

A Theoretical Analysis of Nitrogen and Radiation Effects on Radiation Use Efficiency in Peanut

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Abstract

Radiation use efficiency (RUE) of well-watered crops, measured as grams of biomass accumulated for each megajoule of intercepted total solar radiation, is affected by the level of leaf nitrogen in the canopy and has been related to the canopy specific leaf nitrogen (SLN; g N m⁻² leaf area). A number of field experiments on peanut have measured RUE values greater than current theories predict on the basis of their canopy SLN levels. It is possible that these discrepancies between measured and theoretical values may be caused by non-uniform distribution of SLN in the canopy, incident radiation level, and/or the influence of diffuse radiation. In this study, we developed a theoretical framework to predict the consequences of these factors on RUE in peanut and used it to explain the causes of discrepancies between theory and practice.

The framework is structured to determine photosynthesis of a layered crop canopy by distributing incident radiation among sunlit and shaded leaves in each layer. It allows for variation in incident direct and diffuse radiation associated with location (latitude), time of year, time of day, and atmospheric condition, which is expressed as the degree of transmission of extra-terrestrial radiation. It also allows for variation in photosynthetic capacity associated with average SLN of the canopy and its distribution in the canopy. Daily canopy photosynthesis, intercepted radiation, and RUE are obtained by numerical integration of instantaneous values calculated at specific times of the day.

The framework predicted experimentally determined RUE values accurately and quantified the contribution of each major factor to variation in RUE. On clear days, with high canopy SLN, RUE was predicted to be 1.1 g MJ⁻¹. The major cause of previous underestimation of RUE was found to be variation in RUE associated with the level of incident radiation flux density as affected by the degree of atmospheric transmission. RUE increased by up to 0.4 g MJ⁻¹ as atmospheric transmission decreased from 0.75 (clear sky) to 0.35 (heavy cloud). However, varying incident radiation by changing time of year or latitude did not affect RUE. Partitioning incident radiation into direct and diffuse components and consideration of canopy gradients in SLN both had significant effects on RUE, but of a lesser magnitude than effects of degree of atmospheric transmission. The former caused increases in RUE of up to 0.15 g MJ⁻¹, while the latter caused increases of up to 0.13 g MJ⁻¹ at low canopy SLN. Hence, by quantifying the understanding of plant physiological processes and integrating appropriately to the canopy scale, this theoretical framework has explained the causes of discrepancies between measured RUE and previous theoretical estimates.

Keywords: radiation use efficiency, model, specific leaf nitrogen, nitrogen gradients, diffuse radiation, peanut.

Introduction

Crop radiation use efficiency (RUE, g MJ⁻¹) is the amount of biomass accumulated for each unit of total solar radiation intercepted by the leaf canopy. It is frequently used in calculating accumulation of crop biomass. In peanut

(*Arachis hypogaea* L.), as in other species, RUE varies with nitrogen status of leaves (Sinclair *et al.* 1993); Wright *et al.* 1993). Sinclair *et al.* (1993) derived the theoretical response of RUE to specific leaf nitrogen (SLN, g N m⁻² leaf area) in peanut by quantifying the curvilinear response of leaf carbon dioxide exchange rate to SLN and substituting this response into the general framework for calculating crop RUE set out by Sinclair and Horie (1989). They showed that RUE increased curvilinearly with SLN so that at high SLN, RUE was high, but increased little in response to further increase in SLN. At low SLN, RUE was low, but was predicted to increase rapidly with increase in SLN.

Field observations of RUE and SLN in peanut have not been totally consistent with the theoretical response derived by Sinclair *et al.* (1993). RUE has responded to SLN in the manner predicted, but RUE values have been greater than expected. Wright and Hammer (1994) measured a RUE value 32% greater than expected from the theory at the SLN measured in their field experiment in north-east Australia. Similarly, Sinclair *et al.* (1993) reported a RUE value 27% greater than expected in the field experiment of Bennett *et al.* (1993) in south-east U.S.A. In other field experiments, values of RUE found by Wright *et al.* (1993), were also greater than expected.

Wright and Hammer (1994) have suggested that discrepancies between measured and theoretical RUE values may be caused by non-uniform distribution of SLN in the canopy, incident radiation level, and/or the proportion of diffuse radiation. Theoretical calculations to date have assumed a uniform distribution of SLN in the leaf canopy. Studies in other species (Hirose and Werger 1987; Pons *et al.* 1990) have found gradients in leaf nitrogen in canopies, with low concentrations at the bottom and high concentrations at the top. In both studies, the nitrogen gradient was calculated to enhance canopy photosynthesis by at least 20% over that calculated for an equivalent total canopy nitrogen distributed uniformly throughout the canopy. Sinclair *et al.* (1993) suggested that this factor alone might explain the difference between actual and theoretical RUE in their data for peanut. Wright and Hammer (1994) measured the canopy profile of SLN in their field experiment on peanut and found a marked decline in SLN from the top to the base of the canopy.

Radiation level and the proportion of diffuse radiation have been hypothesized to affect RUE (Murata 1981; Sinclair *et al.* 1992). Murata (1981) presented theoretical relationships that showed a decrease in RUE as solar radiation increased. This was supported by data collated for rice, soybean, and sugar beet, which showed a rate of decline in RUE of 2–4% for each megajoule increase in total solar radiation. Sinclair *et al.* (1992) used a theoretical derivation to show that RUE increased as the fraction of diffuse radiation increased and the total radiation decreased. This finding was consistent with the high RUE measured in glasshouse experiments.

