

Leaf Nitrogen Content, Photosynthesis and Radiation Use Efficiency in Peanut¹

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ABSTRACT

It has been hypothesized that a close correlation exists between specific leaf nitrogen content (SLN, g N m⁻² leaf area) and leaf carbon exchange rate (CER), and crop radiation use efficiency (RUE). This association has not been investigated previously in peanut (*Arachis hypogaea* L.) so the objective of this research was to obtain such data under greenhouse and field conditions. In the greenhouse study differing nitrogen fertilizer treatments for a non-nodulated cultivar resulted in leaves with a wide range of SLN and CER. A strong, positive association between SLN and CER was found. In the field little variation in either SLN or CER was observed through much of the growing season in four commercial cultivars. Consistent with the observation of stability in SLN and CER, RUE based on total, intercepted solar radiation was found to be constant at 1.00 g MJ⁻¹ through the growing season. However, the observed RUE was 29% greater than a theoretical RUE calculated assuming a uniform distribution of SLN in the canopy. One possibility is that RUE of peanuts may be enhanced by a non-uniform SLN distribution within its leaf canopy. In any event, the results of both the greenhouse and field tests showed that peanut CO₂ assimilation is closely linked to leaf SLN.

Key Words: Specific leaf nitrogen content, leaf carbon exchange rate, radiation use efficiency.

Plant N content has profound influences on crop productivity (e.g., Sinclair, 1990). Carbon dioxide exchange rates (CER) are especially sensitive to N levels in leaves. Sinclair and Horie (1989) reviewed leaf photosynthetic data from soybean (*Glycine max* L. Merr.), rice (*Oryza sativa* L.), and maize (*Zea mays* L.), and concluded that much of the variation in leaf CER within a species was associated with leaf N expressed on a unit leaf area basis. As a consequence of this close relationship, Sinclair and Horie argued that canopy radiation use efficiency (RUE, g biomass accumulated per MJ intercepted total solar radiation) must also be intimately related to leaf N.

In peanut (*Arachis hypogaea* L.) the effects of leaf N on CER have been studied only to a limited extent. Bhagsari and Brown (1976) measured the photosynthetic activity and N concentration (per unit weight) of leaves of 31 peanut genotypes. The correlation coefficients between leaf N

concentration and CER for three experiments were not high ($r = 0.53, 0.37, \text{ and } 0.08$). However, Bhagsari and Brown did not analyze the relationship between CER and N per unit leaf area (specific leaf N, SLN), which has been recently suggested as the variable more likely to result in a high correlation with CER (Sinclair and Horie, 1989).

Radiation use efficiency of well-watered peanut has been observed in only a few studies. The data obtained by Gardner and Auma (1989) for two peanut cultivars (Pronto and Florunner) can be recomputed to calculate a RUE equal to 0.8 g MJ⁻¹. Stirling *et al.* (1990) reported a RUE for peanut of 0.98 g MJ⁻¹ for the period of 44 to 94 days after sowing. Wright *et al.* (1993) measured RUE in a field experiment designed to examine the growth of non-nodulated peanut genotypes grown at two locations in Australia. Nitrogen fertilizer treatments, which ranged from 0 to 26 g N m⁻², were used in the study to induce variation in RUE. The observed RUE values ranged from 0.57 to 1.00 MJ⁻¹, excluding very late season observations, at Kingaroy and from 0.74 to 1.26 g MJ⁻¹ at Bundaberg. The variation in RUE among treatments at Bundaberg was closely associated ($r^2 = 0.74$) with SLN. At Kingaroy, RUE tended to be lower and SLN was higher when compared to Bundaberg, and no correlation between the two variables was found. Wright *et al.* (1993) concluded that cool night temperatures at Kingaroy may have inhibited the full expression of RUE.

To examine in greater detail the possible linkage between leaf N, leaf photosynthesis rates and crop RUE, greenhouse and field experiments were conducted. Greenhouse experiments using a non-nodulated peanut genotype were done to measure directly the relationship between leaflet CER and SLN. Field experiments were established to monitor leaf N, CER, and RUE.

