Single Leaf Carbon Exchange and
Canopy Radiation Use Efficiency of Four Peanut Cultivars[1]

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ABSTRACT

Knowledge of the interception of solar radiation by crop canopies and the use of that radiation for carbon assimilation is essential for understanding crop growth and yield as a function of the environment. A field experiment was conducted in 1990 at Gainesville, FL to determine if differences in single leaf carbon exchange rate (CER), canopy radiation interception, radiation use efficiency (g dry matter produced per unit of solar radiation intercepted), and increase in seed harvest index with time exist among several commonly grown peanut (*Arachis hypogaea* L.) cultivars. Four cultivars (Early Bunch, Florunner, Marc I, and Southern Runner) were grown in field plots on a Kendrick fine sand (a loamy, siliceous, hyperthermic Arenic Paleudult) under fully irrigated, intensive management. Total crop and seed dry matter accumulation were determined, and canopy radiation interception measured at weekly intervals. CER of uppermost, fully expanded sunlit leaves were determined at midday at 2-wk intervals. Single leaf CER's were similar among cultivars (25 to 35 μmol CO_2 m^{-2} s^{-1}) and relatively stable throughout most of the season, before declining during late seed filling. Although interception of radiation differed somewhat among cultivars during early canopy development, total crop dry matter accumulation was linearly related to the cumulative amount of radiation intercepted by all four cultivars (r^2=$\geq$0.99). Radiation use efficiency was similar among all cultivars with a mean of 1.00 g dry matter accumulated per MJ of intercepted solar radiation. The increase in seed harvest index with time was linear ($r^2 \geq 0.94$) and the rates of increase were similar among the Early Bunch, Florunner, and Marc I cultivars (0.0058 d^{-1}), but lower (0.0043 d^{-1}) for the later maturing Southern Runner cultivar. Results from this study indicated that the primary differences among these four cultivars were in early-season development of the leaf canopy and resultant radiation interception and the rate of seed growth, rather than the capacity to assimilate carbon dioxide.

Key Words: *Arachis hypogaea*, biomass, harvest index, light interception, photosynthesis, seed growth.

Interception of solar radiation for use in carbon assimilation is fundamental to crop production. Many management practices (i.e. irrigation, pest control, plant density, etc.) are implemented to ensure that the crop canopy develops rapidly for interception of incident radiation and to maintain the canopy in a healthy condition so that high photosynthetic activity can be maintained throughout the crop life cycle.

Total biomass accumulation of a peanut crop is dependent on the integrated carbon exchange rates (CER) of single leaves throughout the total leaf canopy. Although there are several reports concerning leaf CER of peanut (summarized by Ketring *et al.*, 1982), relatively few studies have examined the season-long responses of various peanut cultivars.

Dry matter accumulation of crops has traditionally been described through use of crop growth analysis, often including computation of crop growth as a function of time (crop growth rate). However, crop biomass accumulation may better be described as a function of the cumulation of intercepted radiation (Monteith, 1977), rather than with respect to time. Radiation use efficiency (RUE) has been defined as the amount of biomass accumulated per unit of solar radiation intercepted by the crop canopy (g dry matter accumulated per MJ intercepted solar radiation). Estimates of RUE ranging from 0.8 to near 1.4 g MJ^{-1} for peanut grown under near optimal conditions have been reported (Bell *et al.*, 1987; Stirling *et al.*, 1990; Wright *et al.*, 1992; Bell *et al.*, 1992). However, very few studies have focussed on the possibility that peanut cultivars may differ in RUE.

Since peanut seeds are the crop component of commercial importance, prediction of seed growth as a function of total crop biomass would be desirable. In several other crops including soybean (*Glycine max.* L.) and maize (*Zea mays* L.), the harvest index (ratio of seed mass to total crop biomass) has been shown to increase linearly during the reproductive phase of growth (Spaeth and Sinclair, 1985; Muchow, 1990). Such a linear relationship provides a convenient way to describe the accumulation of seed mass as a function of crop biomass, provided the beginning of the linear phase can be predicted. Although seed growth of peanut has been studied with respect to dry matter increase

with time, the possibility that peanut seed harvest index increases in a linear manner with time has apparently not been fully examined.