Water limitation (Chapman 1989) and cool night temperature (Bell *et al.* 1992) also affect RUE in peanut, but we will not consider these factors in this study. Neither of these factors was responsible for the discrepancies between measured and theoretical RUE values in the field experiments of Wright and Hammer (1994), Wright *et al.* (1993), and Sinclair *et al.* (1993) mentioned earlier. All of those experiments were conducted with water and night temperature non-limiting.

There has not been an adequate integration of existing theories on factors affecting RUE to explain the discrepancies between measured and theoretical RUE values. Existing frameworks deal with single factors. Sinclair and Horie (1989) and Sinclair *et al.* (1993) deal with the effect of average canopy SLN. Sinclair *et al.* (1992) deal with the effect of proportion of diffuse radiation. Hirose and Werger (1987) and Pons *et al.* (1990) deal with the effect of nitrogen gradients in the canopy. Each of these frameworks takes differing approaches, making an assessment of relative effects of the various factors difficult. An integrated theory on RUE is required so that causal factors can be isolated in a manner that shows their relative importance.

Our objectives in this study were:

- (i) to develop a theoretical framework to predict the effects on RUE of average canopy SLN, SLN distribution in the canopy, radiation level, and the proportion of diffuse radiation; and
- (ii) to use the theoretical framework to compare the relative influence of nitrogen and radiation factors on RUE in peanut, and hence, to attempt to explain the causes of discrepancies between measured RUE values and values predicted from current theories.

Theoretical Framework to Predict Radiation Use Efficiency

This theoretical framework extends the approach presented by Sinclair and Horie (1989) to allow general consideration of nitrogen gradients in the leaf canopy, the level of incident radiation, and the proportion of incident radiation that is diffuse.

Crop radiation use efficiency (RUE, g MJ⁻¹) on any day is calculated as the ratio of crop biomass accumulated that day (BIO, g m⁻² day⁻¹) to total solar radiation intercepted by the canopy that day (RAD, MJ m⁻² day⁻¹) [equation (1)]. The same calculation can be applied to intervals longer or shorter than 1 day.

$$\text{RUE} = \text{BIO}/\text{RAD}. \quad (1)$$

Crop biomass increment (BIO) is determined from canopy CO₂ assimilation rate (C , mg CO₂ m⁻² day⁻¹) and the conversion ratio [B , mg biomass (mg CO₂)⁻¹] [equation (2)]. The conversion ratio (B) combines factors allowing for biochemical conversion and maintenance respiration. A value of 0.34 was used for B following the reasoning of Sinclair and Horie (1989), who used this approach for soybean.

$$\text{BIO} = C * B/1000. \quad (2)$$

Canopy assimilation rate (C) is calculated by accumulating the instantaneous assimilation rates of sunlit leaves (C_{sun} , mg CO₂ m⁻² s⁻¹) and shade leaves (C_{sh} , mg CO₂ m⁻² s⁻¹) over five canopy layers and integrating the instantaneous rates over the daylight period [equations (3) and (4)]. A layered canopy was introduced to take account of potential effects on C , and hence on RUE, of the vertical distribution of SLN in the canopy. The daily integration was achieved using the three-point Gaussian method (Goudriaan 1986) [equation (4)]. Using

this method, C is calculated at three specific times in the day ($t = 1, 2, 3$), and a weighted average of those three values enables very accurate approximation of the daily integral. If the time of day (TIME) is taken as a fraction of the daylength (DL, hours), then solar noon will occur at a TIME of 0.5. We assume that the daily time course of incident radiation, and thus C , is symmetrical about solar noon. Hence, we apply the three-point Gaussian integration to half the day, which fixes the TIME values for the three calculations as 0.06, 0.25, and 0.44.

$$C(t) = \sum_{l=1}^5 \{C_{\text{sun}}(l, t) + C_{\text{sh}}(l, t)\}, \quad t = 1, 2, 3 \quad (3)$$

$$C = 3600 * DL * \{C(1) + 1.6 * C(2) + C(3)\} / 3.6. \quad (4)$$

The instantaneous assimilation rates, C_{sun} and C_{sh} , are calculated from the product of leaf area index of sunlit or shade leaves (LAI_{sun} or LAI_{sh} , m^2 leaf m^{-2} ground) and the assimilation rate per unit leaf area, which is given by an asymptotic exponential equation of radiation flux density (Boote and Jones 1987; Boote 1991) incident on either sunlit leaves or shade leaves (I_{sun} or I_{sh} , $\text{MJ m}^{-2} \text{s}^{-1}$) (Sinclair and Horie 1989) [equations (5) and (6)]. The assimilation rates per unit leaf area asymptote to the leaf potential for CO_2 assimilation rate per unit leaf area (C_{max} , $\text{mg CO}_2 \text{ m}^{-2} \text{s}^{-1}$), which was determined as 1.8 for peanut (Sinclair *et al.* 1993). The light use efficiency at low light (E , $\text{g CO}_2 \text{ MJ}^{-1}$) was set at 5.0 (Ehleringer and Björkman 1977). The values of C_{sun} and C_{sh} are calculated for each of the five canopy layers (l) at each of the three times of day (t) required for the Gaussian integration in equation (4).

$$C_{\text{sun}}(l, t) = \text{LAI}_{\text{sun}}(l, t) * C_{\text{max}}(l) * \{1.0 - \exp[-1000 * E * I_{\text{sun}}(l, t) / C_{\text{max}}(l)]\}, \quad (5)$$

$$C_{\text{sh}}(l, t) = \text{LAI}_{\text{sh}}(l, t) * C_{\text{max}}(l) * \{1.0 - \exp[-1000 * E * I_{\text{sh}}(l, t) / C_{\text{max}}(l)]\}. \quad (6)$$