Materials and Methods

Leaf N and CER in Greenhouse. On March 12, 1991, GA T-2400 N.N. (non-nodulating) peanut seeds were sown one per pot into 14-L plastic pots containing a fine, washed builder's sand. Twelve pots containing uniform seedlings were selected and irrigated approximately three times per week with a complete nutrient solution (Ra-Pid-Gro Products, Chevron Chemical Co., San Francisco, CA) until 23 April. Following one month of growth during which all nutrients were readily available, soil in all pots was leached with copious amounts of water on 23 April to remove residual N. Soil was again leached with water the following day. Subsequently, all plants were irrigated approximately three times per week with a full-strength Hoagland's solution with N deleted. To obtain leaves over a wide range of nitrogen levels, the plants were separated into five treatments with differing amounts of N added. Calcium nitrate was added to the pots at various times after 23 April to give total nitrogen applications of 0, 0.042, 0.25, 0.29, and 0.84 g N pot⁻¹.

On 7 to 9 May, leaflet CER were measured under saturating photosynthetically active radiation (greater than 1000 $\mu\text{mole m}^{-2} \text{ s}^{-1}$) by briefly enclosing individual leaflets in a 0.25-L portable chamber system

¹Mention of company names or commercial products does not imply recommendation or endorsement by the United States Department of Agriculture over others not mentioned.

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(Model 6200, Li-Cor, Inc., Lincoln, NE). The leaflets were selected among the various N treatments in order to sample a range of leaves with differing coloration. At the time of measurement, leaves from the three lowest N treatments were yellowing and appeared N deficient. Immediately after measuring CER, the leaflet lamina were harvested and their areas were measured (Delta-T area meter, Decagon Devices, Inc., Pullman, WA). In addition to the leaflet on which CER was measured, the other three leaflets of the leaf were harvested to form a single leaf sample for N determination. The four leaflets were dried at 80 C, weighed, ground to 1-mm particle size and leaf N was determined by Kjeldahl analysis. The Kjeldahl analysis yielded a measure of leaf N per unit dry weight, and this was subsequently converted to mg N m⁻² leaf area by multiplying by the specific leaf area of each sample.

Leaf N and CER in Field. Leaf CER were measured in a field experiment previously described by Bennett *et al.* (1992) in which the growth and development of four peanut cultivars was reported. Briefly, this experiment was established on 15 May 1990 on a Kendrick fine sand (loamy, siliceous, hyperthermic Arenic Paleudults) at Gainesville, FL. Four cultivars (Florunner, Early Bunch, Southern Runner, and Marc I) were sown in large replicated plots (180 m²) with rows 61 cm apart to give a plant density of 15 plants m⁻². Each cultivar was replicated three times in a randomized complete block design.

Beginning 27 days after sowing, CER were measured (Model 6200, Li-Cor, Inc., Lincoln, NE) on three leaflets in each plot at 2-wk intervals. Photosynthetic rates were measured at mid-day on mature, recently expanded leaflets on the second or third leaf from the stem apex and the leaves were judged to be normally exposed to direct, incident radiation. The leaflet lamina were harvested following the CER measurement and leaflet area was determined. The individual leaflets were combined with the other three leaflets of each individual leaf for determination of leaf N content by Kjeldahl analysis.

Canopy N and RUE Measurements. Growth analysis from the comparison of the four peanut cultivars described briefly above and in detail by Bennett *et al.* (1993) provided data to examine the relationship between leaf N content and RUE. For each cultivar, weekly harvests were made of the above ground plant mass from 1.22 m² of each plot. These samples were dried in a forced-air oven at 64 C and weighed. Pod mass was estimated in the later part of the season by a complete harvest of three plants from each plot and determination of the fractional dry weight of pods relative to above ground weight.

