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Photosynthesis in Peanut (**Arachis**) Genotypes[1]

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ABSTRACT

Research was undertaken to assess the variation in photosynthetic capacity within the genus **Arachis** and to determine associations between photosynthesis and other leaf characteristics. Photosynthetic rates of attached leaves of thirty-one peanut genotypes, including six wild (**Arachis** L.) species and twenty-four genotypes of the cultivated species, **Arachis hypogaea** L., were measured by gas exchange. Genotypes of **A. hypogaea** showed a range in photosynthetic rates from 24 to 37 mg CO_2 dm^{-2} hr^{-1}. Florunner, a recently developed US cultivar, consistently had higher photosynthetic rates than most other peanut genotypes. The rates were approximately 41 and 30 mg CO_2 dm^{-2} hr^{-1} in two pot experiments and a field test, respectively. Wild species had generally lower photosynthetic rates than did **A. hypogaea. A. pintoi** Krap. et Greg. had the lowest rate of photosynthesis and the lowest specific leaf weight in the three experiments. Photosynthetic rate was positively correlated, though weakly, with percent nitrogen and chlorophyll content of leaves in two out of three experiments. Specific leaf weight was positively correlated with photosynthesis in only one out of three experiments. Stomatal frequency and photosynthetic rates were negatively correlated. The relationship between photosynthesis and leaf characteristics is discussed.

Key words: **Arachis hypogaea,** Specific leaf weight, Leaf characteristics, Chlorophyll, Stomatal frequency, Groundnuts.

During the last decade, variations in photosynthetic rates of major food and grain (4,6,7,9,14,19), fiber (8), and forage (26) crops have been documented. Variation in photosynthetic capacity of soybean (*Glycine max* L.) has been related to mesophyll and stomatal resistance and ribulose-1, 5-diphosphate carboxylase activity (6,3). Differences in photosynthesis of several species were related to photosynthate translocation rates (17). In maize (*Zea mays* L.), dwarf bean (*Phaseolus vulgaris* L.) and willow (*Salix viminalis*) both RUDP carboxylase activity and physical resistance to CO_2 diffusion in the leaf have been implicated in photosynthetc variation (28). Chlorophyll concentration was found to be associated with photosynthetic rate at low light intensity in experiments by Gabrielsen (11) but in other studies has been found not to be correlated with photosynthesis (22). Specific leaf weight (SLW) and photosynthetic rates in alfalfa (*Medicago sativa* L.) (26) and soybean cultivars (6) have been found to be positively correlated. Photosynthesis was not related to the number and arrangement of stomata in a large number of plant species, including maize and sugarcane (*Saccharum officinarum* L.) (16). There was no control of photosynthesis by stomatal resistance in sugarcane (20) nor was there any correlation between photosynthetic rate and stomatal number, stomatal length or leaf density thickness (19). Others have observed that cultivars of *Phaseolus vulgaris* L. (21) and maize (15) with lower stomatal frequency had higher photosynthetic rates. The present investigation was undertaken to establish whether variation in rates of photosynthesis occurs among genotypes of cultivated peanut (*Arachis hypogaea* L.) and wild *Arachis* species and to relate the variations, if any, in photosynthetic rates to leaf characteristics.

Materials and Methods

Thirty-one peanut genotypes were used in this study. They represent twenty major peanut growing countries and areas in South America where **A. hypogaea** and wild **Arachis** species are endemic. Seeds were obtained from the Southern Regional Plant Introduction Station, ARS, USDA, Experiment, Georgia. The wild species selected for study were **A. duranensis** Krap. et Greg. (unpubl.), **A. villosa** Benth., **A. monticola** Krap. et Rig., **A. villosulicarpa** Hoehne, **A. pintoi** Krap. et Greg. (unpubl.) and **A. sp.** glabrata?, cv. Arb).

Plants were grown outdoors in 19 liter pots in 1971 and 1972. Seeds of each genotype were planted in two pots in 1971 and in one in 1972. Plants were thinned to four per pot and were supplied with Hoagland's solution weekly. Plants were also grown at approximately 1 meter spacing in two replications in the field during 1972. Before planting, an application of 34 kg of N, 32 kg of P, and 28 kg of K per ha was made. The soil used in all three experiments was an Appling sandy loam.