The potential assimilation rate per unit leaf area (C_{max}) is a function of specific leaf nitrogen (SLN, g N m^{-2} leaf area) (Sinclair and Horie 1989) as quantified for peanut by Sinclair *et al.* (1993) [equation (7)]. This equation results in a nearly linear response of C_{max} to SLN from the intercept at 0.6 g N m^{-2} to about 2.0 g N m^{-2} at which the carbon exchange rate is $1.0 \text{ mg m}^{-2} \text{s}^{-1}$. At higher values of SLN, carbon exchange rate increases less rapidly with increase in SLN and approaches a maximum value of $1.8 \text{ mg m}^{-2} \text{s}^{-1}$ at very high SLN. Values of C_{max} are calculated for each of the five canopy layers (l) to allow for variation in SLN throughout the canopy.

$$C_{\text{max}}(l) = 1.8 * \{2.0 / (1.0 + \exp[-0.9 * (\text{SLN}(l) - 0.6)]) - 1.0\}. \quad (7)$$

The SLN of each layer can be calculated from the linear decline in SLN with cumulative LAI from the top of the canopy (Wright and Hammer 1994). If the

SLN of leaves averaged over all five canopy layers is SLN_{av} and the gradient in SLN is SLN_{grad} , then SLN in each layer can be calculated from equations (8) and (9). Equation (8) gives the SLN at the very top of the canopy (SLN_o , $g\ N\ m^{-2}$) given LAI_{tot} , which is the LAI for the entire canopy. Equation (9) gives the SLN in a canopy layer given $\sum LAI_m$, which is the accumulated LAI from the top of the canopy to the mid-point of that canopy layer. Layers are numbered from the top of the canopy. Wright and Hammer (1994) reported a value of 0.14 for SLN_{grad} . However, these equations have been structured to allow consideration of any SLN_{grad} , any SLN_{av} , and any canopy LAI profile.

$$SLN_o = SLN_{av} + SLN_{grad} * LAI_{tot}/2, \quad (8)$$

$$SLN(l) = SLN_o - SLN_{grad} * \sum LAI_m(l). \quad (9)$$

The radiation flux density, incident on either sunlit leaves or shade leaves (I_{sun} or I_{sh} , $MJ\ m^{-2}\ leaf\ s^{-1}$), is calculated from the incident direct beam radiation (I_{dir} , $MJ\ m^{-2}\ ground\ s^{-1}$) and incident diffuse radiation (I_{dif} , $MJ\ m^{-2}\ ground\ s^{-1}$), the proportion of the incident radiation intercepted by the leaf canopy (F), and the leaf area index of sunlit or shade leaves (LAI_{sun} or LAI_{sh} , $m^2\ leaf\ m^{-2}\ ground$) [equations (10) and (11)]. In a manner similar to Sinclair *et al.* (1992), we assumed that sunlit leaves are exposed to both direct beam and diffuse radiation, whereas the shade leaves are exposed to diffuse radiation and radiation scattered from the sunlit leaves. The scattering coefficient (SCAT) was set at 15% (Boote 1991), representing the total proportion of light transmitted through the sunlit leaves or reflected from them into the canopy. Values of I_{sun} and I_{sh} are calculated for each of the five canopy layers (l) and three times of day (t). We assumed that light scattered from sunlit leaves in any layer (l) was uniformly distributed over the leaf area of shade leaves in the same layer (l) and the layer immediately lower in the canopy ($l+1$).

$$I_{sun}(l, t) = I_{dir}(t) * F(l, t)/LAI_{sun}(l, t) + I_{dif}(t) * F(l, t)/\{LAI_{sun}(l, t) + LAI_{sh}(l, t)\}, \quad (10)$$

$$I_{sh}(l, t) = I_{dif}(t) * F(l, t)/\{LAI_{sun}(l, t) + LAI_{sh}(l, t)\} + SCAT * \{I_{sun}(l-1, t) * LAI_{sun}(l-1, t)\}/\{LAI_{sh}(l-1, t) + LAI_{sh}(l, t)\} + SCAT * \{I_{sun}(l, t) * LAI_{sun}(l, t)\}/\{LAI_{sh}(l, t) + LAI_{sh}(l+1, t)\}. \quad (11)$$

The leaf area index of sunlit or shade leaves (LAI_{sun} or LAI_{sh} , $m^2\ leaf\ m^{-2}\ ground$) is calculated by considering the sun angle (α), the proportion of intercepted radiation (F), and the shadow projection coefficient (G), which was set at a value of 0.5 (Sinclair and Horie 1989). Equations (12) and (13) yield

the values of LAI_{sun} and LAI_{sh} for each of the five canopy layers (l) and three times of day (t), given the total LAI in each layer:

$$LAI_{\text{sun}}(l, t) = F(l, t) * \sin\{\alpha(t)\}/G, \quad (12)$$

$$LAI_{\text{sh}}(l, t) = LAI(l) - LAI_{\text{sun}}(l, t). \quad (13)$$

The proportion of intercepted radiation (F) is calculated via an exponential equation on LAI, the form of which depends on the sun angle (α) and the shadow projection coefficient (G) (Duncan *et al.* 1967). We used this approach to determine the cumulative F from the top of the canopy to the base of a canopy layer ($\sum F$), based on the accumulated LAI from the top of the canopy to the base of the layer ($\sum LAI_b$) [equation (14)]. F for each canopy layer was then calculated by difference [equation (15)]:

$$\sum F(l, t) = 1.0 - \exp\{-\sum LAI_b(l) * G/\sin[\alpha(t)]\}, \quad (14)$$

$$F(l, t) = \sum F(l, t) - \sum F(l-1, t). \quad (15)$$

The total incident radiation at any time (I_o , MJ m⁻² ground s⁻¹), consists of direct beam (I_{dir} , MJ m⁻² ground s⁻¹) and diffuse (I_{dif} , MJ m⁻² ground s⁻¹) components. At any instant, I_o , I_{dir} , and I_{dif} depend on latitude (LAT), day of year (DAY), time of day (TIME), and the atmospheric transmission ratio (RATIO). On clear days, RATIO takes daily values from 0.7 to 0.8 (Bristow and Campbell 1984; Spitters *et al.* 1986; Meinke *et al.* 1994). Hence, we assumed a value of 0.75 for clear skies. Under such conditions, 23% of the radiation reaching the Earth's surface in a day is diffuse (Spitters *et al.* 1986). This thus represents 17% of the extra-terrestrial insolation for the day. As the transmission coefficient for diffuse radiation is insensitive to solar elevation and cloud conditions (Collares-Pereira and Rabl 1979), this proportion can be used for any time of day. Hence, I_{dif} can be simply calculated from extra-terrestrial radiation, which depends only on the solar constant (1360 J m⁻² s⁻¹; Bristow and Campbell 1984) and sun angle (α) [equation (16)]. The diurnal pattern of atmospheric transmission of direct beam radiation is more complex (Spitters *et al.* 1986), so we obtain I_{dir} by difference [equation (17)] once I_o is calculated:

$$I_{\text{dif}}(t) = 0.17 * 1360 * \sin\{\alpha(t)\}/1\,000\,000, \quad (16)$$

$$I_{\text{dir}}(t) = I_o(t) - I_{\text{dif}}(t). \quad (17)$$

The total incident radiation at any time (I_o , MJ m⁻² ground s⁻¹) is obtained from the daily integral of solar radiation reaching the Earth's surface (S_g , MJ m⁻² day⁻¹), the daylength (DL, hours), and the time of day (TIME) via equation (18), which was adapted from Charles-Edwards *et al.* (1986):

$$I_o(t) = S_g * \{1.0 + \sin(2\pi * \text{TIME}(t) + 1.5\pi)\}/(\text{DL} * 3600). \quad (18)$$

The daily integral of solar radiation (S_g) is calculated as the product of the daily extra-terrestrial irradiance (S_o , MJ m⁻² day⁻¹) and the atmospheric transmission ratio (RATIO) [equation (19)].

$$S_g = S_o * \text{RATIO}. \quad (19)$$

Using this method of calculating I_{dir} and I_{dif} allows the ratio of the two to vary throughout the day and the proportion of diffuse radiation to increase on cloudy days (i.e. RATIO < 0.75) in the manner reported by Spitters *et al.* (1986). On cloudy days, I_{dif} does not differ from clear days unless the calculated I_o is so low that $I_o < I_{\text{dif}}$. Under such heavy cloud conditions, we assume $I_{\text{dif}} = I_o$ and $I_{\text{dir}} = 0$.

Calculation of the daily extra-terrestrial irradiance (S_o , MJ m⁻² day⁻¹) is achieved using the equation derived by Milankovitch (1930). The procedure is set out clearly by Brock (1981). The approach requires the day of year (DAY) and latitude (LAT), which is negative in the southern hemisphere. The solar declination (DEC), appropriate daylength attributes and DL are calculated from DAY and LAT. These variables and the solar constant are used in the Milankovitch equation to determine S_o .

The sun angle at any time (α) is calculated from DEC, LAT, DL, and TIME using equation (20), which was adapted from Spitters *et al.* (1986). The variables LAT, DEC, and α are in units of radians, DL is in hours, and TIME is expressed as a fraction of the daylength.

$$\sin\{\alpha(t)\} = \sin(\text{LAT}) * \sin(\text{DEC}) + \cos(\text{LAT}) * \cos(\text{DEC}) * \cos\{\text{DL} * (\text{TIME}(t) - 0.5) * \pi/12\}. \quad (20)$$

In order to calculate RUE via equation (1), it only remains to calculate the radiation intercepted by the canopy for the day (RAD, MJ m⁻² day⁻¹). This is achieved by determining the amount intercepted by the entire leaf canopy at each of the three calculation times [equation (21)] and using three-point Gaussian integration to find the daily integral [equation (22)], in a similar manner to that used for the canopy assimilation rate in equations (3) and (4).

$$\text{RAD}(t) = I_o(t) * \sum F(5, t), \quad (21)$$

$$\text{RAD} = 3600 * \text{DL} * \{\text{RAD}(1) + 1.6 * \text{RAD}(2) + \text{RAD}(3)\} / 3.6. \quad (22)$$

The theoretical framework defined by equations (1) to (22) enables prediction of radiation use efficiency for any given latitude, day of year, atmospheric transmission ratio, canopy leaf area profile, canopy specific leaf nitrogen, and canopy gradient in specific leaf nitrogen.

Evaluating Effects of Nitrogen and Radiation

To evaluate the effects on RUE of average canopy SLN, canopy gradient in SLN, and partitioning radiation into direct and diffuse components, four hypothetical

scenarios, incremental in features, were examined. In all scenarios, the theoretical framework was used to predict RUE for average canopy SLN ranging from 0.7 to 3.1 g N m⁻², which covers the range found in field experiments on peanut (Bell *et al.* 1992; Sinclair *et al.* 1993; Wright and Hammer 1994). The leaf area profile was set to one unit of LAI in each of the five canopy layers. This approximated the profile measured by Wright and Hammer (1994). The latitude was set at 25° S., which corresponds to the main peanut growing area in Australia and the location of the field experiments (Wright and Hammer 1994). Daily incident radiation levels were varied by varying DAY from 1 (1st Jan.) to 176 (20th May) in 35 day increments, and by varying RATIO from 0.75 (clear sky) to 0.25 (heavy cloud) in 0.10 increments.