The fraction of photosynthetically active radiation intercepted by the crop canopies was measured weekly using a line quantum sensor (Model 191SA, Li-Cor, Inc., Lincoln, NE). Near midday on sunny days the sensor was placed at the soil surface across the peanut rows and radiation beneath the crop canopy was normalized with respect to the incident radiation. Although the midday measurement gave the minimum radiation interception, over 75% interception was found after day 40 and over 95% interception after day 57. From the measured values of the fraction of intercepted radiation for each cultivar, the total cumulative amount of intercepted radiation was calculated. Radiation use efficiency for each cultivar was calculated by linear regression of a plot of cumulative biomass versus cumulative total solar radiation intercepted by the crop. During the period of seed growth, seed mass was energy adjusted by multiplying the seed mass by 1.65 (Bennett *et al.*, 1993).

In addition to the determination of leaf N on the leaves from which CER was measured, all leaves from the weekly 3-plant subsample in each plot were combined and retained for N analysis. After determining the leaf area of the sample, the leaves were dried at 70 C, weighed and ground for N analysis by the Kjeldahl procedure.

Results

Leaflet N and CER in Greenhouse. Application of differing N levels to the non-nodulated peanut cultivar resulted in leaf N concentrations between 12 and 64 mg N g⁻¹. Leaflet CER ranged 0.08 to 1.50 mg CO₂ m⁻² s⁻¹. The high CER obtained for leaves with high N concentrations was equal to or greater than the CER for field leaves exposed to midday irradiances, which confirmed that the greenhouse leaves were radiation saturated during the CER measurements. The plot of leaflet of CER versus leaf N concentrations (Fig. 1) showed a positive association. A

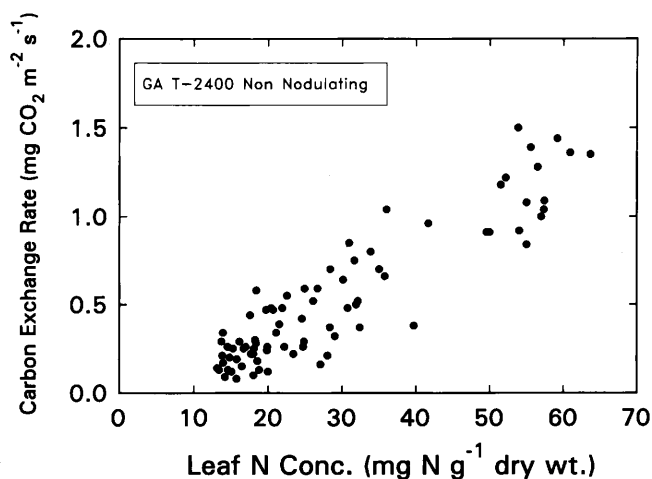


Fig. 1. Leaflet carbon exchange rates plotted against nitrogen concentration of leaves harvested from non-nodulating cultivar GA T-2400 grown in a greenhouse under a range of nitrogen fertility. The linear regression for these data is $y = 0.0236x - 0.160$ ($r^2 = 0.84$).

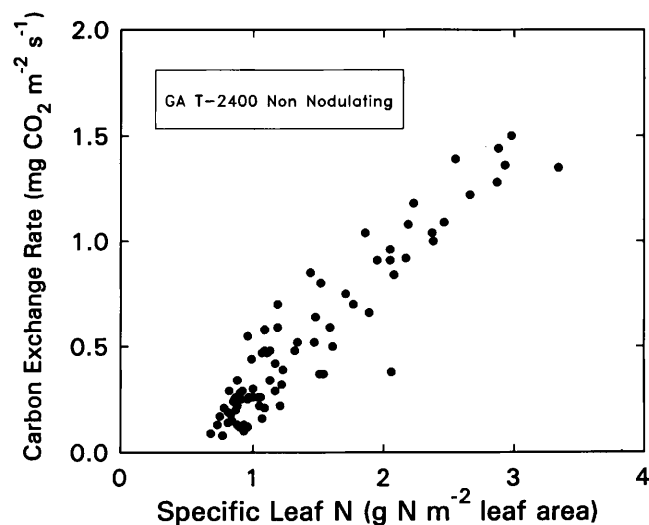


Fig. 2. Leaflet carbon exchange rates plotted against nitrogen per unit area of leaves harvested from non-nodulating cultivar GA T-2400 grown in a greenhouse under a range of nitrogen fertility. The linear regression for these data is $y = 0.555x - 0.256$ ($r^2 = 0.88$).

linear regression of these data resulted in $r^2 = 0.84$ and an error MS = 0.024.