Seeds for the two pot experiments were planted during the first week of June each year. The field experiment was planted on May 19. Plants in pots were watered once daily in early stages of growth and twice daily in later stages. Field grown plants were watered with sprinkler irrigation 5 times during the growing season to supplement rainfall.

Measurements of net photosynthesis (Pn) and other leaf characteristics for both experiments were made during late July and up to August 20. The rates of Pn of attached, fully expanded leaves were measured by differential infrared gas analysis of CO_2. In 1971, the youngest fully expanded leaf on a given branch was enclosed in a plexiglass chamber composed of two halves which were clamped together. The lower half was water-cooled to help control air and leaf temperature. Leaf temperature was maintained at 30 ± 1 C and was measured by a thermocouple pressed against the underside of the leaf. A nylon thread wound on the upper and lower halves of the chamber positioned the leaf midway between the walls of the chamber. The light intensity was 32 klux at the leaf surface and was measured with a Weston Model 756 illumination meter. Light was provided by three 300 watt incandescent lamps immersed in water. The water bathing the lamps was approximately 10 cm deep under the

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lamps providing an infrared filter.

During 1972, all the Pn measurements were made in sunlight from 70 to 100 klux. Pn was measured between 8 a.m. and 6 p.m. depending upon the weather conditions. The chamber used in Pn determinations was made after the air seal principle and specifications of Wolf et al. (30) with some modifications. The leaf temperature was 30 ± 3 C. The CO_2 concentration in air passed over the leaf surface varied between 320 and 360 ppm. The reference and sample air streams were passed through drying colums of $CaSO_4$ before entering the infrared gas analyser. Measurements of Pn were made on leaves of similar age to that used in the 1971 experiment.

Nitrogen and chlorophyll concentrations were determined on leaves on which Pn was measured. Leaf nitrogen estimations were made by the Micro-Kjehdahl method. Chlorophyll determinations were made according to Arnon's technique (1). Leaf samples were combined for chlorophyll and nitrogen analysis to provide sufficient tissue. Leaf area was measured with a polar planimeter in 1971. In 1972, leaf boundaries were drawn on paper and the outlined areas were subsequently measured with the planimeter. Stomatal counts were made in 1972 from leaf impressions made with Rhoplex silicon rubber material as suggested by Horanic and Gardener (18). Counts were made on upper and lower leaf surface impressions by making counts in three microscope fields of view on one leaf per genotype.

Results

The rates of Pn of various peanut genotypes along with data pertaining to leaf characteristics for 1971 are presented in Table 1. Statistically significant differences were found in the Pn rates, chlorophyll concentration, percent leaf nitrogen and specific leaf weight (SLW) among the peanut genotypes. The range in Pn of *A. hypogaea* was from 29 to 41 mg CO_2 dm^{-2} hr^{-1} for a genotype from Turkey (P.I. No. 169294) and for Florunner, a US cultivar, respectively. Among the wild species, the two genotypes of *A. monticola* had significantly higher Pn rates than *A. pintoi*.

Table 1. Net photosynthesis† and leaf characteristics† of peanut (Arachis) genotypes, 1971.