Scenario I

In scenario I, RUE values for the various combinations of SLN_{av}, DAY, and RATIO, were predicted assuming no gradient of SLN in the leaf canopy (i.e. SLN_{grad} = 0) and that incident radiation was not partitioned into direct and diffuse components, which was achieved by setting $I_{dif}(t) = 0$. Under these circumstances, predicted RUE increased in a curvilinear manner with increase in SLN_{av}, increased at all SLN_{av} levels as RATIO decreased, but was unaffected by change in incident radiation level associated with DAY at all SLN_{av} and RATIO levels (Fig. 1). The response of RUE to SLN_{av} predicted by Sinclair *et al.* (1993) was similar to that predicted using our framework with a RATIO value of 0.55 at either DAY (Fig. 1). However, our predictions of RUE differ markedly at high and low RATIO levels (Fig. 1), even in the absence of SLN gradient and diffuse radiation effects.

The response of RUE to SLN_{av} was consistent with that reported previously by Sinclair and Horie (1989) and Sinclair *et al.* (1993) (Fig. 1). Variation in SLN_{av} caused major change in RUE. However, our predictions of the influence of radiation level differ with those previous studies. We found that changing the level of incident radiation by varying time of year (DAY) had no effect on the response of RUE to SLN_{av}, but that reducing atmospheric transmission (RATIO) at any time of year, increased RUE at all SLN_{av} levels. Sinclair and Horie (1989) reported only minor sensitivity of RUE to incident radiation.

Our finding of little effect of DAY on RUE is similar to the lack of response to sun elevation (α) reported by Sinclair and Horie (1989), although they related this outcome to time of day rather than day of year. Sinclair and Horie (1989) used the solar radiation flux density at midday (I_m) and modified this by the sine of sun elevation (α) to represent the daily cycle. They found little change in RUE when α was varied. However, $I_m \sin(\alpha)$ is not a good representation of the diurnal trend in incident radiation, which is better described in equation (18) (Charles-Edwards *et al.* 1986). Using this equation, RUE varies with TIME in a day, being lowest at solar noon and highest early and late in the day (data not shown). The variation in α examined by Sinclair and Horie (1989) relates to variation in DAY in our framework. The lack of response to DAY is caused by similar effects of change in α on LAI_{sun} and S_o , which cancel out when calculating RUE on any DAY. Insensitivity to α associated with change in DAY also implies little effect on RUE of varying latitude. When we varied LAT (data not shown), the resultant RUE changed little.

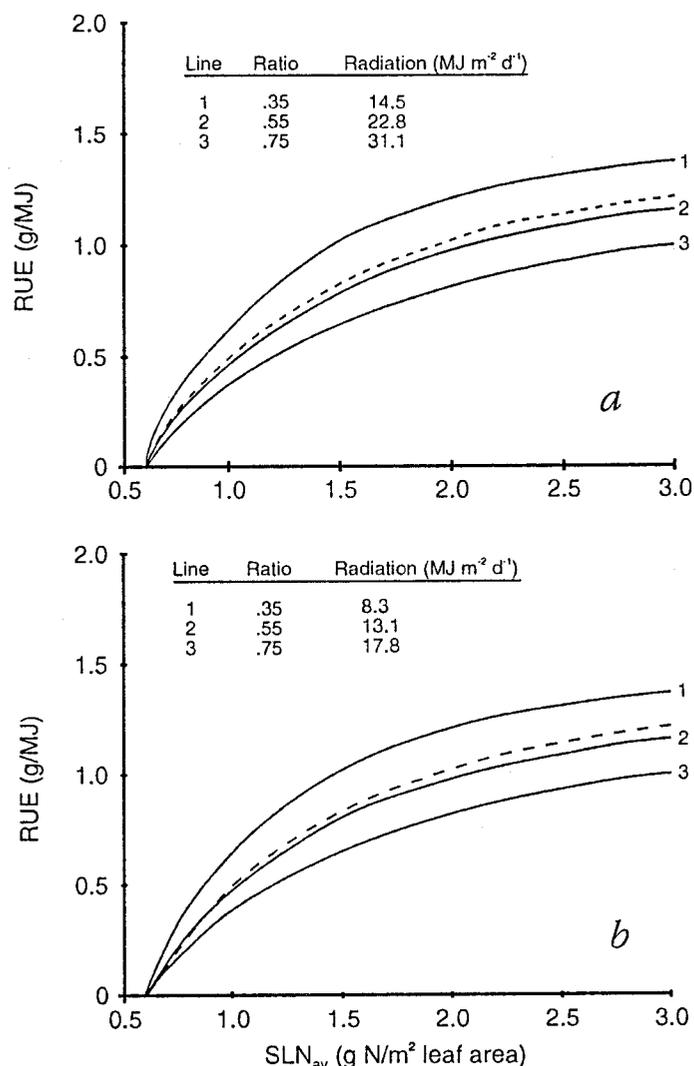


Fig. 1. The predicted response of radiation use efficiency (RUE) to canopy average specific leaf nitrogen (SLN_{av}) for three levels of incident radiation flux density associated with three levels of atmospheric transmission (RATIO). The predictions were made assuming no canopy gradient in SLN and no diffuse radiation component for (a) day 1 of the year at latitude 25° S., and (b) day 141 of the year at latitude 25° S. The response predicted by Sinclair *et al.* (1993) is included for comparison (broken line). That response is insensitive to level of incident radiation flux density.