Expression of leaf N levels on a per unit area basis improved the association between leaf N and CER (Fig. 2). The linear regression of CER versus SLN gave a $r^2 = 0.88$ and an error MS = 0.018. To match the exponential form of the relationship between CER and SLN used by Sinclair and Horie (1989) for soybean, rice, and maize, the data in Fig. 2 could be represented by,

$$CER = 1.8 [2 / (1 + \exp(-0.9 * (SLN - 0.6))) - 1] \quad (1)$$

This response function indicated that CER became zero at a SLN of 0.6 g N m⁻², which was intermediate between that reported for soybean and rice (Sinclair and Horie, 1989).

Peanut had a higher, extrapolated maximum leaf CER ($1.8 \text{ mg CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) than those observed for soybean and rice, but the rate of increase with increasing SLN was lower (coefficient -0.9).

Leaflet N and CER in Field. Leaflet CER observed for four cultivars in the field (Fig. 3a) was similar among cultivars throughout the season. For all cultivars, CER tended to be slightly higher early in the season, fairly constant through the bulk of the season, and decreased dramatically late in the season. For the middle part of the season, CER were approximately $1.3 \text{ mg m}^{-2} \text{ s}^{-1}$ for all cultivars, which was near the maximum CER observed in the greenhouse study. No changes in CER were associated with the beginning of seed growth which occurred at about 60 DAS in all four cultivars (Bennett *et al.*, 1993). The major difference among cultivars appeared at the end of the season, where the CER decline in Southern Runner was delayed with respect to the other cultivars.

The SLN under field conditions was also stable through most of the season for the exposed leaves on which CER was

measured (Fig. 3b). The SLN for the first measurement period was higher than observed during the remainder of the season. After day 35, the mean SLN for these exposed leaves for all cultivars was 2.12 g N m^{-2} (s.e. = 0.03). Substitution of the mean SLN for the exposed leaves into Equation (1) derived for the non-nodulated genotype, gives a CER estimate for these field leaves of $1.1 \text{ mg m}^{-2} \text{ s}^{-1}$, which is only slightly less than the experimentally observed value.

Leaf N and RUE Measurements. The analysis of biomass accumulation and cumulative light interception gave a stable value for RUE of 1.00 g MJ^{-1} (s.e. = 0.01, $r^2 = 0.99$) through the season among the four cultivars (Bennett *et al.*, 1992). This stability in RUE is consistent with the observed stability in leaf CER through most of the season (Fig. 3a) and the constancy in SLN for the exposed leaves used in the CER measurements (Fig. 3b).

The SLN values for all leaves obtained from the 3-plant sample (Fig. 3c) also showed little variation among cultivars and through the season, except for early in the season when all leaves were newly expanded. The mean value of SLN for all leaves on the plants of all four cultivars after day 35 was 1.37 g N m^{-2} (s.e. = 0.01). This value was substantially less than the SLN obtained for the exposed leaves used in the CER measurements (2.12 g N m^{-2}).

