentration differentials were minimised by using air saturated with water vapour. A correlation between stomatal aperture and visible damage provided supporting evidence, but causality was not proven. Transects taken across leaves treated with low CO$_2$ air showed that stomatal apertures were greater over the visibly damaged areas than over adjacent areas. The results presented in Fig. 2 were taken from leaf-surface replicas obtained by using a spray-on plastic film (Nufix, W. Lewis Pty. Ltd., Sydney).

These findings raise several points of importance. For some areas to become water stressed while adjacent areas do not, there must be significant resistance to lateral and longitudinal transport of water between different parts of the leaf. However, the exact nature of this resistance is not clear. It is known that the major supply vessels run longitudinally in the leaf, and it can be demonstrated (by cutting a section from one side of the lamina at the proximal end) that lateral supply of water can sustain high transpiration rates.

It is also interesting that such high rates of CO$_2$ release can be sustained by a leaf which under some conditions can return to near-normal CO$_2$ exchange rates. If, as the visible damage suggests, only small areas of the leaf are affected, then the actual CO$_2$ flux from these areas would be perhaps an order of magnitude higher than that indicated by measurements made on the total area enclosed in the leaf chamber.
Fig. 2. - Correlation of stomatal aperture with areas of leaf visibly altered by low CO₂ treatment. Two transverse transects are shown.
It must be emphasised that the unusual response to low CO$_2$ concentrations occurred in healthy plants that gave entirely satisfactory and consistent results under environmental conditions that were identical in every other respect. It is perhaps not surprising that effects of the type described are rather unusual. Few, if any, detailed studies of gas exchange have been made previously on *Pennisetum typhoides*, and the low CO$_2$ concentrations required to cause damage would not normally be encountered in the field.

REFERENCES


A USER-ORIENTED MODEL OF THE PENETRATION, PROPAGATION, AND ABSORPTION OF RADIATION WITHIN PLANT CANOPIES

SUMMARY

A mathematical model for simulation of the penetration, propagation, and absorption of radiation within plant canopies is presented. The model is based on well known theory but incorporates several important features in the description of canopy structure and optical properties not available in any single model previously published.

The above-crop radiation is specified according to solar elevation and the direct and diffuse proportions of the radiation. The description of the canopy includes the leaf and soil optical properties appropriate to the wavelength under consideration, and the vertical profiles of leaf area and leaf angle. Multiple reflections and transmissions can be taken into account.

The predictions of the downward and upward travelling flux densities are compared with comparable measurements made in canopies of six different species of known architecture, under both clear and overcast skies. Good agreement is obtained in all cases except those where the crop was sufficiently water stressed to cause changes in the canopy which violated assumptions made in the model.

The model, and its relationship to others previously published, is discussed in this paper. The computer program developed to provide the numerical solution of the model is described by McPherson and Torssell (1970; Chapter 4) in sufficient detail to enable others to use the model for their own purposes.
A. INTRODUCTION

The transfer of radiant energy from the environment to the plant's photosynthetic system involves processes which vary widely in their efficiency. Many of these processes can be modified, and this provides a widely recognized opportunity for some influence to be exerted on plant growth through management and plant breeding. An important example of processes that can be modified in this way are those involved in the absorption of photosynthetically active radiation (PAR) by the leaves. These processes are essentially physical in nature and involve the penetration, propagation and absorption of radiation in the complex array of leaves, stems, and sometimes reproductive organs, that make up the plant canopy.

Radiation has the characteristic features of being directional and only instantaneously available to the absorbing surfaces. This poses special problems in predicting the absorption of radiation by plant canopies. It is also difficult to understand how the radiation is used, since photosynthesis is a non-linear function of flux density. Consequently, the spatial distribution, as well as the total quantity of radiation flux densities absorbed by the canopy must be determined.

A powerful approach that has been adopted to meet many of these problems is to assemble relevant information in the form of mathematical relationships, thus allowing important interactions among the various components to be analysed. Experiments on such mathematical models test the validity of the assumptions incorporated and, if they are satisfactory, the model can then be used as an efficient means of predicting the outcome of modifications to the
real plant canopy by management or breeding. Although several models have been developed, the present authors found that no single model satisfied all their requirements, and that modification was impractical.

The scope of the model presented here has been restricted to the prediction of only those parameters that could be thoroughly tested by techniques available to the authors. It was realized that the relation between canopy architecture and crop growth could only be understood when that between radiation flux density and rate of photosynthesis was also taken into account. However, it was clear that the description of the radiation environment alone had not been adequately validated, and this was regarded as an important first step towards the construction of a useful growth model.

The aims, theory, testing, and application of the radiation model are presented in this paper.

B. REVIEW OF LITERATURE

There is an extensive literature on the theory of penetration, and absorption of radiation within plant canopies. Anderson (1964, 1969, in press) and Reifsnyder (1967) have provided thorough and critical reviews of theory and measurement techniques. It is clear, however, that a need remains for more accurate and more useful data on light penetration into field crops, and for these to be more effectively utilized. Several mathematical models have recently been developed to help our understanding of the interception of radiation by plant canopies. These models vary widely in their
generality, realism, and precision, and thus in their usefulness to plant physiologists, plant breeders and agronomists. In this literature review attention will be focused on these particular aspects.

The theory used for computing the penetration of direct (unintercepted) radiation has been developed in a variety of ways but the basic relationships are the same in most cases, and allow for the exponential decrease of radiation flux with cumulative leaf area. Most of this work follows from the application of Beer's Law by Monsi and Saeki (1953).

The basic formula initially used by Monsi and Saeki is given by:

\[ I = I_0 \exp(-KF) \]  

(1)

I and \( I_0 \) are the flux densities below and above a given layer of leaves, F is the leaf area within that layer, and K is the extinction coefficient which here is an empirical constant. The empiricism of the extinction coefficient has been reduced in more recent work, firstly by using information on the angle of radiation propagation, \( \beta \), and the leaf angle, \( \alpha \), (both taken here with respect to the horizontal) to derive a term for "effective leaf area." The actual leaf area is adjusted to the area projected in the direction of the radiation, assuming that leaf orientation about the vertical axis (azimuth) is random. Also an allowance is made for the increase in optical path length for radiation travelling at any non-vertical angle through the canopy. The resulting relationships, such as those developed by Reeve (Wilson, 1960), are given by:
\[ I = I_0 \exp\left(-\frac{F'}{\sin \beta}\right) \] (2)

where \( F' \) is the leaf area projected in the direction of radiation travel and \((\sin \beta)\) adjusts for optical path length.

The incident radiation, \( I_0 \), is usually considered in two parts; direct sunlight and diffuse skylight. Direct sunlight is assumed to consist of parallel beams of radiation incident at a given angle, \( \beta \), to the horizontal. Information on solar azimuth is not required if the simplifying assumption is made that leaves are randomly oriented about the vertical axis. Skylight is usually treated in the same way as direct sunlight by considering the radiation from each altitude, \( \beta \), separately, and by weighting for the sky brightness at that elevation. Skylight is either assumed to be isotropic, often termed uniform overcast sky (UOC), or to increase in brightness as \( \beta \) approaches zenith, (e.g. the standard overcast sky, SOC, Moon and Spencer, 1942). Comparisons by Anderson (1966) and Cowan (1968) show that penetration of skylight from SOC and UOC skies differ. However, the differences would not be important when direct sunlight comprised the majority of the incident radiation.

Leaf angle is described in a variety of ways. De Wit (1965) uses a distribution function of angle which applies to the entire vertical profile. The analytical solution provided by Verhagan and Wilson (1969) is restricted to horizontal leaves only, while that of Cowan (1968) describes the case for horizontal, vertical, or randomly oriented leaves. Chartier (1966) and Ross and Nilson (1968) have analytical solutions where leaf angle can be defined, but this has the important restriction of uniform angle throughout the profile. This restriction does not apply to the numerical solution of Duncan et al. (1967).
A second modification of K involves the incorporation of information on leaf optical properties and estimation of the fate of intercepted radiation. It is here that the greatest variety of approaches is seen. Most models allow for propagation of intercepted sunlight and skylight, though Duncan et al. (1967) consider the reflection and transmission of sunlight only. De Wit (1965), Ross and Nilson (1968), Nilson (1968), Cowan (1968), Allen et al. (1970), and Idso and De Wit (1970) incorporate a scattering function for the leaves. Leaf transmission and reflection coefficients are defined separately by Duncan et al. (1967), and by Verhagen and Wilson (1969). Cowan, Ross, Nilson, Allen et al., and Idso and De Wit include a reflection coefficient for the soil. Nilson (1968) makes provision for multiple reflection and transmission which was found to be significant for wavebands where absorption is low. The upward flux is often ignored, but is considered by Cowan (1968), Nilson (1968), Ross and Nilson (1968), Verhagen and Wilson (1969), Allen et al. (1970), and Idso and De Wit (1970). In all cases it is assumed that the scattered radiation is completely diffuse.

Allen et al. (1970) have applied the Kubelka and Munk (K-M) two parameter theory. This application assumes uniform distribution of leaf angles, and output is the average radiant flux density with height. Direct application to photosynthesis is therefore difficult. With the purpose of overcoming the limitations of the K-M theory, Idso and De Wit (1970) presented a theory based on the light-distribution function of De Wit (1965). Their new De Wit-Idso (D-I) theory includes an iterative procedure for calculation of intercepted radiation using coefficients of scattering for direct, diffuse, and once-intercepted radiation.
Attempts have been made to provide a more direct approach than those described so far and to trace, theoretically, the fate of individual beams of radiation as they move through the canopy. The analysis presented by Monteith (1965) deals only with horizontal leaves which are assumed to transmit radiation rectilinearly, and no account is taken of reflected radiation. Although Armstrong (1969) has used more realistic assumptions, his model has not yet been fully developed and tested.