Cultivar or P.I. number	Species	Pn	Chl	%N	SLW
Florunner	A. hypogaea	41	5.3	4.5	5.9
Florigiant	"	40	5.8	4.6	5.5
Starr	"	38	4.7	3.7	5.5
288914	"	38	4.3	3.8	6.7
196734	"	37	4.0	3.7	5.9
158839	"	37	4.0	3.3	5.5
239039	"	36	4.1	3.1	5.9
230328	"	36	3.6	3.5	5.5
314817	"	35	4.1	3.2	4.5
290570	"	35	4.9	4.0	5.3
207530	"	35	4.6	3.5	5.5
162861	"	35	4.9	3.9	5.9
145681	"	35	4.4	3.4	5.0
138870	"	35	4.5	3.4	5.5
261977	"	34	3.9	3.4	6.2
259636	"	34	4.5	3.4	5.3
234419	"	34	4.2	3.2	5.9
117846	"	34	3.7	3.0	6.2
314980	"	33	3.6	2.8	5.9
149268	"	33	4.9	4.1	5.5
119240	"	33	3.3	3.0	6.7
279618	"	32	5.3	3.8	5.9
161897	"	31	4.4	3.2	4.2
169294	"	29	3.9	3.0	5.9
Mean	"	35	4.4	3.5	5.5
263393	A. monticola	33	5.3	4.0	5.5
210553	A. monticola	33	5.1	3.7	4.0
118457	A. sp. (glabrata?)	31	2.6	2.3	8.3
210555	A. villosa	29	4.8	3.0	5.0
263396	A. villosulicarpa	28	3.2	2.4	5.0
219823	A. duranensis	27	4.6	3.4	4.0
338314	A. pintoi	22	3.0	3.3	3.4
Mean Wild Species		29	4.1	3.2	4.8
No. of observations per genotype		7	2	2	6
Overall standard error‡		2.5	0.1	0.1	0.53
		**	**	**	**

** Significant differences occurred among genotypes at the .01 probability level.

† Units for measurements are as follows: Net photosynthesis (Pn)-mgCO_2dm^{-2}hr^{-1}; Chlorophyll (Chl)-mg g^{-1} dry weight; Nitrogen (%N)-% of dry matter; Specific leaf weight (SLW)-mg dry weight cm^{-2}.

‡ Standard error used for calculating Duncan's multiple range values.

Florigiant, a US cultivar, had significantly higher chlorophyll concentration (5.8 mg/g dry wt) than other peanut genotypes (Table 1). The percent leaf nitrogen of the genotypes varied from 2.3 to 4.6. Florigiant and Florunner had significantly higher percent leaf nitrogen (4.6 and 4.5%, respectively) than all the other genotypes. *A. pintoi* had significantly lower SLW than most of the other genotypes. *A. sp.* (glabrata?) had the highest SLW ie, 8.3 mg cm^{-2}.

Table 2 shows Pn rates and other leaf characteristics for peanut genotypes in 1972. Florunner again had the highest Pn rates of 41 and 30 mg CO_2 dm^{-2} hr^{-1} in the pot and field experiments, respectively, though not significantly different from all the other genotypes. *A. pintoi* and *A. villosulicarpa* had the lowest Pn during 1972. The overall average rate of Pn of the genotypes was lower in the 1972 field and pot experiments as compared with the 1971 experiment. Few genotypes had as high Pn rates in 1972 as in 1971. The 1972 pot experiment average for cultivated genotypes was 27 mg dm^{-2} hr^{-1} compared to 35 mg dm^{-2} hr^{-1} for the 1971 experiment. We have no explanation for the lower rates in 1972.

Chlorophyll concentration of the peanut genotypes varied from 4.0 to 6.2 and 4.0 to 7.2 mg gm^{-1} of dry matter in the field and pot experiments, respectively, in 1972. The average percent nitrogen in the leaves was 3.3 and 3.6 for the pot and the field experiments, respectively. *A. pintoi* had significantly lower SLW than most of the other genotypes in 1972 field experiment. There were no significant differences in SLW in the 1972 pot experiment.

Wide variations in the stomatal numbers (upper and lower surfaces combined) per unit leaf area were recorded among the peanut genotypes. *A. villosulicarpa* had higher stomatal frequency (848 and 770 mm^{-2} in the pot and field experiments, respectively) than other genotypes in the experiments of 1972. Stomatal frequency was greater in the wild species than *A. hypogaea*, except that *A. monticola* had a frequency similar to cultivated genotypes. Spaced plants in the field had fewer stomata per unit leaf area (371 mm^{-2}) as compared with pot grown plants (399 mm^{-2}). These stomatal frequencies are similar to those reported recently for 474 cultivated peanut genotypes (23).

The correlations between Pn rates and leaf characteristics of peanut genotypes are shown in Table 3. There was a positive correlation between chlorophyll and Pn and between percent leaf nitrogen and Pn in two out of the three experi-

Table 2. Net photosynthesis† and leaf characteristics† of peanut (Arachis) genotypes, 1972.