Our finding of a significant effect of RATIO on RUE, is associated with an effect of radiation level that is not connected to, nor negated by, a concurrent change in sun angle. This finding conflicts with the suggestion of Sinclair and Horie (1989), that RUE is only slightly dependent on I_m . However, in subsequent studies that examined the sensitivity to I_m , Sinclair *et al.* (1992) found RUE increased as I_m decreased. This was consistent with the earlier study of Murata (1981) and is consistent with our finding on the effect of RATIO on RUE. The effect is caused by the more efficient use of light by sunlit leaves at low light levels. This efficiency continues to increase as incident radiation flux density decreases as per the partial derivative of equation (5) with respect to I_{sun} . This effect may not be as pronounced in species with the C₄ photosynthetic pathway, due to less responsiveness of the assimilation rate to increasing radiation in those species.

The impact on RUE of variation in RATIO is of sufficient magnitude to demand consideration when comparing theoretical and measured values of RUE. RUE does not vary with incident radiation level in general. It does not vary with DAY and LAT, but it does vary with RATIO. This suggests that observations collated by Murata (1981) for a range of species and by Manrique *et al.* (1991) for potato, showing decrease in RUE with increase in incident radiation, were

probably associated with differences in RATIO among experiments, not differences in location (i.e. LAT) or season (i.e. DAY).

Our findings on the impact of RATIO on RUE are important in ascribing causality to observed variation in RUE. Stockle and Kiniry (1990) reported an association of RUE with vapour pressure deficit (VPD), with RUE decreasing as VPD increased. Kiniry *et al.* (1992) used this association in a simulation analysis for sunflower over a wide range of environments. The association of RUE with VPD is likely caused by the effect of RATIO. As cloud cover increases, RATIO decreases and we would predict RUE to increase. In such situations, VPD often decreases, leaving a casual (not causal) association between VPD and RUE. It is inappropriate to use such a casual association, rather than a causal one, in extrapolating via simulation models. If VPD changes for some reason other than a change in RATIO, as would be the case with a change in moisture content or temperature of the air mass, the simulated outcomes would be spurious.

Scenario II

In scenario II, RUE values for the various combinations of SLN_{av} and RATIO, were predicted assuming no gradient of SLN in the leaf canopy (i.e. $SLN_{grad} = 0$), but incident radiation partitioned into direct and diffuse components as set out in the theoretical framework. Calculations were performed for 1st January (DAY = 1) only, following the finding in scenario I that DAY had only very minor effects on RUE.

Adding the partitioning of incident radiation into direct and diffuse components resulted in increases in RUE of 0.06 to 0.15 g MJ⁻¹ (Fig. 2). The level of increase was least at high RATIO and greatest at low RATIO. Expressed as a percentage, the changes in RUE corresponded to increases of 7 to 23%. The lower percentage increases were predicted on clear days (RATIO = 0.75) with high SLN_{av} . The higher percentage increases occurred on cloudy days (RATIO = 0.35) at relatively low SLN_{av} .

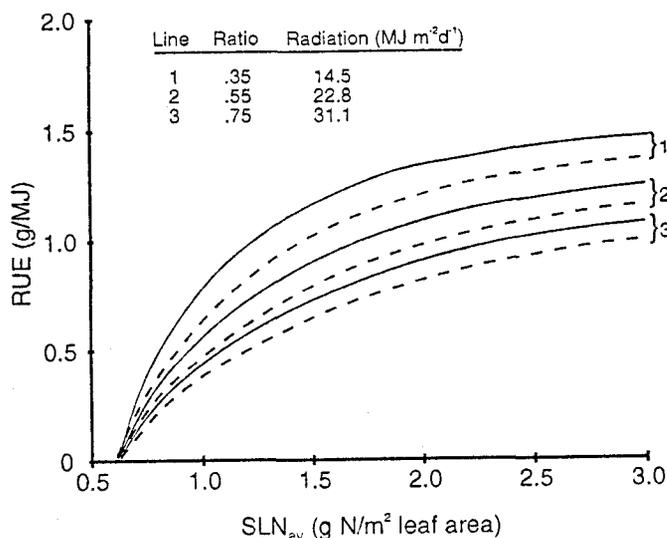


Fig. 2. The predicted response of radiation use efficiency (RUE) to canopy average specific leaf nitrogen (SLN_{av}) for three levels of incident radiation flux density associated with three levels of atmospheric transmission (RATIO). The predictions were made for day 1 of the year at latitude 25° S., assuming no canopy gradient in SLN and incident radiation partitioned into direct and diffuse components (solid lines). The predictions for the same circumstances, but without partitioning incident radiation into components [as per Fig. 1(a)] are included (broken lines) for comparison.

The increase in RUE resulting from the partitioning of incident radiation into direct and diffuse components was caused by the diffuse component being spread over the areas of sunlit and shade leaves. In the absence of consideration of

a diffuse component, shade leaves receive only radiation scattered from sunlit leaves. The introduction of the diffuse component decreases the radiation flux density on sunlit leaves but increases it on shade leaves. The increase in canopy efficiency results from the balance of changes in efficiency of the sunlit and shade leaves. There is little change in efficiency of shade leaves as they are operating at low radiation levels, but the efficiency of sunlit leaves is increased by the reduction in radiation flux density incident on them. Hence, canopy efficiency increases.

