

Photosynthetic Traits of Selected Peanut Genotypes^{1, 2}

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ABSTRACT

These studies were undertaken to identify photosynthetic traits of the cultivated peanut (*Arachis hypogaea* L.) that might be used in breeding programs designed to increase yield. Net photosynthesis (Pn), CO₂ compensation point (Γ), stomatal diffusion resistance to water vapor and stomatal frequency were measured on 32 diverse genotypes. Pn was measured on 3 and 4 week old plants in a semi-closed compensating system, Γ by initial introduction of CO₂-free air and equilibration thereof, and stomatal resistance with a diffusion porometer; photorespiration and mesophyll diffusion resistance to CO₂ were calculated. At high light (1400 μE m⁻²s⁻¹ PAR) eight genotypes had Pn rates of 20 to 30, seventeen 31 to 40 and seven 41 to 43 mg CO₂ dm⁻²h⁻¹. At any given light level tested Pn rates of a given genotype were significantly different from other genotypes. Only three genotypes showed any tendency toward photosaturation at 1400 μE m⁻²s⁻¹ PAR. Photosynthetic rate and photorespiration were positively correlated ($r = 0.92$, $P < .001$). Stomatal density for the 32 genotypes averaged 168 and 154 mm⁻² on adaxial and abaxial surfaces. Neither stomatal density nor stomatal resistance to water vapor diffusion was correlated with Pn. In all instances, resistance to water vapor diffusion of the adaxial surface was less than that of the abaxial surface. Pn was negatively correlated ($r = -0.98$, $P < .001$) with mesophyll resistance which suggests that somewhere within the residual resistance system lies the reason(s) for differences in Pn amongst the genotypes tested.

Key Words: Carbon Dioxide Exchange Rate, Photorespiration, Mesophyll resistance, Leaf resistance, Stomatal resistance and density, Groundnut, *Arachis hypogaea* L.

Considerable effort is being made by crop scientists to identify photosynthetically superior genotypes for use in plant breeding. Leaf photosynthetic rates are reported to be closely related to economic yield for several crops (7, 8, 11, 13). However, high leaf photosynthetic rate does not necessarily equate with greater economic yield; there are many factors that must be considered (5). In the case of the cultivated peanut (*Arachis hypogaea* L.) it appears that measurements of leaf photosynthesis of plants grown under a controlled environment can be useful in learning more about its photosynthetic potential. It has been shown that in the field the cultivated peanut grown both in Georgia (USA) and Zimbabwe (S. Africa) had a greater daily growth rate and higher photosynthetic efficiency than rice, wheat or cotton (19). The crop growth rate of peanut cultivars has also been shown to be much higher than the crop growth rate of soybeans (4). Under growth conditions in a controlled environment (17), the net photosynthetic rate (Pn) of the cultivar NC4 (52 mg dm⁻²h⁻¹ at 1546 μE m⁻²sec⁻¹ PAR) exceeds the recorded rates of

nearly all other C₃ species somewhat similarly grown (compare with reference 5, table 1 and reference 23, table 8.1). The Pmax for individual peanut leaves has been calculated to be 77 mg dm⁻²hr⁻¹ (22). Light saturation under an artificially controlled environment as has been reported for other C₃ species did not occur with any of the nine peanut genotypes in prior tests (17). Thus, the cultivated peanut appears well suited to growth and development at least under our controlled environmental conditions.

The few Pn measurements recorded suggests that cultivated peanut genotypes may vary widely in their Pn rate (1, 17), however, no extensive study has been made. The work reported herein was undertaken to assess a wide germplasm base of the cultivated peanut for variance in photosynthetic capacity. Measurements of the CO₂ compensation point (Γ), leaf resistance to water transfer and stomatal frequency further enabled approximations of photorespiration and mesophyll resistance and their relationships to Pn to be determined.