The success of a model must be judged largely by the resemblance it bears to the object or system it represents. There is a noticeable lack of satisfactory tests for this resemblance in published radiation models. This is due, in part, to the real difficulties of obtaining meaningful descriptions of canopy structure and the radiation environment within it. However, in many cases models do not supply output suitable for effective testing. The models of De Wit (1965), and Duncan et al. (1967), estimate the interception of PAR by the canopy and also its photosynthetic utilization, but do not allow for intermediate testing of the radiation estimates. The radiation data from De Wit is given as a frequency distribution of intercepted light with leaf angle. Although Duncan et al. (1967) provide calculations of horizontal flux density, this data is calculated in quite a different way to the radiation actually used as input to the photosynthetic section of the model. In both these cases the final output of photosynthetic production is the only quantity that could be meaningfully tested against experimental results. The radiation model of Chartier (1966) provides estimates of downward horizontal flux density, and those of Cowan (1968), Ross and Nilson (1968), Nilson (1968), Verhagen and Wilson (1969), Allen et al. (1970), and Idso and De Wit (1970) include, in addition,
the upward flux. Chartier provides a comparison of his model's prediction of the within-crop radiation with measured $K$ values reported by other workers. Other tests have been reported by Allen et al. (1970), and Idso and De Wit (1970) but these are limited to results for only one canopy and one waveband in each case.

Finally, it is worth noting that few of the models that have been developed are readily accessible to the agronomists, plant breeders, plant physiologists, or teachers, who might otherwise make use of the valuable information they can yield. This is because complex mathematical relationships or involved computer programs that are inadequately described, provide a significant barrier to the worker in related fields who can not afford the time to unravel these for himself.

C. OBJECTIVES AND DESCRIPTION OF THE MODEL

The objectives of this work are to provide a simulation model which is comprehensive and realistic, and to establish the validity of the model by testing it against radiation measurements made in field canopies of known architecture.

1. Specification of radiation

Radiation input and output are given as horizontal flux densities so that direct comparison can be made with the measurements from plane horizontally-oriented sensors. Incoming radiation is separated into direct sunlight and diffuse skylight, since their penetration into the crop must be treated somewhat differently. These quantities are easily measurable with standard solarimeters and a shading ring.
Upward as well as downward horizontal fluxes are computed so that their relative significance may be assessed. Incorporation of upward fluxes also permits the comparison of crop albedo estimates with measured values.

No account is taken here of the effect of spatial heterogeneity of radiation flux density on the utilization of PAR by the photosynthetic system. However, the model is designed so that this information can be easily included.

2. Canopy architecture

The description of canopy architecture includes the leaf optical properties and the distribution of leaf area and leaf angle with height. Waveband is, in effect, specified by the leaf optical properties which are wavelength-dependent. Leaf optical properties show a marked discontinuity at a wavelength of approximately 0.7 µ and radiation is therefore considered in two classes: one where absorption by leaves is high, PAR (taken as 0.4 - 0.7 µ waveband); the other where leaf absorption is low, the near infrared (NIR) waveband (0.7 - 3.0 µ). Provision is made for combination of the radiation profiles computed for these two wavebands to give results in the entire short-wave (0.4 - 3.0 µ) waveband. This feature is included because the short-wave radiation is a widely used measure even if it is not directly applicable to photosynthesis.

Leaf angle can be specified separately for each layer. This is an important feature seldom incorporated even though it has been suspected for some time that leaf angle, which varies with time and height in the canopy, is one of the key parameters.
affecting the efficiency of PAR utilization by crops. It is assumed that leaf angle is constant within each layer. However, a large number of layers could be used in the computation to incorporate data on the variability of leaf angle at any given height. A second assumption, which is widely used, is that leaf orientation is at random about the vertical axis.

3. Penetration

The penetration of radiation through a layer of leaves is described by the exponential decay of unintercepted radiant flux with cumulative "effective leaf area" (eq. 2). The procedure followed is based on that described by Duncan et al. (1967). It is used to determine the penetration of any radiation travelling through the canopy in a specified direction, regardless of whether it is direct sunlight, skylight, or previously intercepted radiation that has been reflected or transmitted. Sunlight is assumed to consist of parallel rays of radiation travelling at an angle, $\beta$, to the horizontal. Specification of solar azimuth is not necessary because of the assumption that leaf azimuth is random.

Skylight is dealt with in a similar way by the usual procedure of assuming that the radiation arriving at a given point from small areas of the sky also consists of parallel rays. The sky, which is assumed to be uniformly bright, is divided into six concentric segments subtending equal solid angles. The radiation from each of these segments is regarded as having an elevation angle, $\beta$, equal to the elevation of the mid-point of each segment (skyzone), and is treated in the same manner as direct sunlight. Again azimuth angle need not be specified.
Radiation travelling through the canopy as a result of reflection and/or transmission is treated in essentially the same way as skylight. The source and direction of this radiation is discussed in the following section.

4. Propagation

The exponential decay of sunlight and skylight with effective leaf area does not, in itself, account for radiation arising from reflection and transmission within the layer in question. Therefore, where the leaves give significant reflection and transmission of intercepted radiation this must be taken into account separately. The quantity of radiation intercepted in each layer is given by equation 2. In calculating the proportion of radiation travelling in specified directions after reflection and transmission it is necessary to take into account the combined effect of the angle of incoming radiation, $\beta$, and leaf angle at each leaf azimuth position. These calculations are crucial in any model used for estimating the variability of incident or absorbed flux density on leaves. Such information is necessary for computing net photosynthesis correctly because of the non-linearity of this response to PAR flux density. In this model, information on the heterogeneity of flux densities is not extracted, as the planned field tests were restricted to measurement of the spatial average of radiant flux density through a horizontal plane. The actual relationships used are described in more detail by McPherson and Torssell (1970; Chapter 4), and the underlying theory is discussed by De Wit (1965) and Duncan et al. (1967).

A major problem in radiation models is accounting for the number of quantities and directions of radiation which increase with each reflection or transmission. To overcome this problem all
reflected or transmitted radiation is allocated to one of twelve angle categories; six for radiation travelling in directions below the horizontal (downward), and six for those above (upward). Again, the need for classification with respect to azimuth angle was obviated by the assumption of random leaf azimuth orientation.

The passage of reflected and transmitted radiation is followed upward and downward through the canopy from the layer of origin in a series of stepwise processes. As this radiation passes through each layer the unintercepted portion is calculated from the exponential relationship as before (eq. 2). From the intercepted radiation, the quantities of re-reflected and re-transmitted radiation are calculated. An iterative loop in the computer program is used to follow the reflected and transmitted radiation in this way until the quantity remaining (i.e. that which has not left the upper crop surface or been absorbed by leaves or soil) is negligibly small.

The importance of the contribution of radiant flux from reflection and transmission varies with leaf optical properties, and so, consequently, does the importance of being able to take into account multiple reflections and/or transmissions. The effect of the number of calculation cycles made by the iterative loop on simulation results is shown in Fig. 1. The approach toward stability of the calculated "albedo" (the ratio of radiant flux leaving the upper surface of the canopy, to that entering it) provides an index of the approach toward energy conservation where all the significant fluxes of radiation have been taken into account. Where absorption is high, for example in the photosynthetically active waveband, only first and second order reflections and transmissions
Fig. 1. - The effect of the number of iterations on the calculated "albedo" for absorption applicable for PAR (T = R = 0.10), NIR (T = R = 0.40) and for no absorption (T = R = 0.0). Soil reflectivity in all cases equal to T plus R.
need be computed. However with low absorption, using optical properties
more typical of the near-infrared waveband, approximately twelve
iterations are required before an acceptably high proportion of
the radiation movement is accounted for. These results apply
strictly only to the conditions specified, and would vary in detail
if, for example, leaf angle was changed. The approximate computing
times quoted are for the Fortran IV program described by McPherson
and Torssell (1970; Chapter 4) and apply to the time required
for its execution, in pre-compiled form, on the CSIRO CDC3600 computer.

5. Absorption

Absorbed radiation can be accounted for directly or indirectly.
An indirect method is most convenient where attention is limited
to horizontal flux density, and this method is followed here. As
the penetration of all forms of radiation is followed from layer
to layer, a count is kept of the flux passing upward or downward
through each layer interface. This cumulative quantity gives the
flux density at each interface and is an output from the model.
The radiation absorbed is based on these quantities by calculating
the difference between the net flux density above and below each
particular layer.

A direct estimate of absorbed radiation can be made while
partitioning the intercepted radiation into reflected, transmitted,
and absorbed categories. The absorbed radiation could at this stage
be classed into different levels of flux density for the subsequent
calculation of net photosynthesis.
D. MODEL TESTS

A comparison of results was made with two published models (Cowan, 1968; and Verhagen and Wilson, 1969) which provided output in a form compatible with this model. The three models use the same basic theory but differ considerably in the way it is used. In Fig. 2a it can be seen that for a horizontal-leaved canopy with leaf optical properties appropriate to PAR (R = T = 0.10), good agreement was obtained for the predicted downward and upward horizontal flux density of radiation. Cowan also gave results where leaf optical properties typical of the NIR waveband (R = T = 0.40) were used. Agreement for the predicted total downward and upward flux density and unintercepted downward flux density was good in this case also (Fig. 2b).

To test the validity of the model and the assumptions it incorporates in a more direct way, measured and predicted radiation profiles were compared for canopies of four grasses and two legumes. The crops were grown under supplementary irrigation during the 1970 wet season in Katherine, northern Australia, a low latitude monsoonal area (132.3°E. longitude, 14.3°S. latitude). Measurements were made under both clear and overcast conditions. The results were expressed in all cases as the radiant flux density passing upward or downward through unit area of horizontal plane.

Most of the measurements were made using instruments sensitive to shortwave radiation (SW, 0.4 - 3.0 µ) which includes the photosynthetically active waveband (PAR, 0.4 - 0.7 µ) and the near-infrared waveband (NIR, 0.7 - 3.0 µ). This provided a well balanced test. Absorption by plant leaves is high for PAR, and leaf angle
Fig. 2. - Downward and upward horizontal flux densities of radiation in the PAR (a) and NIR (b) wavebands calculated for horizontal leaves, using the models of Cowan (1968) (■), Verhagen and Wilson (1969) (♦), and the model presented in this paper (▲). The broken line in (b) indicates the component of downward flux due to unintercepted radiation.
and radiation angle play a dominant role. In the case of NIR, absorption is low and the treatment of reflection and transmission assumes much greater importance. For simulation purposes, the PAR and NIR wavebands were treated separately as described earlier. As facilities were not available for measurement of the appropriate leaf optical properties, it was necessary to assume values generally accepted for this type of plant material (PAR, $R = T = 0.10$; NIR, $R = T = 0.40$). These values were used throughout all experiments.

Some measurements were made using instruments sensitive only to PAR in order to provide results less dependent on the assumed optical values. In this waveband of high absorption, reflection and transmission are of reduced importance.