Information concerning the development of a crop canopy, leaf CER's, and RUE with respect to vegetative and reproductive biomass is critical to our understanding of crop growth and productivity of peanut. Accordingly, a field experiment was conducted in 1990 at Gainesville, FL to determine if differences in single leaf CER, canopy radiation interception, radiation use efficiency, and increase in seed harvest index with time exist among several commonly grown peanut cultivars.

Materials and Methods

Cultural Practices

A field experiment was conducted in the summer of 1990 at the Irrigation Research and Education Park on the University of Florida Agronomy Farm at Gainesville, FL. Four peanut cultivars (Early Bunch, Florunner, Marc I, and Southern Runner) were grown in field plots on a Kendrick fine sand. Before sowing, the soil was moldboard plowed and treated with recommended rates of fenamiphos (ethyl-4-(methylthio)-m tolyl isopropylphosphor amidate) and benefin (N-butyl-N-ethyl-α-α-α-triflouro-2,6-dinitro-p-toluidine) to control nematodes and weeds, respectively. The plot area was then disked twice and leveled for sowing. Since maize had been grown on the plots for the previous 3 yr. and supplied with ample nutrients, residual fertility was deemed sufficient for the peanut crop.

On 15 May, seeds of the four cultivars were inoculated with *Bradyrhizobium* spp. and hand-sown at a depth of 7 to 8 cm into open furrows spaced 61 cm apart. Intra-row spacing was approximately 10 cm, resulting in an established plant density near 15 plants m^{-2}. Furrows were then closed and 2.0 cm of irrigation were applied to ensure germination and crop establishment. Each cultivar comprised 15, 14.5-m long rows, replicated three times in a randomized complete block design. Seedlings began cracking the soil on 21 May and emerged on 22 May. Throughout the season, all treatments were irrigated as needed to prevent water deficits using a solid-set, impact sprinkler irrigation system. Leafspot disease was controlled with 10 to 14 d applications of chlorothalonil (tetrachloroisophthalonitrile). Nevertheless, a moderate level of leafspot disease was apparent late in the growing season and some data collected during late seed filling are not presented because of the possible detrimental effects of the disease. Growth of all four cultivars was excellent and, except for the leafspot problem in late season, biotic and abiotic stresses were minimal.

Measurements

Single leaf CER. Rates of single leaf carbon exchange were measured at midday on upper, fully-expanded, sunlit (photosynthetic active radiation, PAR, > 1500 µE m^{-2} s^{-1}) leaflets using a Li-Cor 6200 Portable Photosynthesis System (Li-Cor, Inc.[3], Lincoln, NE) and a 0.25-liter assimilation chamber. Measurements began 27 days after sowing (DAS) and continued at 2-wk intervals until 141 DAS. Three leaflets of each cultivar were measured in each plot and means of the three leaflets were computed and considered as a replicate (3 replicates x 3 leaflets/replicate = 9 leaflets/cultivar on each date). Following measurement, the leaflet was excised from the plant and leaf area was determined with a Delta-T area meter (Decagon Devices, Inc., Pullman, WA).

Crop biomass accumulation. Above-ground biomass plus pods was determined for each cultivar at weekly intervals beginning 16 DAS by harvesting two, adjacent 1-m row lengths (1.22 m^2) from each replicate. A 3-plant subsample was selected from the large sample to measure separately above-ground weight, pod and seed weight. All samples were dried in a forced-air oven at 65 C for approximately 1 wk. Dry weights of the large sample (total mass from the 1.22 m^2 sample), the 3-plant sub-sample, pod sample (from the 3-plant sample), and seed sample (following hand-shelling) were measured. Seed harvest index (SHI) was computed from the 3-plant sample as the ratio of seed weight to total biomass. The estimate of seed weight per unit area was obtained by multiplying SHI by the weight per unit area of the total sample.

Leaf area was determined for one representative plant which was selected from the 3-plant subsample. Leaves were dried, and specific leaf area was determined as the ratio of leaf area to leaf weight. Leaf area index (LAI) was computed as the product of total above-ground biomass per unit area, fraction leaf, and specific leaf area.

Canopy Interception of PAR. Crop canopy interception of PAR was determined at midday on sunny days by measuring PAR above and at the soil surface below the crop canopies using a Li-Cor 191SA line quantum sensor (Li-Cor, Inc., Lincoln, NE). Weekly measurements began 21 DAS and continued until near crop maturity (140 DAS). Canopy interception of PAR was expressed as a ratio of the below-canopy to above-canopy PAR.