Materials and Methods

Plant Growth: Thirty-two genotypes with wide germplasm divergence of *Arachis hypogaea* L. were kindly selected and seeds supplied by R. O. Hammons, peanut breeder, USDA, SEA-AR, Tifton, Georgia (Table 1). Seeds were germinated in damp paper toweling at 27 C. Seedlings were selected for uniformity and transplanted 4 days after sowing into 1.4-liter containers of a peat-vermiculite mix (Jiffy Mix)². The plants were grown in type 1 chambers (16) programmed for 25 C, 60% relative humidity and 350 μl CO₂ liter⁻¹ air for 14-hr photoperiods and 20 C, 90% relative humidity and 400 μl CO₂ liter⁻¹ for 10-hr nyc-toperiods. Light was provided from VHO cool-white fluorescent supplemented with incandescents giving 1.17 J cm⁻²m⁻¹ radiation at the soil surface of which 49% was infrared (340 μE m⁻²s⁻¹ PAR).

Assimilation measurements: Two representative plants were selected from a large population when they were 3 and 4 weeks old for assessments of Pn. The recently, fully expanded leaves from each plant were routinely sealed with caulking gum around the petioles into a plexiglass and metal, water-cooled assimilation chamber. Pn was first measured for a full standard day (340 μE m⁻²s⁻¹ PAR, leaf temperature 25 C, vapor pressure deficit 9 mm Hg) and then measured for several days at increasing and decreasing light intensities. The effect of varying light intensity on Pn was measured only during those hours of the day when the rates of Pn showed minimal change due to endogenous control, i.e., 0900 to 1500 (18). At any light level other than the standard 340 μE m⁻²s⁻¹ PAR the radiant energy was applied for 15-minute intervals. This was sufficient to achieve steady state Pn. Light was normally increased in at least five steps (i.e., 180 to 340, 340 to 570, 570 to 920, 920 to 1150, and 1150 to 1400 μE m⁻²s⁻¹ PAR) and then decreased in reverse order in runs both before and after noon. Light sources were the same as those previously reported (17). Pn measurements taken on each genotype minimally involved two weeks of analysis and each value of Pn in Table 1 is the average of 16 individual measurements. Pn measurements were made in a semi-compensating system (20) where air was circulated through a plexiglass and metal water-cooled leaf chamber at 25 m min⁻¹. The chamber air temperature and VPD were controlled by brining humidified air to the desired dewpoint temperature and reheating it before it entered the leaf chamber. The CO₂ content of the chamber was monitored by a model 315 NDIR Beckman infrared CO₂ analyzer and held at steady state 300 ± 2 μl CO₂ by the compensating system.

CO₂ Compensation Point (Γ) Determination: Fully expanded leaves from two plants were sealed into an assimilation chamber in the semi-closed system for individual Γ measurements. The CO₂ concentration was quickly lowered to near zero in the chamber by purging with CO₂

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²Trade names and company names are included for the benefit of the reader and do not imply preferential treatment of the product by the USDA.

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Table 1. Net photosynthesis of 3- to 4-week old peanut genotypes under various amounts of photosynthetically active radiation (400 to 700 nm). †