All other information on the crop canopy was determined for the exact section of canopy where the radiation profile measurements were made. This included soil reflectivity, and, for every 10 cm layer of canopy, the foliage area, average stem angle, and average leaf angle. Stem area (projected), was treated in the same way as leaf area. Although stem area constituted 15-40% of total foliage area its contribution to absorption was less than this might indicate. This was because of its more vertical orientation, and proportionately smaller contribution near the top of the canopy where most of the absorption occurs.

Comparisons of measured and predicted flux densities were mostly made near solar noon to avoid the possible effects of heliotrophia which is known to occur in *Stylosanthes* (Begg and Torssell, unpublished).
1. Methods

Sampling

Measurement of the radiation in a plant canopy involves considerable sampling problems, firstly in spatial integration due to the physical heterogeneity of the canopy, and secondly in time integration due to the fluctuation in the incoming radiation. To reduce the spatial variation, measurements were made in carefully selected uniform stands, with four replicates provided by four linear, spatially-integrating instruments.

To reduce errors due to fluctuating radiation, all measurements were restricted to either completely clear or uniformly overcast sky conditions. A digital data logging system (Solartron Pty. Ltd.) was used to sample instrument signals by the sequential scanning of 25 channels (at the rate of 1 channel/sec) and to punch the results on paper tape. The system was remotely controlled from the field to give a minimum of 3 scans for each instrument position. A series of remote switches provided a code which was recorded by the logger for later identification of each group of data.

Sensors

The shortwave radiation incident on the canopy surface was measured by two Kipp and Zonen solarimeters. One of these determined global radiation while the other, equipped with a shade ring, determined the diffuse component. The direct component was determined by difference. Solar altitude was determined from information on time of day, latitude, and longitude, using a computer program.
developed by Goodspeed (1970). The downward and upward fluxes of shortwave radiation within the canopy were measured using linear solarimeters (Szeicz et al., 1964). These were modified for use with only one glass cover to reduce their diameter to 2.0 cm and thereby minimize the disturbance of the canopy. The angular sensitivity of these instruments about the major axis closely approximated the required cosine response.

Silicon photovoltaic cells (0.5 x 1.0 cm active area), directly filtered with GG19 and BG38 glass filters (Schott and General, Mainz), provided within-crop measurements of PAR (McPherson, 1969; Chapter 5). To improve the angular sensitivity, surface-roughened opal diffusing perspex was mounted on top of the filters. Three of these instruments were attached 15 cm apart on a linear support and were connected in parallel electrically to provide an integrated signal. This output was shorted by a stable 100 ohm resistor to provide a linear signal response with radiant flux density, and to give the required temperature stability. Further spatial integration was obtained by moving the sensors horizontally through the crop over the measuring area, recording every three seconds to give a total of 13 readings.

Measurements of soil reflectivity were made in the shortwave band using the miniature solarimeter of Bringman and Rodskjer (1968), and in the photosynthetically active waveband using the instruments described above. Reflection in the near-infrared waveband was determined by difference.

Instrument support

The linear solarimeters were supported in the canopy at each end by circular holders welded at 10 cm intervals along 1.2 cm diameter
steel pegs. When the measuring site had been selected the two steel pegs for each of the four instruments were driven into the ground to allow the instruments to be held approximately 13 cm apart at any one height. Thus, the four sensors covered a horizontal area of 50 x 50 cm, providing adequate spatial averaging at each of the 10 cm height intervals.

Immediately after the complete radiation profile was measured the canopy was harvested for leaf area measurement, the pegs and instrument supports giving the exact area and height for stratified sampling. Soil reflectivity was then measured at the same site.

Leaf angle

Two different methods were used for estimating leaf angle. For grass, a 10 cm thick and 50 cm long vertical sample of the stand was pressed together between two boards then removed for determination of the average angle of both leaves and stems. For legumes, leaf angle was estimated from the relationship between actual and projected leaf area as presented by Duncan et al. (1967) in their "Wilson" table. For any given radiation elevation and leaf angle (assuming random azimuth orientation), the table gives the ratio $F'/F$ where $F'$ is the shadow area projected on a plane normal to the sun's rays, and $F$ is the actual leaf area. To determine $F'$ a piece of stem with leaves attached was removed from the crop using a drawing-board arm mounted on a tripod. This maintained the original orientation of the stem and leaves while they were exposed over a sheet of self-developing photographic paper (Studio proof F, Kodak) held normal to the sun's rays. The area of the shadow on this paper gave $F'$. 
2. Results

The plant material used for test purposes fell into three categories:

(a) Young undefoliated canopies with high growth rates and approaching the maximum leaf area index (LAI) of 4.0 – 6.0. There was no evidence of water stress.

(b) Older canopies with slower growth rates than in category (a), having reached maximum LAI. Slight noon water stress was apparent. Some of the canopies in this category were not defoliated while others were continuously defoliated.

(c) Old canopies at seed-setting stage with severe noon and afternoon water stress.

All tests conducted in the unstressed canopies (category a) gave very good agreement between observed and predicted data. This is shown in Fig. 3 which illustrates the profiles for downward and upward travelling flux density of shortwave radiation in a grass canopy (Digitaria ascenedens, summer grass) under clear and overcast sky, and in two legume canopies Stylosanthes humilis, Townsville stylo; Alysicarpus vaginales, buffalo clover) under a clear sky. The correlation between observed and predicted radiation was high ($r = 0.99$). The regression is illustrated in Fig. 4.

Measurements of PAR were introduced towards the end of the growth season when most of the stands available had been continuously defoliated. These stands were very compact, with a leaf area index of 4 within a total height of 10 cm. Despite the obvious problems in
Fig. 3. - Measured (○) and predicted (●) downward and upward horizontal flux densities of shortwave radiation in non-stressed canopies of: *Digitaria adscendens* under (a) overcast and (b) clear sky; *Stylosanthes humilis* (c) clear sky; and *Alysicarpus vaginalis* (d) clear sky.

All data is expressed as percent of above crop radiation, and is plotted against foliage area accumulated from the top of the canopy.
relating leaf area to height accurately, agreements were good for both PAR and SW wavebands. The one case where both PAR and SW measurements were made on the same undefoliated stand also showed good agreement (Fig. 5).

When the same optical properties as those used above were applied to a 1.2 m (4 ft) high almond tree (cv. H-1), the estimate of absorbed radiation was consistently too low. This was the case with the three species mentioned above but adding three other defoliated annual grasses. Reducing the leaf deviation using lower leaf angles did not increase the absorption sufficiently to give agreement with the observed values, confirming that deviation was most unlikely to be caused by errors in the measurements. It was found that increase in the leaf properties (both the sum of K and N and their relative distribution) could explain the results, coupled with that these varied with height in the canopy. It is considered likely that such effects could explain the discrepancy between measured and simulated results.

All the observations were under conditions of severe water stress (Fig. 4). Under water stress in lagoons is negatively phototrophic, thus reducing the interception of radiation (Begg and Terswell, unpublished). When the water stress signal is present, the undefoliated lysimeter leaf distribution is irregular but regular for the canopy. As this situation is not likely to be applicable under the conditions described above, and with the results of the simulations, further work is required to show the canopy. In Figs. 3 and 5 (non-stressed canopies).

Fig. 4. - Regression between measured and predicted horizontal flux densities for the model tests presented in Figs. 3 and 5 (non-stressed canopies).
relating leaf area to height accurately, agreements were good for both PAR and SW wavebands. The one case where both PAR and SW measurements were made on the same undefoliated stand also showed good agreement (Fig. 5).

When the same optical properties as those used above were applied for the canopies classified as slightly stressed (category b), the estimate of absorbed radiation was consistently too low. This was the case with the three species mentioned above and, in addition, three other defoliated annual grasses. Recalculation of absorption using lower leaf angles did not increase the absorption sufficiently to give agreement with the observed values, confirming that the deviation was most unlikely to be caused by errors in leaf angle measurements. It was found that changes in the leaf optical properties (both the sum of R and T and their relative magnitude) could explain the results, provided that these varied with height in the canopy. It is considered likely that such effects would explain the discrepancy between measured and simulated results, but in the absence of field measurements on leaf optical properties no direct experimental evidence can be offered to support this.

All the observations made under conditions of severe water stress (category c), were in *Stylosanthes* canopies. Under water stress, this legume is negatively phototrophic, thus reducing the interception of radiation (Begg and Torssell, unpublished). When there is severe stress the leaflets cluster together. The leaf distribution is then no longer random and irregular gaps form in the canopy. As this model assumes random leaf distribution it is not likely to be applicable under the conditions described above, and would be expected to overestimate absorption by the canopy. Results confirmed this. Observations taken for the morning, noon,
Fig. 5. - Measured (○) and predicted (■) downward and upward horizontal flux densities in non-stressed canopy of *Stylosanthes humilis* for (a) PAR (0.4 - 0.7 µ) and (b) shortwave (0.4 - 3.0 µ) wavebands.
and afternoon of the same day are shown in Fig. 6. It is significant that the model holds for the morning situation where there is very little water stress. By noon the water stress had increased and the resulting high leaf angle ($\alpha = 83^\circ$), combined with high solar altitude ($\beta = 77^\circ$), caused the direct solar radiation to penetrate to a much greater extent than predicted by the model. The better agreement by 16.15 hr is likely to be due to the decrease in solar altitude ($\beta = 37^\circ$) reducing the importance of the canopy gaps.

Having established the validity of the model it was then possible to use it for simulation. Strictly, the model remains untested outside the range of conditions that were obtained in the field, so results outside this range should be regarded with some caution.

E. EXAMPLES OF SIMULATION WITH THE MODEL

An important use of simulation models is that they can indicate the sensitivity of the system to change in any of the components described. Following are two examples which show how this sensitivity analysis can be applied.

It has not been clear previously whether leaf optical properties could be specified solely in terms of the proportion of intercepted radiation absorbed (with the assumption that $R = T$), or whether $R$ and $T$ should be specified separately. In Fig. 7 the effect of varying the proportions of $R$ and $T$ is examined for two constant values of $(T + R)$, one appropriate to the photosynthetically active waveband, and the other to the near-infrared waveband. As might be expected, an increase in the ratio $R/(R + T)$ is accompanied by a decrease in the absorption by the canopy,
Fig. 6. - Measured (*) and predicted (•) downward and upward horizontal flux densities of shortwave radiation in severely water-stressed stands of *Stylosanthes humilis* at 0930 HRS (a), 1315 HRS (b) and 1615 HRS (c).
and an increase in "albedo". The effect is relatively unimportant in the photosynthetically active waveband, but in the near-infrared waveband it is highly significant. Results are not shown for shortwave radiation but these are intermediate.