Computation of RUE. Radiation use efficiency was computed as the slope of the regression equation for cumulative total solar radiation intercepted vs. crop biomass. The solar radiation incident to the crops was measured at a weather station located within 100 m of the experimental site. The proportion of the incident solar radiation intercepted by each cultivar was estimated from the weekly measurements of canopy interception of PAR.

Although canopy interception of PAR may differ somewhat from interception of solar radiation, there is likely to be only a small difference between PAR and solar radiation interception in this experiment. Because of absorption spectrum of leaves, the measured fraction of interception of PAR was greater than the interception by the canopy of total solar radiation. However, this bias was offset by measuring PAR interception at midday which results in a minimum estimate of interception for the diurnal cycle. Further, both of the above factors influencing interception become susbstantially less significant as the leaf area index of the canopy increases. In this experiment, only the first three measurements were made when PAR interception was less than 0.5 (Fig. 2) and these occurred when biomass accumulation was low. Consequently, potential adjustments in intercepted PAR radiation would have virtually no influence on the computation of RUE.

Statistical analysis

All data were subjected to appropriate analysis of variance using SAS/PC version 6.03 (SAS, 1985.) and LSD (0.05) values were computed for comparison of cultivar means. Linear regression techniques were used to examine the relation of cumulative solar radiation intercepted and total crop biomass, and the change in SHI with time.

Results and Discussion

Single leaflet CER declined very early to relatively stable values over most of the growing season, ranging between 25 and 35 µmol CO$_2$ m^{-2} s^{-1}, before declining sharply during the late seed filling period (Fig. 1). The lower range of CER's observed in this study (25 µmol CO$_2$ m^{-2} s^{-1}) was similar to the maximum rates previously reported for peanut (Bhagsari and Brown, 1976a, 1976b; Henning *et al.*, 1979; Pallas, 1982; Branch and Pallas, 1984), while Trachtenberg and McCloud (1976) observed rates near our upper range for young peanut leaves exposed to high irradiance.
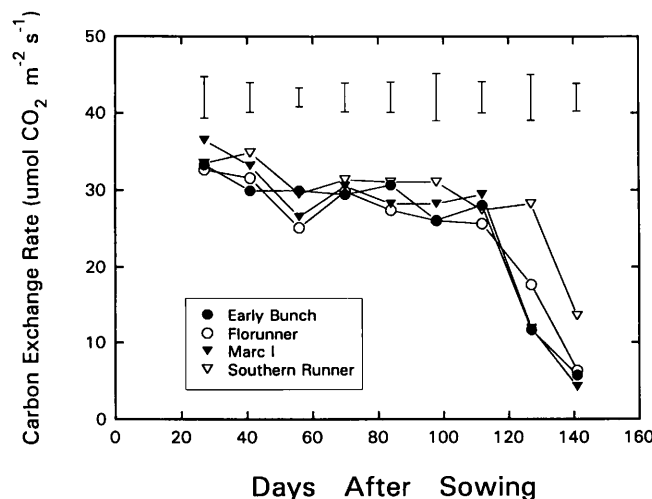

Fig. 1. Single leaflet carbon exchange rates of four peanut cultivars in response to days after sowing in 1990 at Gainesville, FL. Vertical bars above data points on each date are LSD (0.05) values for comparison of cultivar means.
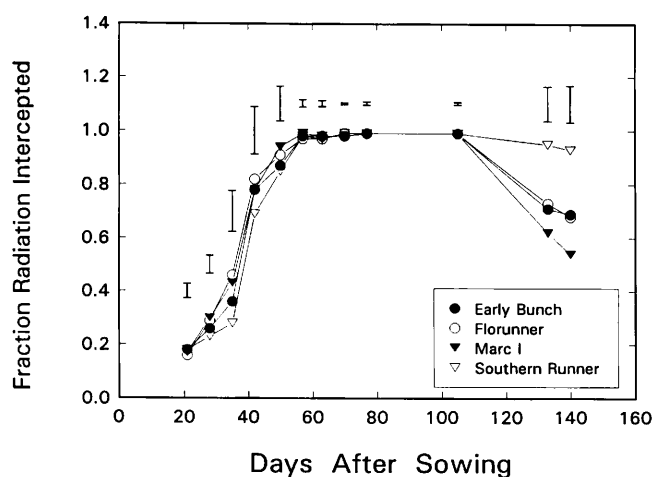
Fig. 2. Fraction photosynthetically active radiation intercepted by four peanut cultivars in response to days after sowing in 1990 at Gainesville, FL. Vertical bars above data points on each date are LSD (0.05) values for comparison of cultivar means.