The balance of changes in efficiency of the sunlit and shade leaves also explains the greater effect on RUE at low RATIO when the diffuse component is introduced (Fig. 2). At low RATIO, incident radiation is low and consequently, there is a greater effect on the efficiency of the sunlit leaves. Decreasing RATIO impacts solely on the direct radiation component, so the greater increase in RUE at low RATIO can be associated with the proportion of diffuse radiation as reported by Sinclair *et al.* (1992). However, it is important to realize that a high proportion of diffuse radiation can only occur at low RATIO and that most of the increase in RUE under such conditions is due directly to the effects of RATIO, as shown in scenario I, rather than to the inclusion of the diffuse component.

Scenario III

In scenario III, RUE values for the various combinations of SLN_{av} and RATIO, were predicted assuming a gradient of SLN of 0.14 in the leaf canopy (i.e. $SLN_{grad} = 0.14$), as measured by Wright and Hammer (1994), and incident radiation partitioned into direct and diffuse components. As for scenario II, calculations for 1st January only were performed.

Incorporating a SLN_{grad} of 0.14 resulted in further increases in RUE, but not over all SLN_{av} values (Fig. 3). Increase in RUE ranged from 0.01 to 0.13 $g\ MJ^{-1}$. This represented percentage increases of 1 to 20%. For SLN_{av} of 2 $g\ N\ m^{-2}$ or more, RUE increased little (5% or less) due to the addition of the canopy gradient in SLN. Percentage increases were greatest at low SLN_{av} and were similar at all three incident radiation levels.

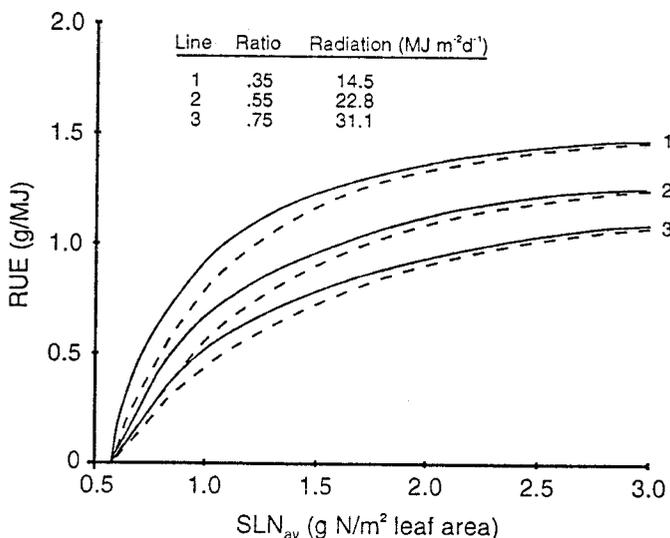


Fig. 3. The predicted response of radiation use efficiency (RUE) to canopy average specific leaf nitrogen (SLN_{av}) for three levels of incident radiation flux density associated with three levels of atmospheric transmission (RATIO). The predictions were made for day 1 of the year at latitude 25° S., assuming a canopy gradient in SLN of $0.14\ g\ N\ m^{-2}$ leaf area per unit leaf area index and incident radiation partitioned into direct and diffuse components (solid lines). The predictions for the same circumstances, but without a canopy gradient in SLN (as per Fig. 2) are included (broken lines) for comparison.

The inclusion of a gradient in SLN in the leaf canopy caused increases in RUE (Fig. 3) because the assimilation capacity of the canopy was improved. Greater SLN in leaves nearer the top of the canopy gave those leaves a greater potential assimilation rate [equation (7)]. As those leaves were intercepting the greater proportion of the incident radiation, this resulted in greater total canopy assimilation for the same amount of intercepted radiation. This effect was more pronounced at low SLN_{av} because similar changes in SLN in a canopy layer have greater impact on potential assimilation rate at low SLN levels [equation (7)]. The effect of introducing the SLN gradient was also more pronounced at low RATIO (Fig. 3). This was because the greater potential assimilation rate caused greater increase in efficiency at low incident radiation levels [equation (5)], than at high radiation levels.

Scenario IV

In scenario IV, RUE values for the various combinations of SLN_{av} and RATIO, were predicted assuming a gradient of SLN of 0.28 in the leaf canopy (i.e. $SLN_{grad} = 0.28$) and incident radiation partitioned into direct and diffuse components. Increasing SLN_{grad} from 0.14 to 0.28 resulted in further, but only small, increases in RUE (Fig. 4). The increases were greater at low values of SLN_{av} , but never exceeded a 5% increase.

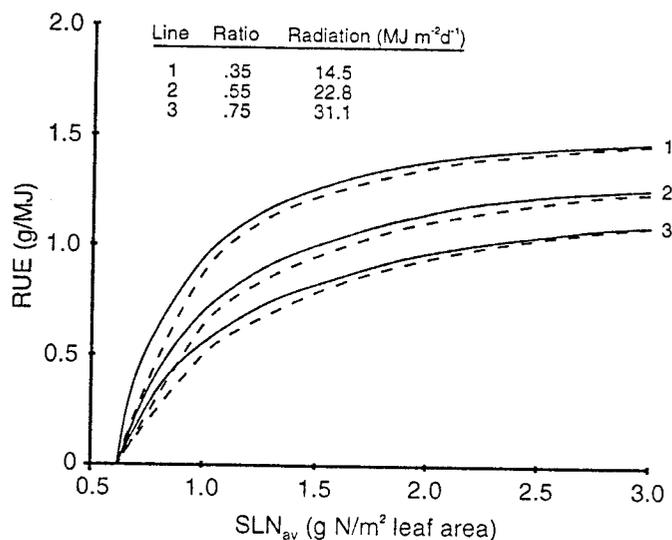


Fig. 4. The predicted response of radiation use efficiency (RUE) to canopy average specific leaf nitrogen (SLN_{av}) for three levels of incident radiation flux density associated with three levels of atmospheric transmission (RATIO). The predictions were made for day 1 of the year at latitude 25° S., assuming a canopy gradient in SLN of 0.28 g N m⁻² leaf area per unit leaf area index and incident radiation partitioned into direct and diffuse components (solid lines). The predictions for the same circumstances, but with a canopy gradient in SLN of 0.14 (as per Fig. 3) are included (broken lines) for comparison.