The magnitude of "albedo" as leaf optical properties is examined for three different leaf tilts. It is clear that as leaf absorption decreases toward zero, "albedo" becomes increasingly sensitive to changing leaf optical properties and the influence of leaf angle, even over a wide range is small.

Although the "albedo" is small and rather insensitive in magnitude, and of direct importance in photosynthesis and indirectly to growth, it proves to be a useful indication of changes in the leaf optical properties. In the NIR absorption wavebands, moreover, it is highly sensitive to leaf optical properties and almost independent of leaf angle. For some species of plants, it appears that leaf angle would provide an easily measured parameter that is highly sensitive to leaf optical properties, and essentially constant for different levels of canopy density. If leaf optical properties vary significantly with some other parameter of importance, such as plant water status, disease, or species differences, the appropriate "albedo" measurement could provide a useful tool for estimating these regularities.

Fig. 7. - The effect of the ratio \( R/(R + T) \) on calculated "albedo" and absorption, for PAR (\( T + R = 0.20 \)) and NIR (\( T + R = 0.80 \)) wavebands.
and an increase in "albedo". The effect is relatively unimportant in the photosynthetically active waveband, but in the near-infrared waveband it is highly significant. Results are not shown for shortwave radiation but these are intermediate.

The sensitivity of "albedo" to leaf optical properties is examined in Fig. 8 for three different leaf angles. It is clear that as leaf absorption decreases toward zero \( T + R = 1 \) the "albedo" becomes increasingly sensitive to changing leaf optical properties, and the influence of leaf angle, even over a wide range, is small.

Although the "albedo" is small and rather insensitive in the waveband of direct importance in photosynthesis, it may nevertheless prove to be a useful indicator. The "albedo" in the low absorption wavebands, such as NIR, is highly sensitive to leaf optical properties and is almost independent of leaf angle. For most established crops this "albedo" would be insensitive to leaf area also. It provides then, an easily measured index that is highly sensitive to leaf optical properties, and essentially independent of canopy structure. If leaf optical properties vary significantly with any growth parameter of importance, such as plant water status, disease, or species differences, the appropriate "albedo" measurement could provide a useful tool for estimating these characteristics.

F. DISCUSSION

The first objective of the field tests was to establish whether the model could describe adequately the penetration, propagation, and absorption of radiation under ideal conditions, with stable and easily described above-crop radiation, and with canopies regular
in leaf angle and area distribution. The results showed that the model is capable of predicting intercepted radiation with good accuracy. Disagreement between measured and predicted radiation was well within the limits that might be expected, taking into account the accuracy in measurements of radiation, leaf area, leaf angle, and canopy structure. It is concluded therefore, that the assumptions included in the model (e.g. random leaf distribution, random azimuth orientation, and Lambertian scattering of reflected and transmitted radiation) are valid for the conditions described.

Fig. 8. - The effect of leaf optical properties on the calculated "albedo" for leaf angles 1°, 45° and 89°.

T = R, and soil reflectivity = T + R.
in leaf angle and area distribution. The results showed that the model could fulfil these requirements for the species studied. Disagreement between measured and predicted radiation was well within the limits that might be expected, taking into account the accuracy of measurements of radiation, leaf area, leaf angle, and canopy height. It is concluded therefore, that the assumptions included in the model (e.g. random leaf distribution, random azimuth orientation, and Lambertian scattering of reflected and transmitted radiation) are valid for the conditions described.

In situations where it is difficult to measure key parameters accurately, less consistent agreement between measured and predicted values must be expected. This situation was encountered in the short and dense canopies which resulted from continuous defoliation. Here, even small errors in height measurement were highly significant. Although it was more difficult to test the model under such circumstances the results indicated that it did describe the radiation environment within these canopies satisfactorily.

By contrast, the field tests showed that the assumptions implicit in the model do not hold for severely water stressed canopies. Leaf clustering in response to severe water stress in *Stylosanthes humilis* gave markedly non-random leaf distribution, and considerable over-estimates of canopy absorption resulted. Difficulties of this type arise because the description of the canopy and radiant flux accounts for variation in only one dimension. Most radiation models are of this type and are suitable only where the scale of heterogeneity in the horizontal plane is small. They can not be applied validly, for example, in crops with widely spaced rows or where other large-scale variability exists, even if this is random in nature.
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A COMPUTER PROGRAM FOR SIMULATION OF
THE PENETRATION, PROPAGATION, AND
ABSORPTION OF RADIATION WITHIN PLANT CANOPIES

SUMMARY

A detailed description is given of a Fortran IV computer program for use in the simulation of the penetration, propagation, and absorption of radiation in plant canopies. The program provides the numerical solution of a mathematical model presented and discussed more fully in a companion paper (McPherson and Torssell, in press; Chapter 3). This paper is a technical description to assist those who may wish to use the program.

Input, describing the above-crop radiation and canopy structure, consists of information on the horizontal flux density of sunlight and skylight, sun elevation, the vertical distribution of leaf area and angle, and leaf and soil optical properties. Output includes layer by layer predictions of the downward and upward flux of radiation and its absorption. An iterative loop permits multiple reflections and/or transmissions to be accounted for.

The program description includes an outline of overall organization, annotated flow charts describing the major sections, and details of input/output control.

Rigorous tests for internal program errors were conducted and the results of these are presented.
A. INTRODUCTION

It has long been recognized that the efficiency of transfer of radiation from the plant's environment to its photosynthetic system is both variable and generally low. A considerable amount of theory has been developed to describe the processes affecting this transfer, with the aim of determining means of improving their efficiency. Unfortunately, because of the complexity of the canopy structure and the variability of the above-crop radiation environment, the mathematics are often complex and the calculations tedious. This tends to restrict the application of such theory, particularly as full descriptions of the calculation procedures are seldom published. Increasing use is being made of simulation models to provide a logical basis for planning crop management procedures, plant breeding, and further experimentation. Consequently, there is a need for full descriptions of these models to be published so that they can be used efficiently, and modified if necessary, by the agronomists, plant breeders, and physiologists involved.

An extensive literature is available on the theory of the penetration, propagation, and absorption of radiation within plant canopies and several models have been developed which formalize these relationships. However, the models vary widely in their generality, realism, and precision, and consequently, in their capacity to provide an operational tool for those wishing to make use of the important information they can yield.

The work described here was initiated when the present authors found that available models did not meet their requirements and could not be readily modified. The model that was developed is presented in a companion paper (McPherson and Torssell, in press;
Chapter 3) where a full discussion is given of the underlying theory with reference to current literature, the main objectives and features of the model, and also the results of field tests conducted to determine its validity. The advantages of the model are seen in its incorporation of several important features not available in any one model so far described, and in the field testing of its performance.

The Fortran IV computer program, developed to cope with the calculations required for the model's solution, is presented here in detail.

B. THEORY SUMMARY AND SEQUENCE OF PROGRAM OPERATION

1. Unintercepted radiation

The decay of direct (unintercepted) radiation penetrating the canopy is taken to be an exponential function of effective leaf area and is given by:

$$ I = I_0 \exp \left( \frac{F'}{\sin \beta} \right) $$

$I$ and $I_0$ are the flux densities below and above a given layer of leaves, $F'$ is the leaf area projected in the direction of radiation propagation, and $\beta$ is the altitude of the radiant source and consequently $(\sin \beta)$ adjusts $F'$ for the increase in optical path length where radiation travels through the canopy at any non-vertical angle.

Skylight is treated in essentially the same way as direct sunlight, by assuming that the sky is uniformly bright and dividing it into concentric skyzones subtending equal solid angle. The
radiation travelling from a given skyzone to a particular point is taken to have \( \beta \) equal to the elevation of the zone midpoint above the horizon. Azimuth effects can be ignored as leaf orientation about the vertical axis is assumed to be at random.

Unless otherwise stated, radiation is described as the flux through unit area of horizontal plane in unit time (horizontal flux density). This has the advantage of direct relation to measurements made with the widely used cosine-corrected plane sensor horizontally oriented, and in addition it simplifies computation if used consistently.

2. Intercepted radiation

The sunlight or skylight intercepted by any given layer of leaves can be determined by equation (1). It is taken as the difference between the \( I \) values appropriate to the two planes delimiting the leaf area in question. The fate of this radiation is governed by the orientation of the leaves intercepting it, and by their optical properties. Subroutine LAMBERT, which is described in detail later, partitions the intercepted radiation by computing the direction and quantity of radiation leaving the leaf. With each interception, radiation is scattered in an increasing number of directions. To overcome the problem of accounting for each of these separately, the radiation is considered in groups according to its direction of travel. The upward and downward fluxes are considered separately, then further subdivided into equal solid angle zones. The separate quantities of radiation are then grouped according to their particular direction of travel with respect to the horizontal. Again, azimuth can be ignored, since random leaf orientation is assumed.
This once-intercepted radiation then has the opportunity to move in its specified directions until it leaves the canopy or is reintercepted. In the case of reinterception the process of re-reflection and/or transmission may be repeated. This is dealt with in a systematic manner and any number of interceptions can be traced using an iterative procedure.

The quantity of intercepted radiation that is subjected to reflection and transmission is governed by the optical properties of the leaves. These vary with wavelength, and the values specified should be appropriate to the waveband of interest. If simulation is required for a waveband in which the optical properties vary significantly, the calculations can be conducted independently on as many subdivisions as are required to obtain groups of similar optical properties. The propagation over the entire waveband can then be calculated by summation of these results.

Provision is made for the combination of two wavebands of differing optical properties. These are the photosynthetically active radiation waveband (0.4-0.7 µ) which has high absorption, and the near-infrared waveband (0.7-3.0 µ) which has low absorption. Summation gives the short wave radiation propagation usually measured by glass-covered radiation sensors (0.4-3.0 µ).

3. Sequence of operations

The overall relationship of program operations is summarized in flowchart form in Figure 1, and the separate program sections are identified. Equation (1) is used to calculate, layer by layer, the penetration of unintercepted radiation from information on
Input data - above-crop radiation canopy structure

Penetration of sunlight

Partition of intercepted sunlight

SUBROUTINE LAMBERT

Penetration of skylight

Partition of intercepted skylight

SUBROUTINE LAMBERT

Propagation of intercepted radiation

Penetration of previously intercepted radiation

SUBROUTINE LAMBERT

SUBROUTINE LAMBERT

Radiation not accounted for = 0

Output of horizontal flux density profiles etc.