Ketring *et al.* (1982) summarized data from studies of peanut CER and reported values ranging from 13 to 41 µmol CO_2 m^{-2} s^{-1}.

Carbon exchange rates were similar among all four cultivars during most of the growing season, with only minor differences in cultivars occurring as rates declined late in the season. The Duncan Multiple Range Test (p=0.05) failed to show significantly different CER for any cultivar as compared to the others on any date prior to 127 DAS. However, the later-maturing Southern Runner cultivar maintained a significantly higher CER than the other three cultivars at both 127 and 141 DAS. Although single leaf CER's have been shown to decline with crop maturity (Henning et al., 1979), the sharp decline observed in this study may have been exacerbated by the incidence of leafspot disease on the last two sampling dates. However, even the CER of the leafspot tolerant Southern Runner cultivar declined rapidly between 127 and 141 DAS, indicating that the decline may in part be due to senescence as related to crop age.

The fraction of radiation intercepted by the canopies of each cultivar increased rapidly between 21 and 57 DAS as leaf area accumulated (Fig. 2). The LAI (averaged over the four cultivars) during this same time interval increased from 0.38 to 4.2 (Ma, 1991). The leaf canopy of Southern Runner developed somewhat more slowly compared to those of the other three cultivars and resulted in slightly lower interception of radiation during the early growth period. For example, mean LAI's for Early Bunch, Florunner, and Marc I were 0.98 and 2.29 at 37 and 44 DAS, respectively, while LAI of Southern Runner was 0.66 and 2.07 on the same dates (Ma, 1991). By 57 DAS, all cultivars had LAI's near 4.0 (Ma, 1991), were intercepting more than 95% of incident radiation, and continued to intercept essentially all radiation until decline of the leaf canopy resulted in lower interception on the last two measurement dates (127 and 141 DAS). The lower fraction of radiation intercepted on those dates was, in part, likely a consequence of the incidence of leafspot disease. The later maturity and leafspot resistance of the Southern Runner cultivar resulted in greater leaf area duration and a higher fraction of radiation interception later in the season, compared to the other three cultivars.

Linear regression (using data pooled from all four cultivars) of cumulative total solar radiation intercepted vs. total crop biomass revealed a close relationship with two distinct slopes (Fig. 3). Data from all four cultivars fit the computed regressions very well, indicating almost identical responses for each cultivar. The slope of the response using radiation interception data below 790 MJ (corresponding to 72 DAS) was somewhat higher than the slope of the response above 790 MJ. Ma (1991) reported that on average these four cultivars reached the R6 (full seed) growth stage (Boote, 1982) between 72 and 76 DAS. Thus, biomass accumulation before 72 DAS was primarily vegetative material (leaves and stems), while biomass accumulated after 72 DAS was increasingly partitioned to reproductive structures (shells and seeds). The much higher metabolic costs of seed formation associated with oil and protein formation should result in a lower slope during the period when seeds are growing.
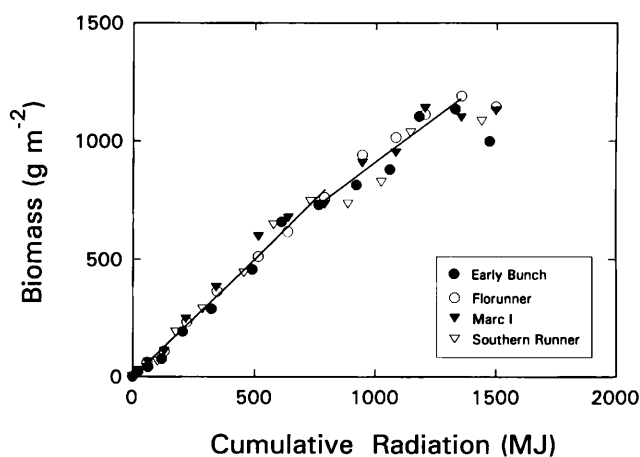

Fig. 3. The relationship of total crop biomass to cumulative intercepted solar radiation for four peanut cultivars grown in 1990 at Gainesville, FL. Linear regression equations: Y = 1.01(X) - 4.25 and Y = 0.76(X) + 150.46 for early and late season, respectively. The last four data points (>1400 MJ) were not included in the regression analysis due to incidence of leafspot disease.