ID	Genotype	Light Intensity, $\mu\text{E m}^{-2}\text{s}^{-1}$					
		180	340	570	920	1150	1400
		mg CO ₂ dm ⁻² h ⁻¹					
1	Aureus	6 ^a ₁	13 ^b ₁	21 ^c _{mn}	24 ^d _{no}	27 ^e _{mn}	29 ^f _{mn}
2	Argentine	14 ^a _o	19 ^b _d	31 ^c _d	33 ^d _e	36 ^e _f	38 ^e _d
3	Comet	6 ^a _{k1}	16 ^b _h	24 ^c _{h1}	29 ^d _{h1j}	32 ^e _{h1}	34 ^f _{hg}
4	Krinkleleaf	10 ^a _e	18 ^b _d	30 ^c _d	35 ^d _{de}	38 ^e _e	42 ^f _{bc}
5	Pearl GI	8 ^a _{ghij}	16 ^b _{fgh}	23 ^c _{ij}	27 ^d _{k1}	28 ^e _{1m}	30 ^f _{1m}
6	Spancross	6 ^a ₁	14 ^b _j	23 ^c _{hi}	28 ^d _{ijk}	31 ^e _i	33 ^f _{h1j}
7	Spanhoma	6 ^a _{k1}	14 ^b _{jk}	18 ^c _o	19 ^d _q	20 ^e _{de}	21 ^e _q
8	Starr	8 ^a _{gh1}	16 ^b _{fgh}	25 ^c _{gh}	29 ^d _{gh1}	31 ^e _{h1}	32 ^e _{h1jk}
9	Tifspan	8 ^a _{gh}	17 ^b _{ef}	25 ^c _{fg}	32 ^d _e	36 ^e _f	37 ^f _{de}
10	White G. 11	7 ^a _{jk}	13 ^b _{k1}	20 ^c _m	22 ^d _{op}	26 ^e _{no}	28 ^f _{no}
11	PI 262129	8 ^a _{h1j}	16 ^b _{gn}	20 ^c _{jk1m}	22 ^d _p	24 ^e _p	25 ^f _p
12	PI 268704	6 ^a ₁	14 ^b _{jk}	21 ^c _{jk1m}	27 ^d _{ef}	29 ^e _{jk}	31 ^f _{k1}
13	Wh. Manyema PI 270773	9 ^a _g	16 ^b _{gh}	27 ^c _{ef}	34 ^d _e	38 ^e _e	41 ^f _c
14	PI 288160	8 ^a _{h1j}	17 ^b _f	21 ^c _{jk1}	23 ^d _{nop}	25 ^e _{op}	26 ^f _o
15	PI 290569	5 ^a _m	13 ^b _{k1}	20 ^c _{mn}	26 ^d _{1m}	29 ^e _{k1}	31 ^f _{k1}
16	PI 299747 Tarapota	5 ^a _m	15 ^b _{ij}	21 ^c _{k1m}	24 ^d _{no}	26 ^e _{no}	28 ^f _{no}
17	Early Runner	14 ^a _{bc}	23 ^b _{ab}	32 ^c _{bc}	35 ^d _{de}	38 ^e _e	39 ^f _{cd}
18	UF334A-B-14	6 ^a ₁	13 ^b ₁	22 ^c _{ijk}	27 ^d _{jk}	31 ^e _{ij}	32 ^f _{ijk}
19	Florigiant	17 ^a _a	23 ^b _{ab}	33 ^c _{ab}	38 ^d _{ab}	41 ^e _{ab}	43 ^f _{ab}
20	Florunner	17 ^a _a	21 ^b _{bc}	32 ^c _{ab}	38 ^d _{ab}	41 ^e _{ab}	43 ^f _{ab}
21	Tifton 8	12 ^a _d	20 ^b _i	28 ^c _e	31 ^d _{fg}	32 ^e _{gh}	34 ^f _{hg}
22	Virginia Bunch 67	6 ^a _{k1}	14 ^b _j	22 ^c _{ijk}	28 ^d _{ij}	31 ^e _{h1}	33 ^f _{gh1}
23	UF 393-7-1	14 ^a _{bc}	22 ^b _{bc}	31 ^c _{cd}	37 ^d _c	40 ^e _{bcd}	42 ^f _c
24	Cook Jumbo (T-1632)	7 ^a _{h1j}	14 ^b _{jk}	21 ^c _{k1m}	28 ^d _{jk}	31 ^e _j	33 ^f _{gh1}
25	Japan Jumbo	10 ^a _e	17 ^b _{efg}	26 ^c _{ef}	35 ^d _{de}	39 ^e _{de}	42 ^f _{bc}
26	Jenkins Jumbo	10 ^a _e	17 ^b _e	28 ^c _e	35 ^d _{cd}	40 ^e _{bcd}	42 ^f _{bc}
27	Korean Jumbo	6 ^a _{k1}	13 ^b ₁	19 ^c _{no}	25 ^d _{mn}	28 ^e _{k1m}	32 ^f _{ijk}
28	Macrocarpa PI 161430	9 ^a _f	17 ^b _{ef}	24 ^c _{gh1}	30 ^d _{hg}	34 ^e _g	37 ^f _{de}
29	Macrocarpa (T-1648)	7 ^a _{jk}	13 ^b ₁	18 ^c _o	24 ^d _{nmo}	28 ^e _{1m}	31 ^f _{jk}
30	Nhambiquara Prp/W PI 263391	6 ^a ₁	15 ^b _j	23 ^c _{hi}	29 ^d _{gh1}	34 ^e _g	36 ^f _{ef}
31	Nhambiquara R/W	6 ^a _{k1}	14 ^b _j	21 ^c _{k1m}	27 ^d _j	31 ^e _{h1}	35 ^f _{fg}
32	Nhambiquara Prp/H PI 221068	7 ^a _{ijk}	14 ^b _j	21 ^c _{jk1m}	25 ^d _{mno}	27 ^e _{nm}	28 ^f _{nm}