Fig. 1. - A flowchart of the more important program sections.
above-crop radiation and plant structure. Sunlight is dealt with first, and the quantity reaching the lower limit of each layer is calculated in turn. Subroutine LAMBERT is used to compute the magnitude of the first reflection and transmission in each layer, and to provide for its storage according to the separate directional classes. Skylight is then treated in an identical manner except that the calculations are repeated six times, one for each skyzone with its appropriate value of $\beta$.

The sequence followed in this calculation and in the subsequent calculation of propagation of reflected and transmitted radiation is illustrated in Figure 2. Firstly, sunlight and skylight are followed downward, layer by layer through the canopy (from $C_1$ to $S_1$), and the proportions of intercepted radiation that is reflected, transmitted, and absorbed by each layer is calculated at each stage. Radiation reflected and transmitted upward is held, for later processing, in storage locations represented by square boxes ($U_1$ - $U_3$). Similarly, radiation reflected and transmitted downward is held in locations represented by circles ($D_1$ - $D_3$). The radiation in the storage locations for upward travelling radiation is then followed upward, with provision for interception within each layer (from $S_2$ to $C_2$). Then, in the same way, the primary reflections and transmissions downward are accounted for (going from $C_3$ to $S_3$). By this stage, the secondary reflections and transmissions are held in storage as described above, available for further computation if the quantity is significant. Radiation intercepted at any stage in the described sequence may thus be re-reflected or re-transmitted, in which case the quantity (with respect to direction) is defined by subroutine LAMBERT and stored. LAMSCAT is simply a subroutine used for determining the quantity...
Penetration and interception of sunlight and skylight. Allocation of primary reflection and transmission.

Penetration and interception of previously intercepted radiation. Allocation of secondary to \( n + 1 \) reflections and/or transmissions, for \( n \) iterations of this loop.

Fig. 2. - Representation of the sequence followed in calculating the penetration and propagation of radiation through a canopy (specified in three layers only, for clarity).
of the reinterception and allocating this radiation to LAMBERT at the appropriate stage. It also returns the results to the main program. Unintercepted radiation is carried forward and added to the radiation reflected and transmitted upward from the next layer.

The procedure for the regrouping of diffuse radiation (sky radiation and reflected and transmitted radiation) according to its direction in each layer is represented diagrammatically, in Figure 3. Diffuse radiation is considered to be composed of a large number of individual rays which may be grouped into directional classes. Each of these is treated in the same way as direct sunlight. For clarity, the number of directional groups is reduced to three downward (denoted A, B, C), instead of the 6 downward and 6 upward actually used. As each of the rays passing into a layer is intercepted there is opportunity for it to be scattered in new directions. To overcome the problem of the increasing number of directions at each interception the radiation leaving each layer is collected into the above-mentioned directional groups, regardless of whether its source is direct penetration, reflection or transmission. At this point in the computation we have followed the once-reflected or transmitted radiation through the canopy, allowing it either to leave the canopy altogether or to be reintercepted. In the latter case the radiation from the second reflection and transmission is stored for further analysis by repeating the steps described above. This is continued in an iterative loop until the quantities remaining are sufficiently small to be ignored.

This then, accounts for the propagation of radiation through the crop. To interpret this in terms of a measurement at a particular point, a count is made of the quantity of radiation passing a unit
Fig. 3. - Penetration and propagation of diffuse radiation (i.e. skylight, reflected, and transmitted radiation) represented for two layers of canopy. Only three of the twelve angle classes used in practice (six upward, six downward) are shown here (denoted A, B, C).
area of plane at that point. This count is taken at the horizontal layer interfaces, and is made separately for upward and downward-travelling flux.

4. Subroutine LAMBERT

Intercepted radiation may be reflected, transmitted, and absorbed. Subroutine LAMBERT is used to determine the relative proportion of these quantities and the direction of propagation of the reflected and transmitted components. The reflection and transmission coefficients are specified for the waveband under consideration, and these determine the quantity of radiation leaving the leaf. The direction of propagation is calculated on the assumption that scattering is complete (Lambertian). That is, the leaf scatters radiation uniformly in all directions. The fraction of illuminated leaf surface facing upward or downward is calculated using information on leaf angle and elevation of the radiation source, and relating these for each of the six leaf azimuth positions in turn. Together with the assumption of Lambertian scattering, this permits calculation of the proportion of radiation reflected at angles above and below the horizontal. Complimentary calculations are used for transmitted radiation. The direction of propagation is specified by grouping the reflected and transmitted radiation in each of the upward or downward hemispheres into six elevation angle classes which are the same as those used for skylight.

Two leaf azimuth cases are sufficient to represent all possible cases in relation to direction of radiation. Fig. 4a represents the case where the upper surface of the leaf is illuminated and Fig. 4b the case with the lower surface illuminated. The radiation reflected from point 0, on the leaf, COF, (solid arrows) is assumed
Fig. 4. - An illustration of the directional allocation of radiation reflected and transmitted from point, 0, on a leaf COF. Two leaf azimuth positions, representative of all those possible, are shown (a and b). (a) refers to the case where radiation is intercepted by the upper surface and (b) by the lower surface of the leaf. The alphanumeric sector labels refer to variable names used in subroutine LAMBERT.
to be completely and uniformly scattered and therefore the flux distribution can be represented by a hemisphere, the flux travelling within any solid angle being proportional to that solid angle.

Firstly, the total reflected radiation is separated into that travelling above or below the horizontal and added for all azimuth positions \((R_{UP1} + R_{UP2} \text{ and } R_{DN1} + R_{DN2} \text{ respectively})\). Secondly, it is necessary to further subdivide this radiation into that travelling at angles greater than or less than leaf angle (e.g. \(R_{UP1}\) is divided into \(R_{A1}\) and \(R_{B1}\) respectively). A similar, but separate, procedure is followed for transmitted radiation (broken arrows, Fig. 4) to allow for the situation where the reflection and transmission coefficients are unequal. Finally, the total amount of radiation travelling upward in each of the sectors \(AOB, BOC, COD\) (Fig. 4a), \(AOC, COB, BOD\) (Fig. 4b) and downward in the sectors \(AOP, FOE, EOD\) (Fig. 4a), \(AOE, EOF, FOD\) (Fig. 4b) is determined and is divided equally among the number of skyzones with mid-angles falling within each particular sector.

C. DETAILS OF PROGRAM STRUCTURE AND OPERATION

1. Input/Output

The main program and subroutines are executed once for each set of conditions specified for above-crop radiation, leaf area, leaf optical properties, and leaf angles. Three external logic loops, regulated by a control card, allow for successive calculations with several different combinations of this input data (Fig. 5). The geometric table "WILSØN" (Duncan et al. 1967), giving the ratio between the leaf shadow on a plane normal to the sun's rays and the actual leaf area, is also required as input.

For each set of specified conditions the output consists of a listing of upward and downward horizontal flux densities through
Main program and subroutines executed for current values of leaf angle, above-crop radiation, and leaf optical properties.

Proceed for NLEAF different leaf angle profiles.

Proceed for NRAD different above-crop radiation environments.

Proceed for NOPT different leaf optical properties.

If only one set of optical properties bypass calculation for short-wave radiation.

If optical switch set at 1 calculate short-wave profiles, otherwise bypass.

Add profiles for pairs of optical properties (PAR, NIR)

Write shortwave profiles computed above

Main program and subroutines: MULTIRAD and LAMBERT, LAMSCAT.

Write results for current optical properties and store them.

Fig. 5. Logic providing input/output control and calculations for short-wave radiation.
each of the layer interfaces, the radiation absorbed by each layer, and the sum of absorption over all layers. A term is printed to indicate the error involved if the downward fluxes only are used in the absorption calculation. Also listed is the ratio of the flux density of radiation upward to that travelling downward at the crop surface ("albedo"), and a count of the number of reflections and/or transmissions followed in the iterative loop.

As mentioned earlier (B2), provision is made for the summation of the profiles computed for the photosynthetically active (PAR) and near infrared (NIR) wavebands, in order to give profiles and accompanying data in the short-wave band. This option is specified on a control card (Fig. 5).

2. Details of program structure

Details of the structure of the more important program sections are provided in the annotated flowcharts (Fig. 6-10).

D. PROGRAM TESTS

The tests reported here are limited to those that were designed to ensure that the program itself was free of errors. The results of tests of the basic assumptions included in the model are presented in the companion paper (McPherson and Torssell, in press; Chapter 3).

Layer identification was checked by providing marked discontinuities of leaf area and leaf angle data, and results were compared to ensure the discontinuities occurred where expected.
Downward flux of direct sunlight at top of canopy (interface (1)).

Count of direct sunlight passing horizontal interface (1).

Sun elevation (radians). In COMMON with subroutine LAMBERT.

Select row in WILSON table appropriate to sun elevation.

Proceed layer by layer using appropriate leaf areas and angles.

Select column in WILSON table appropriate to leaf angle.

Compute penetration of direct sunlight through layer (J) from: I=Io exp (effective leaf area).

Count direct sunlight passing layer interfaces.

Flux of direct sunlight intercepted by leaves of layer (J). In COMMON with subroutine LAMBERT.

Subroutine LAMBERT computes here the quantity (with respect to direction) of first reflection and transmission of direct sunlight, assuming Lambertian scattering.

Hold direct sunlight reflected and transmitted downward by leaves of layer (J), at angles (I). PDN(I) in COMMON with subroutine LAMBERT.

Hold direct sunlight reflected and transmitted upward by leaves of layer (J), at angles (I). PUP(I) in COMMON with subroutine LAMBERT.

Hold direct sunlight reflected upward by the soil at angles (I), assuming Lambertian scattering.

Fig. 6.—Program section 2. Penetration of unintercepted sunlight through the canopy and the primary reflections and transmissions.
Count skylight passing interface (1) and accumulate.

Proceed skyzone by skyzone (M) using appropriate elevation angle.

Mid-zone angle (radians) for skyzone (M). In COMMON with subroutine LAMBERT.

Select row in WILSON table appropriate to skyzone elevation.