The increases in RUE showed the same pattern as the initial increases associated with including the first part of the SLN gradient (scenario III) for the same reasons. However, these increases were smaller in magnitude because of the lesser effect on potential assimilation rate of further increase in SLN of the top canopy layers [equation (7)]. Hence, this gradient is approaching the optimal point for this canopy configuration, where loss of assimilation capacity in a layer caused by the reduction in N (and, hence, SLN) is just offset by the concomitant gain in the layer(s) receiving the N.

Comparison with Experimental Studies

The theoretical framework was used to predict RUE for the experiments of Wright *et al.* (1993), Wright and Hammer (1994), and Sinclair *et al.* (1993).

For each experiment, the LAT, DAY, I_o , and SLN_{av} were known for the period over which RUE was determined. We assumed SLN_{grad} was 0.14 (Wright and Hammer 1994). The average value of RATIO for the measurement period was determined and used in calculating the predicted RUE. The predicted values were compared with those measured in the experiments and with the predictions using the framework set out by Sinclair *et al.* (1993). The predictions of RUE from Sinclair *et al.* (1993) are based on an adaptation for peanut of the general framework set out by Sinclair and Horie (1989). In that framework, RUE is predicted to vary substantially with SLN_{av} , but is predicted as insensitive to I_o . In addition, gradients in SLN and the partitioning of radiation into direct and diffuse components are not considered.

The theoretical framework accurately predicted the experimentally measured values of RUE (Table 1). The prediction residuals were within the error of measurement. In all cases, the theoretical framework used in this study predicted the measured outcomes better than the Sinclair *et al.* (1993) framework. The predictions using our framework were from 0.13 to 0.24 g MJ⁻¹ higher than predicted using the framework of Sinclair *et al.* (1993). Hence, by including the effects of radiation and nitrogen distribution, the discrepancies between measured RUE values and values predicted from previous theories have been explained.

Table 1. Comparison of predicted and measured radiation use efficiencies (RUE, g MJ⁻¹) for three field experiments in peanut where average specific leaf nitrogen in the canopy (SLN_{av} , g N m⁻² leaf area) and the ratio of incident solar radiation at ground level to extra-terrestrial incident radiation (RATIO) were known

Where available, standard errors of measured RUE values are included in parentheses after the value. Predictions of RUE were made using the theoretical framework presented here (H&W) and using the framework of Sinclair *et al.* (1993) (SBB)

Location	Latitude	SLN_{av}	RATIO	RUE		
				Measured	H&W	SBB
Bundaberg ^A	25.0° S.	1.39	0.54	0.90	0.92	0.77
		1.63	0.54	1.18	1.02	0.89
		1.19	0.48	0.79	0.89	0.65
		1.48	0.48	1.12	1.04	0.82
Bundaberg ^B	25.0° S.	2.07	0.47	1.40 (0.14)	1.25	1.04
Gainesville ^C	29.7° N.	1.35	0.51	1.01 (0.01)	0.98	0.78

^A Experiment reported by Wright *et al.* (1993). The values given are derived from nitrogen treatments imposed on a non-nodulating cultivar giving high or low SLN_{av} for intervals between harvests 2 and 4 (RATIO = 0.54) and harvests 3 and 5 (RATIO = 0.48).

^B Experiment reported by Wright and Hammer (1994).

^C Experiment reported by Sinclair *et al.* (1993).

The three main factors contributing to the explanation of discrepancies between the measured RUE values and values predicted from previous theories could be ranked in importance from this analysis. Radiation effects associated with variation in atmospheric transmission (RATIO) had the greatest effect with differences in RUE of about 0.4 g MJ⁻¹ between clear and very cloudy days (Fig. 1). The separation of incident radiation into direct and diffuse components was the next most important factor, conferring increases in RUE up to 0.15 g MJ⁻¹ (Fig. 2). The least effect was attributed to canopy gradients in SLN, which conferred increases in RUE of up to 0.13 g MJ⁻¹ at low SLN_{av} , but had much less effect at higher SLN_{av} .

Conclusions

The intent of this study was to develop a framework suitable for explaining the causes of discrepancies between RUE values measured in the field and values predicted from current theories. By integrating quantitative relationships that capture the physiological responses of the crop canopy with relationships defining the radiation environment, a suitable and general theoretical framework was developed. By using the framework in an incremental analysis of hypothetical scenarios, it was shown that variation in the amount of incident radiation, associated with changes in atmospheric attenuation, had greatest effect on RUE for a broad range of SLN. Changes in the amount of incident radiation associated with time of year or latitude had little effect on RUE. The separation of incident radiation into direct and diffuse components and canopy gradients in SLN both affected RUE, but to a lesser extent. Finally, comparisons of predicted RUE with values of RUE measured in field experiments, were presented and showed that the theoretical framework was able to explain the causes of discrepancies between observations and previous theories.

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