*Means within each column followed by the same subscript letter and means within each row followed by the same superscript letter are not significantly different at the 1% probability level as determined by Duncan's Multiple Range Test.

†Each value of P_n is the average of 16 individual 15-minute measurements.

free air and then equilibration of CO₂ between the leaves and chamber air was allowed to estimate Γ . Preliminary studies showed no change in Γ by varying the light intensity. Light intensity was routinely 340 $\mu\text{E m}^{-2}\text{s}^{-1}$, leaf temperature 25 C and vapor pressure deficit 9 mm Hg. An estimation of photorespiration for each genotype at 340 $\mu\text{E m}^{-2}\text{s}^{-1}$ was derived by extrapolating from the rate of apparent photosynthesis at 300 $\mu\text{l CO}_2 \text{ l}^{-1}$ air and Γ concentration. The estimate of photorespiration (Y intercept) was used to further estimate total leaf resistance (R_1) to CO₂ (2):

$$R_1 = \frac{\Gamma}{\text{Y intercept}} = 0.648.$$

Stomatal Frequency and Diffusion Resistance: Diffusive resistances to water vapor [boundary (r_a) + (r_s)] of the adaxial and abaxial surfaces of recently fully expanded leaves were measured on populations of 3-, 4-, and 5-week-old plants. Measurements reported were taken during mid-day under standard growing conditions with a Lambda diffusion porometer (Model 65) calibrated according to Kanemasu, *et al.* (10). They were taken in a random manner from abaxial and adaxial surfaces. CO₂ control in the plant growth chambers was aided by face masks expelling expired air.

The reciprocal of the diffusive resistance of a leaf to CO₂ was determined by summing the reciprocals of measurements from the adaxial and abaxial epidermis and multiplying by 1.605 (8) to convert to CO₂ resistance. The mesophyll resistance (r_m) to CO₂ for each genotype was estimated from the relationship $R_1 = r_a + r_s + r_m$. Stomatal frequency

was assessed by the silicon rubber method (21) and leaf area was measured with a Lambda portable area meter (Model LI-3000). Stomatal impressions of both the adaxial and abaxial surface of four different fully expanded leaves from different plants were taken from the 32 genotypes. Several fields from each impression were individually measured and counted at approximately 100 X.

Results and Discussion

In all 32 genotypes an endogenous rhythm in P_n was found as previously reported (18). Table 1 indicates the diversity in the photosynthetic rate of the 32 genotypes tested. In some instances P_n rates were twofold higher than those of other cultivars. All P_n rates were found to be significantly different amongst genotypes at similar light levels. In most all instances a statistically significant lack of photosaturation was evident at 1400 $\mu\text{E m}^{-2}\text{s}^{-1}$. The leaves of the peanut genotypes grown under our fluorescent incandescent lighting system were not light saturated in their photosynthetic rate at low light intensities as has been found for soybeans, a point of importance. Γ of a given genotype remained constant over all light levels. A high correlation by the least squares method of regression analysis ($r = 0.92$, $P = <.001$) was found between the estimates of photorespiration and photosynthetic rate (Fig. 1). This finding is similar to that recently published by McCaskin and Canvin (12) and is in accord with evidence that carboxylase and oxygenase functions appear on the same enzyme (14). Although probably a very conservative estimate, at least 15 - 20% of total photosynthesis in the lines was photorespired.