Downward flux of skylight at top of canopy (interface (I)) from each of 6 skyzones.

Proceed layer by layer (J) using appropriate leaf areas and angles.

Select column in WILSON table appropriate to leaf angle.

Compute penetration of skylight through layer (J) from: I=Io exp (effective leaf area).

Count skylight passing layer interfaces and accumulate.

Flux of skylight intercepted by leaves of layer (J). In COMMON with subroutine LAMBERT.

Subroutine LAMBERT computes here the quantity (with respect to direction) of first reflection and transmission of skylight, assuming Lambertian scattering.

Hold skylight reflected and transmitted downward by leaves of layer (J), at angles (I). PDN(I) in COMMON with subroutine LAMBERT.

Hold skylight reflected and transmitted upward by leaves of layer (J), at angles (I). PUP(I) in COMMON with subroutine LAMBERT.

Accumulate skylight, from all skyzones, penetrating to soil surface.

Hold skylight reflected upward by the soil at angles (I), assuming Lambertian scattering. Accumulate.

Fig. 7.- Program section 3. Penetration of unintercepted skylight through the canopy and the primary reflections and transmissions resulting.
Establish value to test whether sufficient reflections and transmissions have been accounted for.

Take radiation reflected upward from soil, at angles (1) as input to subroutine LAMSCAT. DIFS\textsuperscript{SR} (I) in COMMON.

Count above radiation passing soil interface and accumulate.

Proceed upward layer by layer using appropriate leaf areas and angles.

Adjust loop index (JJ) to layer identification index (J) which increases downwards.

Subroutine LAMSCAT calculates interception by layer (J) of previously-intercepted radiation passing upward. It allocates the separate directional components to subroutine LAMBERT for calculation of (N + 1)th reflection and/or transmission and returns results to the main program.

Hold downwards radiation from (N + 1)th reflection and/or transmission and accumulate.

Radiation passing into layer above, (J-1), is the sum of radiation from Nth reflection and/or transmission upward from layer (J), and the same from lower layers that has passed unintercepted through them and layer (J).

Count above radiation as it passes layer interface (J) and accumulate.

Hold upward radiation from (N + 1)th reflection and/or transmission.

Fig. 8(a).- Program section 4. Flow of reflected and transmitted radiation through the canopy accounting for secondary to N reflections and transmissions (continued on Fig. 8(b)).
Take radiation reflected and transmitted downward through upper surface of canopy as input to subroutine LAMSCAT. This value will always be zero.

Count above radiation passing interface (I) and accumulate.

Proceed downward layer by layer using appropriate leaf areas and angles.

Subroutine LAMSCAT calculates interception by layer (J) of previously-intercepted radiation passing downward. It allocates the separate directional components to subroutine LAMBERT for calculation of (N + 1)th reflection and/or transmission and returns results to the main program.

Hold upward radiation from (N + 1)th reflection and/or transmission and accumulate.

Radiation passing into layer below, (J + 1), is the sum of radiation from Nth reflection and/or transmission downward from layer (J), and the same from upper layers that has passed unintercepted through them and layer (J).

Count above radiation as it passes layer interface (J + 1) and accumulate.

Hold downward radiation from (N + 1)th reflection and/or transmission.

Hold radiation from (N + 1)th reflection and/or transmission that is incident on soil and reflected upward by it at angles (I), assuming Lambertian scattering.

Test significance of each directional value of radiation travelling upward or downward from (N + 1)th reflection and/or transmission. Continue to (N + 2)th reflection and/or transmission if significant.

Fig. 8(b).- Continuation of Fig. 8(a).
SELECT COLUMN IN WILSON TABLE APPROPRIATE TO LEAF ANGLE FOR LAYER (J). (J) IN COMMON WITH PROGRAM MULTIRAD.

PROCEED ANGLE BY ANGLE, EACH BEING EQUIVALENT AND NUMERICALLY EQUAL TO THE ELEVATION OF THE SKYZONES.

APPROPRIATE RADIATION ELEVATION (RADIANS). IN COMMON WITH SUBROUTINE LAMBERT.

SELECT ROW IN WILSON TABLE APPROPRIATE TO CURRENT RADIATION ELEVATION.

RADIATION INCIDENT ON LAYER (J) APPROPRIATE TO CURRENT RADIATION ELEVATION.

COMPUTE PENETRATION OF RADIATION THROUGH LAYER (J) FROM:

I = 10 exp (EFFECTIVE LEAF AREA).

FLUX OF RADIATION INTERCEPTED BY LEAVES OF LAYER (J). IN COMMON WITH SUBROUTINE LAMBERT.

SUBROUTINE LAMBERT COMPUTES HERE THE QUANTITY (WITH RESPECT TO DIRECTION) OF THE REFLECTION AND TRANSMISSION OF RADIATION CURRENTLY BEING DEALT WITH. ASSUME LAMBERTIAN SCATTERING.

ACCUMULATE FOR EACH ANGLE, THE RADIATION REFLECTED AND TRANSMITTED UPWARD.

ACCUMULATE FOR EACH ANGLE, THE RADIATION REFLECTED AND TRANSMITTED DOWNWARD.

STORE RADIATION PENETRATING THROUGH LAYER (J) WITH RESPECT TO ITS ANGLE OF PROPAGATION (MMM).

**Fig. 9.- Subroutine LAMSCAT.** Determination of the quantity of radiation reintercepted by each layer and allocation of this radiation to subroutine LAMBERT.
Proceed for six leaf azimuth positions representative of the full 360°.

Determine from radiation elevation and leaf angle, whether the normal to the leaf surface illuminated is above or below the horizontal (for current leaf azimuth).

Leaf area projected in direction of radiation propagation for current leaf azimuth.

Accumulate projected areas for leaves that have their normals above the horizontal.

Ratio of projected areas with upward-facing normals to total projected area.

Compliment of above.

Fraction of hemisphere surface, hemisphere base at leaf angle, that falls below horizontal.

Compliment of above i.e. the fraction of radiation reflected from a leaf, with normal above (or below) horizontal, that actually travels upward (or downwards).

Area of hemisphere surface subtending angles greater than leaf angle.

Fraction of hemisphere surface, SURFWITH, that subtends angles greater than leaf angle.

Radiation reflected upward and downward with the direction of propagation related to the horizontal and to leaf angle. Assumes Lambertian scattering. See text and Fig. 4 for explanation.

Fig. 10(a).- Subroutine LAMBERT. Partitioning of intercepted radiation with respect to the direction and quantity of the radiation leaving the leaf (continued on Fig. 10(b)).
Radiation transmitted upward and downward with the direction of propagation related to the horizontal and to leaf angle. Assumes Lambertian scattering. See text and Fig. 4 for explanation.

Fig. 10(b).- Continuation of Fig. 10(a).
Overall program operation was checked by ensuring that there was conservation of energy under a wide range of conditions. "Albedo", being the ratio of ingoing to outgoing radiation at the canopy surface, was used as the indicator of conservation where absorption by leaves and soil was set to zero. Under these conditions, when radiation leaving the crop must be the same as that entering, the "albedo" should be unity. Results of such calculations of "albedo" at zero leaf and soil absorption is given in Table 1, showing that approach to unity was very good for a range of sun elevation and leaf angle. A combination of various reflection and transmission coefficients gave similar results (Table 2). Where absorption is zero (reflection + transmission coefficient = 1.0 along the matrix diagonal), values of unity indicate zero computational error. In the case where radiation is absorbed by the crop and soil (reflection + transmission coefficient <1.0), the albedo is less than unity but conservation of energy is confirmed by accounting for these absorbed quantities. The value thus obtained should also equal unity and is given in brackets in Table 2.

REFERENCES


"ALBEDO" FOR VARIOUS LEAF ANGLES AND SUN ELEVATIONS SHOWING CONSERVATION OF ENERGY

<table>
<thead>
<tr>
<th>Leaf Angle</th>
<th>Sun Elevation</th>
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<tr>
<td>1°</td>
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<td>22°</td>
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</tr>
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<tr>
<td>89°</td>
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Conditions for the calculations: Leaf and soil absorption zero, skylight = 50% of total radiation.
<table>
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<th>Leaf Reflection Coefficient 0.00</th>
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<td>1.00</td>
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</tr>
</tbody>
</table>

Conditions for the calculations: Soil reflection coefficient = Leaf transmission + leaf reflection coefficients, leaf angle = 22°, sun elevation = 45°, skylight = 50% of total radiation.
PHOTOCELL-FILTER COMBINATIONS FOR MEASURING PHOTOSYNTHETICALLY ACTIVE RADIATION

SUMMARY

Unacceptably large errors can occur when unfiltered sensors, commonly in use for physiological studies, are used to estimate the amount of radiant energy available for photosynthesis.

To overcome this difficulty several photocell-filter combinations have been selected by a theoretical analysis to give a spectral response suitable for measuring the flux density of photosynthetically active radiation (PAR) under a range of natural and artificial light sources. The "ideal response" (equal response to photons in the 400-700 nanometre (nm) waveband) has been closely approximated using silicon photodetectors. This enables the low-cost construction of PAR sensors which have the advantages of reliability, linear response, low temperature coefficient, rapid response, and a wide range of possible physical and electrical configurations.

A. INTRODUCTION

Our understanding of plant growth in relation to its environment is hindered by an inability to describe the light environment adequately. This inability is due, in part, to a lack of suitable light measuring devices. The disadvantages of many instruments currently in use include bulk, slow response, high temperature sensitivity, low output level, fragility, and high price. Most important, however, is their unsatisfactory spectral response leading to large errors in the measurement of photosynthetically
active radiation (PAR). This problem has been discussed by several authors and a range of spectrally adjusted sensors suggested. Federer and Tanner (1966b) indicated a combination using a selenium photocell and gelatin filter. More stable glass filters were used by Gaastra (1968) whose most satisfactory spectral correction was using selenium photocells and also thermopile solarimeters. In the latter case it was necessary to filter differentially two sensors to achieve a net output with the required spectral response. Norman et al. (1969) made use of the silicon photocell which has the same advantages as the selenium photocell but is less prone to fatigue. However, their instrument has the disadvantages of using gelatin filters and requiring the differential filtering of two photocells.

This paper reports the results of a theoretical examination of the suitability of a wide range of photocell-filter combinations for measuring PAR. The aim in this selection of cell-filter combinations is to permit the use of more stable components (both sensors and filters) in simpler configurations than those in combinations previously reported, and to give improved spectral response.