To obtain an "energy equivalent" RUE across the entire season, seed weight can be adjusted to account for the increased metabolic costs associated with seed formation. Penning de Vries and van Laar (1982) concluded that 0.7 g vegetative biomass could be produced from 1 g of glucose. Similarly, Sinclair and deWit (1975) calculated that only 0.43 g of peanut seed was produced per 1 g glucose. The ratio of these parameters (1.63) is the "adjustment" by which seed mass was multiplied to obtain equivalent vegetative weights, and consequently RUE, throughout the growing season. Consequently, an adjusted total crop biomass was recomputed and the data for cumulative total solar radiation intercepted vs. energy adjusted crop biomass were plotted (Fig. 4). The relationship was linear ($r^2 \geq 0.99$) from 0 to approximately 1350 MJ of radiation intercepted.

The slopes of the regressions shown in Figs. 3 and 4 define RUE or the efficiency with which intercepted solar radiation is used to accumulate dry matter. The RUE's for the four cultivars were almost identical and means averaged over the four cultivars are given in Table 1. Using data from Fig. 3, RUE was 1.01 g MJ^{-1} before 72 DAS, and declined to 0.76 g

MJ⁻¹ between 72 and 100 DAS. After the energy adjustment was applied to account for seed composition, RUE was 1.00 g MJ⁻¹ for the entire period between 0 and 100 DAS (Table 1, Fig. 4). Following 100 DAS (>1400 MJ) there was little accumulation of biomass, maybe as a result of leafspot and/or leaf senescence, and these data were not included in the regression analyses. Radiation use efficiencies of near 1.0 g MJ⁻¹ for vegetative growth are similar to other values reported for peanut (Stirling *et al.*, 1990; Bell *et al.*, 1992; Wright *et al.*, 1992) as well as those of other C_3 crops (Kiniry *et al.*, 1989).
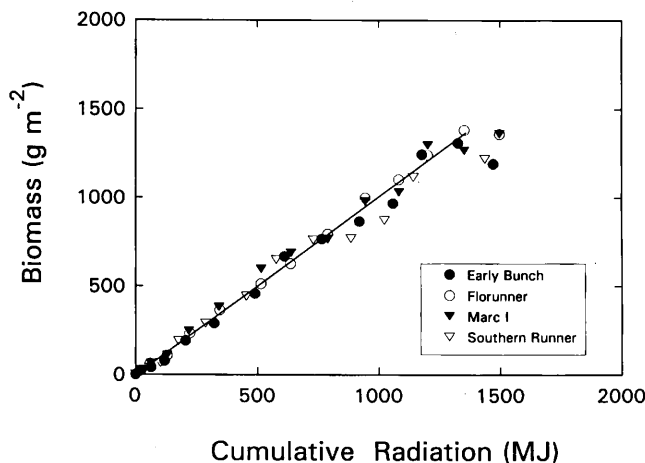

Fig. 4. The relationship of total crop biomass (corrected for metabolic costs of seed constituents) to cumulative intercepted radiation for four peanut cultivars grown in 1990 at Gainesville, FL. The last four data points (>1400 MJ) were not included in the regression analysis due to incidence of leafspot disease. Regression equation: Y = 1.00(X)-0.417.

Data presented in Figs. 2 and 3 and Table 1 indicate that under the near optimal growing conditions biomass accumulation of peanut can be estimated from measurement of the crop's interception of solar radiation. We next examined the relationship between seed biomass and harvested biomass. In other crops such as soybean (*Glycine max* L.) and maize (*Zea mays* L.), SHI has been shown to increase in a linear manner with time during the seed filling period (Spaeth and Sinclair, 1985; Muchow, 1990). Data presented

Table 1. Radiation use efficiency (RUE) averaged over four peanut cultivars for various time intervals during the 1990 growing season at Gainesville, Florida.