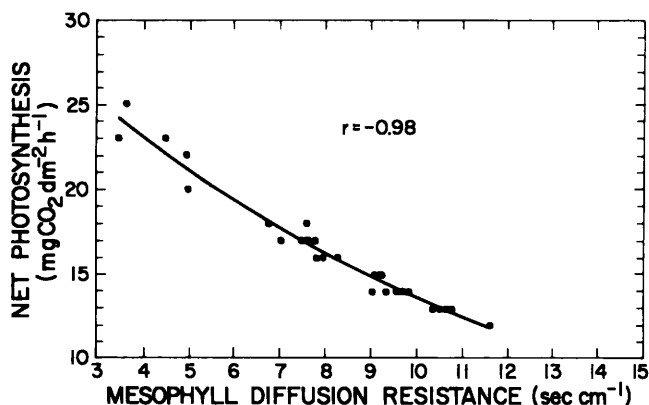


Fig. 1. Relationship of net photosynthesis of peanut to photorespiration at 25 C, vapor pressure deficit 9 mm Hg and 340 $\mu\text{E m}^{-2}\text{s}^{-1}$ as determined by regression analysis by the method of least squares fit and described by curve type $Y = A + \frac{B}{X}$.

Stomatal density (Table 2) was very nearly the same for all 32 genotypes and compared favorably with the few values recorded in the literature (1, 15). One entry, White Manyema PI 270773 (ID #13), had an unusually high number of stomata per mm². For a few lines a higher stomatal density seemed to be associated with small leaflets. Regression analyses showed no correlation between P_n and stomatal frequency; nor was a correlation found between P_n and boundary layer and stomatal resistance to CO₂. It is therefore assumed that the boundary layer and stomatal resistances were not of significance in causing the differences in P_n between genotypes. In all instances the resistances of the adaxial surface was less

than the resistance of the abaxial surface to water vapor movement, verifying corollary studies (15). On the other hand mesophyll resistance (r_m) evidently was very significant in determining photosynthesis (Fig. 2). This is demonstrated both in a high negative correlation of Pn with

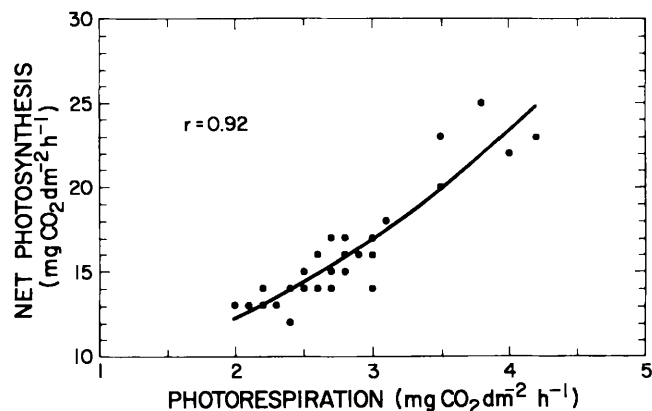


Fig. 2. Relationship of net photosynthesis of peanut to mesophyll diffusion resistance to CO_2 at 25 C, vapor pressure deficit 9 mm Hg and $340 \mu\text{E m}^{-2}\text{s}^{-1}$ as determined by regression analysis by the method of least squares fit and described by curve type $Y = A^{bx}$.