1. Spectral response

It is important first to determine which property of radiation controls its photosynthetic activity. According to the Einstein law of photochemical equivalence, there is a simple integral relationship between the number of molecules changed photochemically and the number of photons absorbed (Rabinowitch, 1951). This applies regardless of the energy of the photon,
provided that it falls within the requisite waveband. Any excess energy is dissipated as heat. PAR should therefore be measured in terms of photon, and not energy, flux density.

The radiant energy used by plants in photosynthesis comes from a small section of the electromagnetic spectrum, the visible waveband. To determine the amount of energy available for plant growth we must measure only this photosynthetically active radiation. The most direct and satisfactory method of achieving this is to use sensors which have a spectral response similar to that of photosynthesis (the action spectrum). Alternatively, if the spectral response of the sensor and the spectral output of the source is known, the quantity of PAR can be calculated. The spectral output of the source is seldom known with sufficient accuracy, however.

Little information is available on the action spectrum of the photosynthetic system in intact leaves. Rabinowitch (1951) reported some early work but interpretation of these results is uncertain because of the varying spectral absorption of the tissue. The quantum yield of carbon dioxide uptake determined by Björkman (1968) for three species indicates an essentially equal photosynthetic response to photons from the lower limit of the measurements (450 nm) to approximately 700 nm. Response in the 700 nm region is complicated, however, by the Emerson enhancement effect. In the absence of reliable data representative of a wide range of species it is assumed here firstly, that photosynthetic activity is restricted to the 400-700 nm waveband, and secondly, that all photons within this waveband contribute equally to photosynthesis. The first aspect is the most important in the measurement of PAR as the balance of
radiation at wavelengths greater and less than 700 nm varies widely among light sources. The primary aim of this survey is then, to select cell-filter combinations with a minimum of sensitivity at wavelengths greater than 700 nm (emittance of wavelengths below 400 nm is negligible for most light sources used in physiological studies and would in any case be substantially filtered if a protective glass cover is used). The second aspect, the assumption of equal photosynthetic response to photons within the 400-700 nm waveband, is of less importance. Fig. 1 gives the "ideal" photon response and the corresponding energy response which follows from photon energy being inversely proportional to wavelength.

The basic unit of the Einstein (E) suggested by Brooks (1964), and Federer and Tanner (1966b) conveniently reduces the large numbers that would result if photon numbers were used. One Einstein is defined as Avogadro's number of photons (6.023 \times 10^{23}). The flux density of full sunlight in the 400-700 nm waveband (taken as 45 mw/cm²) is equivalent to approximately 200 \times 10^{-9} \text{ E/cm}^2\text{sec}.

Calibration of the photon sensor must be carried out under a source of known spectral composition and of known emittance in terms of photon flux units (E/cm² sec). Sunlight on a clear day provides a convenient calibration source. Published curves of its spectral composition (Gates, 1962; Moon, 1963) give sufficient accuracy for most purposes. A thermopile solarimeter is satisfactory for measuring the incident radiation flux density in energy terms. Assuming this standard instrument responds equally to energy at all wavelengths within its range the photon sensor can be calibrated as follows.
Fig. 1. Spectral sensitivity of ideal photon response sensor in terms of (———) photon numbers, and (---) energy.
The energy flux density within the 400-700 nm waveband, $\phi_v$, for a given flux density, $\phi$, within the standard instrument's sensitivity waveband (say 400-3000 nm) is given by:

$$\phi_v = \phi \frac{\int_{400}^{700} \phi_\lambda \, d\lambda}{\int_{400}^{3000} \phi_\lambda \, d\lambda} \text{ (Joule/m}^2 \text{ sec)}$$

where $\phi_\lambda$ = the monochromatic energy flux density.

The visible flux expressed in photon flux units, $\phi'_v$, is given by:

$$\phi'_v = \frac{\int_{400}^{700} \phi_\lambda \, d\lambda}{h \cdot c \cdot 6.023 \cdot 10^{23}} \text{ (Einstein/m}^2 \text{ sec)}$$

where: $\lambda$ = wavelength (m); $h$ = Planck's constant ($6.626 \cdot 10^{-34}$ Joule sec); $c$ = velocity of propagation of light ($2.998 \cdot 10^8$ m/sec); $6.023 \cdot 10^{23}$ = Avogadro's number.

2. Departure from photon response

If the spectral response of a sensor deviates from the required photon response it will only give a true reading from a source with the spectral characteristics of the one it was calibrated under. The deviation of such a sensor under any given light source
can be calculated using a procedure outlined by Federer and Tanner (1966b). Two ratios are required. First, the ratio of the sensor output in the light being measured, \( O \), to its output in the calibration source, \( O_c \), given by:

\[
\frac{O}{O_c} = \frac{\int S \lambda L \lambda d\lambda}{\int S_c \lambda L_c \lambda d\lambda} \tag{3}
\]

where \( S \) is the relative response of the sensor, and \( L \) is the relative emittance of the light source, over all wavelengths under consideration. Subscript or superscript \( c \) denotes the calibration source.

Secondly, a similar ratio for the output of an ideal photon response sensor (indicated by superscript ') under the given light source, \( O' \), to its output in the same calibration source, \( O_c' \), is given by:

\[
\frac{O'}{O'_c} = \frac{\int S' \lambda L' \lambda d\lambda}{\int S_c' \lambda L_c' \lambda d\lambda} \tag{4}
\]

Combining eq. 3 and 4 we obtain the photon response ratio \( R \):

\[
R = \frac{O/O_c}{O'/O'_c} = \frac{\int S \lambda L \lambda d\lambda}{\int S_c \lambda L_c \lambda d\lambda} \cdot \frac{\int S' \lambda L' \lambda d\lambda}{\int S_c' \lambda L_c' \lambda d\lambda} \tag{5}
\]

Departure of this ratio from unity indicates the departure of the sensor from ideal photon response under the given light source. The value of \( R \) is independent of absolute light levels and absolute sensor response.
The photon response ratio is derived from several spectral curves. It is not always possible to define these curves precisely due to: variation in spectral emissivity of light sources and limitations in its measurement; variation in spectral response among individual photocells, and in spectral transmission of filters; or uncertainties regarding the exact ideal photon response. Errors in any one of these curves, or in their integration, can lead to significant errors in $R$. Although these errors would normally not exceed a few percent the ratios should not be applied too rigorously, but used as a means to minimise spectral errors in the measurement of PAR.

B. RESULTS AND DISCUSSION

The departure from ideal photon response was calculated for sensor-filter combinations involving all possible combinations of 10 solid-state photodevices with 64 filters. The filters were used singly and in pairs with two thicknesses (that required to obtain the manufacturer's transmission curve and double the thickness). The suitability of the spectral response of each combination was examined by calculating a photon response ratio for each of sixteen different light sources typical of the range encountered in plant physiological studies. Spectral curves were characterised using points every 25 nm from 375 nm - 1000 nm wavelength. The computer program integrated the curves using Simpson's approximation. Sunlight on a clear day (Gates, 1965) is taken as the calibration source. The sources of data used to define the spectral properties of photocells, filters, and light sources are quoted in Tables I and II. The combinations showing least deviation from ideal photon response
### TABLE I

**PHOTON RESPONSE RATIOS (R) OF SELECTED PHOTOCELL–FILTER COMBINATIONS UNDER VARIOUS LIGHT SOURCES**

<table>
<thead>
<tr>
<th>Photocells</th>
<th>Filters¹</th>
<th>Light Sources²</th>
<th>XBF</th>
<th>XBO</th>
<th>W¹</th>
<th>E²</th>
<th>corn</th>
<th>pine</th>
<th>oak</th>
<th>maple</th>
<th>blue</th>
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</thead>
<tbody>
<tr>
<td>Silicon photodiode SD-100</td>
<td>466/1446 + 466/1439</td>
<td>0.76</td>
<td>1.00</td>
<td>1.01</td>
<td>0.99</td>
<td>0.99</td>
<td>1.00</td>
<td>1.07</td>
<td>1.07</td>
<td>1.04</td>
<td>1.01</td>
</tr>
<tr>
<td>(EG and G, Boston, U.S.A.)</td>
<td>W85 + BG38*</td>
<td>0.32</td>
<td>1.03</td>
<td>1.03</td>
<td>0.94</td>
<td>0.95</td>
<td>1.00</td>
<td>1.26</td>
<td>1.29</td>
<td>1.02</td>
<td>1.04</td>
</tr>
<tr>
<td>Silicon photovoltaic cell</td>
<td>BG38* + GG19*</td>
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<td>1.03</td>
<td>1.02</td>
<td>0.95</td>
<td>0.96</td>
<td>1.02</td>
<td>1.26</td>
<td>1.29</td>
<td>1.02</td>
<td>1.05</td>
</tr>
<tr>
<td>(Int. Rect. Corp., U.S.A.)</td>
<td>BG38* + W81B*</td>
<td>0.35</td>
<td>1.03</td>
<td>1.03</td>
<td>0.95</td>
<td>0.96</td>
<td>1.01</td>
<td>1.23</td>
<td>1.26</td>
<td>1.04</td>
<td>1.05</td>
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<td>Limits of expected cell</td>
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<td>0.93</td>
<td>0.96</td>
<td>1.01</td>
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<td>1.27</td>
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<td>1.02</td>
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<tr>
<td>to cell peak spectral response</td>
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<td>1.02</td>
<td>1.02</td>
<td>0.96</td>
<td>0.96</td>
<td>1.02</td>
<td>1.25</td>
<td>1.29</td>
<td>1.02</td>
<td>1.05</td>
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<tr>
<td>variation</td>
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<td>high</td>
<td>BG38* + W81B*</td>
<td>0.35</td>
<td>1.00</td>
<td>1.00</td>
<td>0.97</td>
<td>0.97</td>
<td>1.02</td>
<td>1.20</td>
<td>1.26</td>
<td>1.01</td>
<td>1.03</td>
</tr>
<tr>
<td>Selenium photovoltaic cell</td>
<td>UG3 + GG4*</td>
<td>0.25</td>
<td>1.00</td>
<td>1.01</td>
<td>0.95</td>
<td>0.96</td>
<td>0.99</td>
<td>1.18</td>
<td>1.20</td>
<td>1.05</td>
<td>1.01</td>
</tr>
<tr>
<td>(Int. Rect. Corp., U.S.A.)</td>
<td>W81EF + W81EF</td>
<td>0.40</td>
<td>1.02</td>
<td>1.02</td>
<td>0.96</td>
<td>0.96</td>
<td>1.01</td>
<td>1.20</td>
<td>1.25</td>
<td>1.05</td>
<td>1.04</td>
</tr>
<tr>
<td>Silicon photodiode LS-222</td>
<td>BG10* + BG10*</td>
<td>0.31</td>
<td>1.02</td>
<td>1.02</td>
<td>0.96</td>
<td>0.97</td>
<td>1.03</td>
<td>1.25</td>
<td>1.28</td>
<td>1.05</td>
<td>1.07</td>
</tr>
<tr>
<td>(Texas Inst., U.S.A.)</td>
<td>W86B + KG3*</td>
<td>0.41</td>
<td>0.98</td>
<td>0.99</td>
<td>0.99</td>
<td>0.99</td>
<td>1.01</td>
<td>1.11</td>
<td>1.16</td>
<td>1.09</td>
<td>1.03</td>
</tr>
<tr>
<td>Silicon Blue photovoltaic cell</td>
<td>(Hayakawa, Japan)</td>
<td>W86B + KG3*</td>
<td>0.41</td>
<td>0.98</td>
<td>0.99</td>
<td>0.99</td>
<td>0.99</td>
<td>1.01</td>
<td>1.11</td>
<td>1.16</td>
<td>1.09</td>
</tr>
</tbody>
</table>