	Days After Sowing		
	0-72	72-100	0-100
	----------(unadjusted)[†]--------		(adjusted)[†]
RUE (g MJ⁻¹)[‡]	1.01 ± 0.02	0.76 ± 0.07	1.00 ± 0.01
r²	0.99	0.88	0.99

[†] Unadjusted or adjusted for differences in metabolic costs required for seed production.

[‡] RUE's are slopes (± standard errors) of the linear regressions shown in Fig. 3 (for 0 to 72 and 72 to 100 DAS), and Fig. 4 (for 0 to 100 DAS).
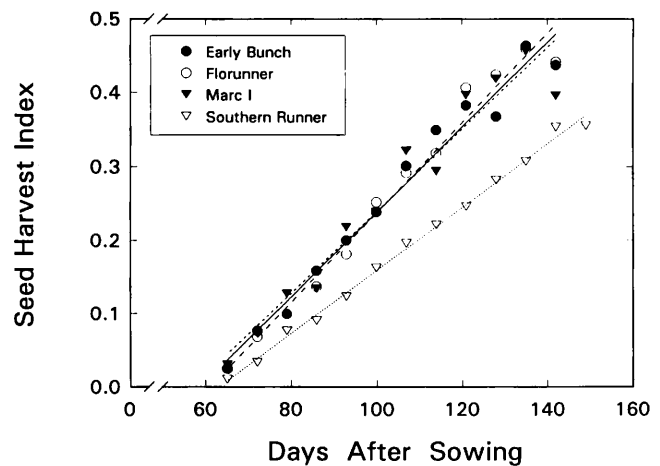

Fig. 5. Seed harvest index (ratio of seed weight to total crop biomass) for four peanut cultivars in response to days after sowing in 1990 at Gainesville FL. Regression equations: Y = 0.0057(X) - 0.3375; Y = 0.0061(X) - 0.3711; Y = 0.0056(X) - 0.3164; Y = 0.0043(X) - 0.2711 for Early Bunch, Florunner, Marc 1, and Southern Runner, respectively.

in Fig. 5 demonstrate that the increase in SHI with time (65 DAS to near maturity) was described well (r²≥0.94) with a linear function for each of the four cultivars. The slopes of the SHI increases (Table 2) were similar for Early Bunch, Florunner, and Marc I, while the later-maturing Southern Runner Cultivar demonstrated a less rapid increase in SHI. The beginning of the linear increase in SHI was 59, 60, 56, and 63 DAS for Early Bunch, Florunner, Marc 1, and Southern Runner, respectively. Even though Southern Runner exhibited a less rapid increase in SHI, crop maturity was later which resulted in a longer seed filling period (Ma, 1991). Final pod yields of the four cultivars did not differ significantly (mean of 531 g m⁻²).

In summary, results of this study suggest that single leaf CER's were relatively constant and similar among cultivars (25 to 35 μmol CO_2 m⁻² s⁻¹) throughout most of the season, before declining during late pod filling. Although radiation interception differed somewhat among cultivars during early canopy development, total crop dry matter accumulation was linearly related to cumulative radiation intercepted in all

Table 2. Rate of increase in seed harvest index (SHI) with time for four peanut cultivars grown in 1990 at Gainesville, FL.

Cultivar	Increase In SHI[†]	r²
	(d⁻¹)	
Early Bunch	0.0057 ± 0.0002	0.98
Florunner	0.0061 ± 0.0002	0.98
Marc I	0.0056 ± 0.0004	0.94
Southern Runner	0.0043 ± 0.0001	0.99

[†] Rates of increase in seed harvest index are slopes (± standard errors) of the linear regressions shown in Fig. 5.

four cultivars. The use of intercepted radiation for accumulation of crop biomass was similar among all cultivars with a mean of 1.00 g MJ^{-1}. The rate of increase in SHI was also linear with time and was similar among the Early Bunch, Florunner, and Marc I cultivars, but lower for the later-maturing Southern Runner cultivar.

We conclude that the primary differences among these four cultivars were in the early-season development of the leaf canopy and the rate of seed growth, rather than the capacity to assimilate carbon dioxide. In this study of four productive, commercially acceptable peanut cultivars differences in RUE's were not detected, but differences in the slope of the increase in SHI were clearly cultivar dependent. The excellent relationship of crop biomass to intercepted radiation and the linear increase in SHI with time, may provide an attractive and relatively simple approach for estimating seed yields of these peanut cultivars.

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