r_m ($r = -0.98$, $P < .001$) as well as a negative correlation of Pn with total leaf resistance ($r = -0.98$, $P < .001$). The resistance of the mesophyll or so called liquid phase is nearly tenfold higher in peanut than the resistance of the boundary layer and stomata to CO_2 transfer and is similar to findings on soybean (6). It appears that peanut photosynthesis is limited more by mesophyll resistance than by photorespiration as may frequently be the case for crop plants (3). The transfer of CO_2 through the liquid phase (which includes physical and biochemical resistance to CO_2 transfer and fixation) is a complex process involving movement through the cell wall, various membranes and cytoplasm and finally carboxylation in the chloroplast by RuBP carboxylase. It is most probable then that differences in photosynthetic rate among peanut genotypes is associated with (i) enzymatic activities, (ii) resistance to CO_2 transfer from the substomatal chamber to the reaction site in the chloroplasts or (iii) efficiency of light utilization. These possibilities are being further studied in our laboratory. The assessment of net photosynthesis of cultivars that are presently important commercially (e.g., Florigiant ID #19 and Florunner ID#20) indicate that they also have the highest Pn of the genotypes studied. This suggests that with present genetic development of runner and virginia market types a rather high photosynthetic potential is being introduced. Interestingly, however, none of the genotypes tested in these studies had a Pn rate as high as our previous report for NC4 (17). NC4 would appear to be an excellent source for incorporating high photosynthetic potential into peanut lines. Pn rates were much lower for the subspecies *fastigiata* market type spanish (ID #1-15). It should be worthwhile to breed into future spanish lines a higher photosynthetic potential. Again these studies as did earlier ones (17) attest to the uniqueness of the peanut to photosynthesize as factored primarily by incident light intensity; this trait probably enables it to respond photosynthetically in a most optimum manner under changing light conditions in

humid or semi-humid regions providing adaptability and high yield potential.

Table 2. Stomatal density, leaflet area, number of stomata per leaflet and resistance to water vapor diffusion for fully expanded leaves of 32 peanut genotypes 3 weeks of age.

ID	Stomatal density		Leaflet area	Stomata/Leaflet		$r_a + r_s$ Resistance	
	Adaxial	Abaxial		Adaxial	Abaxial	Adaxial	Abaxial
	stomata mm^{-2}		cm^2	$\times 10^5$		s cm^{-1}	
1	181	174	13.4	2.42	2.32	2	5
2	172	183	14.1	2.43	2.58	3	6
3	179	174	12.8	2.28	2.22	2	5
4	175	146	12.3	2.12	1.79	3	6
5	176	158	14.0	2.47	2.22	2	7
6	184	168	13.0	2.38	2.18	2	7
7	174	171	10.9	1.89	1.86	3	5
8	162	153	13.1	2.13	2.00	2	5
9	157	171	15.4	2.42	2.63	2	5
10	150	153	11.8	1.77	1.81	2	6
11	152	153	11.5	1.75	1.76	3	9
12	155	154	11.7	1.80	1.80	2	5
13	245	220	8.4	2.05	1.85	2	7
14	150	146	11.6	1.74	1.70	3	4
15	186	177	12.1	2.24	2.14	2	5
16	139	99	10.3	1.42	1.02	2	7
17	160	148	12.5	2.01	1.85	3	6
18	196	170	8.3	1.64	1.41	2	3
19	155	139	11.1	1.71	1.53	3	4
20	169	155	11.9	2.01	1.84	3	5
21	158	128	13.5	2.13	1.73	2	5
22	149	142	19.0	2.84	2.70	3	5
23	181	176	9.5	1.72	1.67	2	6
24	159	152	9.8	1.55	1.47	4	9
25	166	138	13.8	2.30	1.90	3	5
26	145	137	12.9	1.87	1.77	3	5
27	153	140	10.7	1.65	1.50	3	8
28	155	129	11.8	1.83	1.53	2	5
29	167	135	13.4	2.25	1.80	2	6
30	161	145	13.6	2.20	1.97	3	5
31	196	144	8.7	1.70	1.25	2	5
32	162	138	16.2	2.62	2.32	2	5

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