Sinclair and Horie (1989) proposed that RUE was directly related to leaf CER rate, which in turn was dependent on SLN. Using Equation (1) in the calculation of RUE proposed by Sinclair and Horie (1989), a theoretical response curve was generated for peanut RUE as a function of SLN (Fig. 4). The experimentally observed RUE of 1.00 g MJ^{-1} (Bennett *et al.*, 1993) was plotted as a function both of the mean SLN for all leaves (1.37 g N m^{-2}) and of only the exposed leaves on which CER was measured (2.12 g N m^{-2}). The observed RUE was 29% greater than the theoretically expected RUE (0.78 g MJ^{-1}) based on the mean SLN for all leaves, but 7% less than the theoretically expected RUE (1.08 g MJ^{-1}) based on the mean SLN for the exposed leaves:

Discussion

The results from the greenhouse experiment showed a close association between leaflet CER and SLN (Fig. 2). Such a result was consistent with the fact that a high proportion of leaf N is associated with photosynthetic enzymes (*e.g.*, Makino and Osmond, 1991). The CER response curve to SLN for peanut was different than reported for other crops (Sinclair and Horie, 1989) in that the CER was zero at a SLN of 0.6 g m^{-2} and rose slowly with SLN to an extrapolated maximum CER of $1.8 \text{ mg CO}_2 \text{ m}^{-2} \text{ s}^{-1}$. The field measurements also showed a consistency between SLN and leaflet CER for exposed leaves at the top of the canopy because both variables were stable through the season across cultivars. That is, maintenance of leaf SLN in the field was associated with a consistent leaflet CER through the season (Figs. 3a and 3b).

From the relationship between CER and SLN, the theoretical derivation of Sinclair and Horie (1989) indicated that crop RUE was closely associated with SLN. The stability of RUE through the season for the four peanut cultivars is consistent with the observed stability in canopy SLN through the season (Fig. 3c). However, the observed RUE was 29% greater than anticipated by the theory of Sinclair and Horie (1989). The results from the study of Wright *et al.* (1993)

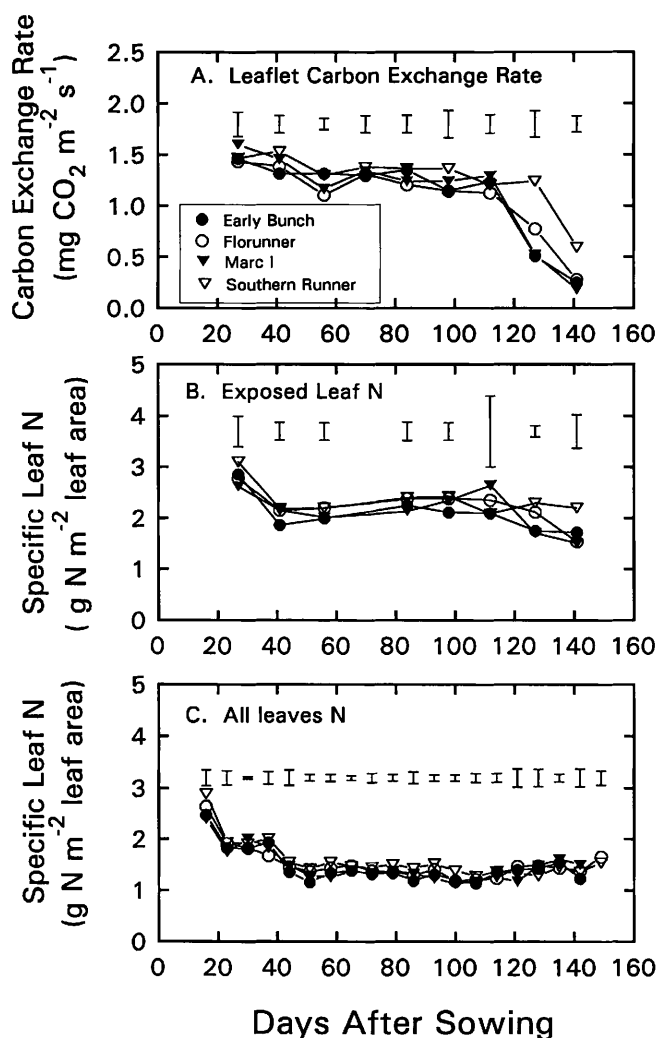


Fig. 3. The seasonal pattern of four peanut cultivars grown under field conditions in (A) leaflet carbon exchange rates, (B) leaf nitrogen per unit area of leaves used in CER measurements, and (C) mean leaf nitrogen per unit area of all the leaves of the canopy. The LSD₍₀₅₎ on each date are represented by the vertical lines at the top of each graph.