¹ Filters: Balzers, Liechtenstein, interference, (numeric notation); Wratten, Eastman Kodak, New York, gelatin absorption, ("W" prefix); Schott and Gen., Mainz, glass absorption, (remainder with alphanumeric notation).
² For explanation of symbols describing light sources see Table II.
³ Average filter transmission in 400–700 nm waveband.
* Double filter thickness used.
TABLE II

PHOTON RESPONSE RATIOS (R) OF PHOTODETECTORS COMMONLY USED IN PLANT PHYSIOLOGICAL STUDIES

<table>
<thead>
<tr>
<th>Light source</th>
<th>Detectors</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
</tr>
</thead>
<tbody>
<tr>
<td>Xenon arc lamps (Osram, Germany)</td>
<td>XBF6000</td>
<td>0.96</td>
<td>0.98</td>
<td>1.22</td>
<td>1.05</td>
<td>1.08</td>
</tr>
<tr>
<td></td>
<td>XBO900</td>
<td>1.03</td>
<td>1.01</td>
<td>1.16</td>
<td>1.09</td>
<td>1.06</td>
</tr>
<tr>
<td>Tungsten lamps of different colour temperature (HOLLAENDER, 1956)</td>
<td>W2854 °K</td>
<td>1.36</td>
<td>1.17</td>
<td>0.88</td>
<td>1.28</td>
<td>0.96</td>
</tr>
<tr>
<td></td>
<td>W3025 °K</td>
<td>1.29</td>
<td>1.14</td>
<td>0.89</td>
<td>1.23</td>
<td>0.97</td>
</tr>
<tr>
<td></td>
<td>W3475 °K</td>
<td>1.00</td>
<td>1.00</td>
<td>0.99</td>
<td>0.98</td>
<td>0.99</td>
</tr>
<tr>
<td>Fluorescent lamps (HOLLAENDER, 1956)</td>
<td>F “daylight”</td>
<td>0.33</td>
<td>0.71</td>
<td>1.41</td>
<td>0.51</td>
<td>1.10</td>
</tr>
<tr>
<td></td>
<td>F “cool white”</td>
<td>0.36</td>
<td>0.72</td>
<td>1.33</td>
<td>0.49</td>
<td>1.06</td>
</tr>
<tr>
<td></td>
<td>F “warm white”</td>
<td>0.39</td>
<td>0.74</td>
<td>1.26</td>
<td>0.47</td>
<td>1.01</td>
</tr>
<tr>
<td>Radiation transmitted through corn crop on clear (c) and overcast (o) day</td>
<td>corn (c)</td>
<td>3.24</td>
<td>2.30</td>
<td>1.20</td>
<td>2.96</td>
<td>1.07</td>
</tr>
<tr>
<td>(YOCUM et al., 1964)</td>
<td>corn (o)</td>
<td>1.50</td>
<td>1.33</td>
<td>1.15</td>
<td>1.43</td>
<td>1.04</td>
</tr>
<tr>
<td>Radiation transmitted through various canopies under clear (C), dark cloud</td>
<td>pine (C)</td>
<td>1.38</td>
<td>1.27</td>
<td>1.28</td>
<td>1.42</td>
<td>1.11</td>
</tr>
<tr>
<td>(DC), white cloud (WC), and overcast (O) sky conditions</td>
<td>pine (DC)</td>
<td>1.11</td>
<td>1.11</td>
<td>1.20</td>
<td>1.14</td>
<td>1.07</td>
</tr>
<tr>
<td>(FEDERER and TANNER, 1966a)</td>
<td>oak (C)</td>
<td>2.54</td>
<td>1.92</td>
<td>1.16</td>
<td>2.35</td>
<td>1.06</td>
</tr>
<tr>
<td></td>
<td>oak (WC)</td>
<td>1.55</td>
<td>1.36</td>
<td>1.17</td>
<td>1.50</td>
<td>1.05</td>
</tr>
<tr>
<td></td>
<td>maple (C)</td>
<td>3.56</td>
<td>2.48</td>
<td>0.91</td>
<td>3.14</td>
<td>0.98</td>
</tr>
<tr>
<td></td>
<td>maple (O)</td>
<td>2.20</td>
<td>1.74</td>
<td>1.15</td>
<td>2.04</td>
<td>1.05</td>
</tr>
<tr>
<td>(FEDERER and TANNER, 1966a)</td>
<td>blue sky</td>
<td>0.39</td>
<td>0.70</td>
<td>1.43</td>
<td>0.63</td>
<td>1.17</td>
</tr>
</tbody>
</table>

2 = silicon blue photovoltaic cell (Hayakawa Electric Co., Japan).
4 = solarimeter (instrument sensitivity extends beyond the 1,000 nm computational limit, therefore errors will be greater than those indicated).
5 = solarimeter filtered to measure 400–700 nm waveband only.
are presented in Table I. Their respective spectral response characteristics are shown in Fig. 2.

The Balzers filters provide the most satisfactory spectral response in combination with a number of cells. Results using the silicon photovoltaic cell (I.R.C.), and silicon photodiode (SD-100) are presented here. Unfortunately these filters are of the interference type, and correct transmission or reflection is achieved only when collimated light is incident at the prescribed angle. A simple optical system could be constructed to meet this requirement but would increase the dimensions and cost of the unit considerably.

More flexible and less expensive alternatives are provided by absorption filters. These give a less desirable spectral correction but perform satisfactorily under scattered light.

Perhaps the most satisfactory combination for physiological studies is that using the silicon photovoltaic cell and absorption filters. A wide range of silicon photovoltaic cells is available commercially at relatively low cost. They have the advantage of good stability, low temperature response, rugged construction, high output level, rapid response, and a range of possible physical and electrical configurations. The smallest cells are suitable for leaf-chamber and whole plant growth-chamber measurements. In addition banks of cells can be built up to give, for example, a linear probe suitable for spatial integration within crops. The departure from ideal photon response is greater than when interference filters are used, but the advantages of simple construction and small size would in general outweigh the disadvantage of slightly increased spectral error.
Fig. 2. Spectral sensitivity at photocell-filter combinations (curves normalised at 550 nm wavelength). A. Silicon photodiode SD-100 and filters (---) 466/1446 + 466/1439, and (---) W85 + BG38*. B. Silicon photovoltaic cell (I.R.C.) and filters (---) BG38* + GG19*, (---) BG38* + W81B*, and (····) BG38 + 466/1446. C. Selenium photovoltaic cell (I.R.C.) and filters (---) UG3 and GG4*, and (---) W81EF*. D. Silicon photovoltaic cell LS-222 and filters (---) BG10* + BG10* and Silicon Blue photovoltaic cell and filters (---) W86B + KG3*. (Symbols used to describe filters are explained in Table I).
The selenium photovoltaic cells have many advantages in common with the silicon cells. In addition they are not sensitive in the infrared which simplifies the filter requirements, and they are available in a wide range of shapes. However, selenium cells suffer from fatigue, particularly at high light intensities. Fatigue is usually temporary and output steadies after about 10 min, but this change in calibration can be as high as 12% even under a moderate light intensity of 100 footcandles (International Rectifier Corporation, 1960).

The spectral response of solid-state photodevices varies from cell to cell. To give an indication of the effect this variation could have, photon response values are given in Table I for the upper and lower limits of the typical range of spectral response given by I.R.C. for silicon photovoltaic cells. These difficulties could be overcome by selecting cells with the required response. SD-100 cells are available with spectral calibration at an extra cost.

In some cases alternative filter combinations are given (Table I). The Wratten gelatin-based filters are desirably thin, flexible, and can be cut easily. They are in general less stable than glass filters, however. The filter combination selected would depend on the nature of the application. The use of filters reduces the effective sensitivity of the photocell. However, those under consideration all have a sufficiently large signal to make this reduction tolerable. The average coefficient of transmission in the 400-700 nm waveband is given for each filter combination in Table I.
Although the best photodetector combinations still deviate from the ideal photon response the errors are zero in full sunlight (by definition), and small under the artificial sources (other than fluorescent). The highest errors occur in the light penetrating plant canopies but these represent extremes. The measurement errors will be least near the top of the crop where the spectral quality is nearer that of sunlight. The majority of the light absorbed by the crop is of this nature.

The uncritical use of sensors with inappropriate spectral response can lead to large errors in the measurement of PAR. The photon response ratios for range of widely used radiation instruments under natural and artificial light sources are given in Table II, and can be seen to deviate considerably from unity. Although the direct filtering of thermopile solarimeters has not been successfully achieved, it is possible to allow for the infrared sensitivity with a difference technique that uses a filter absorbing wavelengths below 700 nm and with a sharp cutoff at that wavelength (RG8, or its replacement RG715, Schott and Gen., Mainz.). The difference between readings with and without the filter gives a measure of the energy within the 400-700 nm waveband. Results indicate that spectral errors using this technique are acceptable (Table I) but for most purposes the directly filtered photocells, discussed earlier, will be more convenient and reliable.

REFERENCES