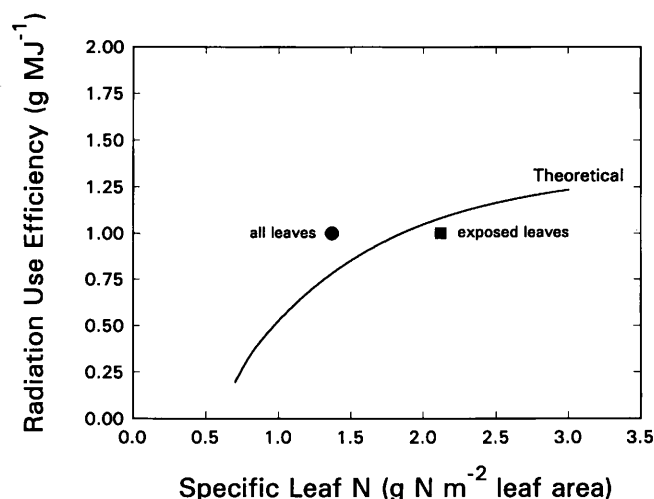


Fig. 4. Radiation use efficiency plotted as a function of leaf nitrogen per unit area. The curve was derived from the theory presented by Sinclair and Horie (1989). The experimentally observed RUE at Gainesville is plotted against both leaf nitrogen content measured for all leaves of the canopy and for only the exposed leaves used in the CER measurements.

with the non-nodulated peanut also lie above the theoretical line ($RUE = 0.924 \cdot SLN - 0.32$). Our results ($RUE = 1.0 \text{ g MJ}^{-1}$ at $SLN = 1.37 \text{ g N m}^{-2}$) are consistent with Wright *et al.* (1993).

The discrepancy between theory and experimental observations may well result from the theoretical assumption that SLN was uniform through the leaf canopy. In our study, the difference in mean SLN between the exposed leaves (2.12 g N m^{-2}) and all leaves (1.37 g N m^{-2}) indicated that N in the peanut canopy was concentrated in the top, exposed leaves. Clearly, leaves deeper in the canopy had to have low SLN to result in an overall mean SLN of 1.37 g N m^{-2} .

The allocation of N to the top leaves allowed the leaves which intercept the bulk of the solar radiation to have higher SLN. A non-uniform SLN distribution potentially allows greater CER by a canopy than could be expected for a uniform SLN. An advantage of the non-uniform SLN has been identified in perennial shrubs by Hirose and Werger (1987) and Pons *et al.* (1989). In both studies, the observed, non-uniform SLN distribution was calculated to have about a 27% advantage in CO₂ assimilation over the uniform SLN distribution. Our experimental observations with peanut in which RUE was 29% greater than anticipated from an assumed uniform SLN distribution, are consistent with the

previous calculations.

Not surprisingly, use of SLN measured for the top, exposed leaves to calculate RUE in the model of Sinclair and Horie (1989) resulted in an over-estimate in the calculated RUE. However, the fact that the theoretical RUE was fairly insensitive to varying SLN at the higher SLN (Fig. 4), resulted in only a 7% difference in the RUE calculated with the inflated SLN obtained from the exposed leaves as compared with the experimental results. A non-uniform distribution of nitrogen in the peanut canopy may have allowed the peanut crop to have greater RUE than possible with a uniform SLN canopy.

Acknowledgments

The authors express appreciation to Dr. W.D. Branch, University of Georgia, Coastal Plain Experiment Station, Tifton, GA for providing seed of the non-nodulating peanut used in this study. Li Ma and Andrew Schreffler were of great assistance in the collection of these data.

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Accepted March 3, 1993