Cultivar or P.I. number	Species	Pot experiment Pn	Chl	%N	SLW	Stomatal no.	Field experiment Pn	Chl	%N	SLW	Stomatal no.
Florunner	A. hypogaea	41	6.7	3.7	5.9	296	30	5.6	3.5	6.7	298
Florigiant	"	27	5.4	2.8	5.3	391	27	5.3	3.4	6.2	315
Starr	"	22	5.1	3.2	6.2	406	23	5.4	3.5	6.2	319
288914	"	21	5.0	3.2	6.7	321	22	5.6	3.6	5.9	393
196734	"	22	4.0	2.8	5.9	412	27	5.5	3.5	5.5	437
158839	"	20	5.8	3.3	6.2	414	28	5.7	3.9	5.5	319
239039	"	27	6.1	3.4	5.9	422	20	6.0	3.7	5.9	329
230329	"	25	5.0	3.0	5.5	334	26	5.4	3.4	5.9	300
314817	"	26	5.1	3.6	6.2	435	18	6.0	3.6	5.9	313
290570	"	27	6.5	3.6	5.3	397	28	5.6	3.2	7.1	327
207530	"	30	6.3	3.8	5.9	393	25	5.7	3.8	5.9	361
162861	"	35	6.0	3.7	5.5	342	20	5.6	3.5	6.7	296
145681	"	24	5.5	3.6	5.9	342	24	6.0	4.5	5.0	304
138870	"	29	5.8	3.5	6.7	427	19	5.3	3.7	6.2	308
261977	"	30	5.8	3.5	5.5	387	20	5.5	3.8	5.0	338
259636	"	26	5.7	3.7	6.7	380	18	5.2	3.6	6.2	310
234419	"	23	4.8	3.2	5.9	270	18	5.4	3.3	5.9	315
117846	"	28	5.5	3.3	5.9	291	19	5.3	3.3	5.5	319
314980	"	25	5.4	3.0	5.5	236	23	5.0	3.2	5.9	319
149268	"	36	5.2	3.2	6.2	359	24	6.2	3.9	5.5	370
119240	"	36	5.5	3.9	5.3	321	21	5.2	3.5	5.9	323
279618	"	23	7.2	3.9	5.5	391	25	5.9	3.7	5.9	332
161897	"	25	4.3	3.4	7.1	365	21	5.2	3.5	6.7	389
169294	"	21	5.9	3.6	5.0	338	23	5.0	3.2	5.9	298
Mean	"	27	5.6	3.4	5.9	361	23	5.5	3.6	5.9	330
263393	A. monticola	25	6.4	3.6	5.0	338	26	5.3	3.9	6.7	336
210553	A. monticola	26	6.7	3.6	4.5	374	23	4.9	3.6	6.2	323
118457	A. sp. (glabrata?)	20	4.7	3.3	6.7	471	17	4.8	3.2	9.1	503
210555	A. villosa	20	4.9	2.6	5.9	613	22	6.2	4.0	6.7	566
263396	A. villosulicarpa	16	5.9	3.5	5.3	848	16	5.2	3.6	6.2	770
219823	A. duranensis	25	5.2	2.4	4.5	568	20	4.5	3.2	7.1	520
338314	A. pintoi	12	5.0	3.0	4.2	500	11	4.0	3.7	4.5	554
Mean Wild Species		21	5.5	3.1	5.0	530	19	5.0	3.6	6.7	510
No. observations per genotype		3	1	1	3	3‡	12	2	2	12	3‡
Overall standard error§		4.0 **	-	-	0.55	-	3.0 *	0.3 **	0.2 *	0.35 **	-

* Significant differences occurred among genotypes at the .05 probability level.

** Significant differences occurred among genotypes at the .01 probability level.

† Units for measurements are as follows: Pn - mg CO_2 dm^{-2} leaf area hr^{-1}; Chlorophyll (Chl) - mg g^{-1} dry weight; Nitrogen (%N) - % of dry weight; Specific leaf weight (SLW) - mg dry weight cm^{-2}; Stomatal number - mm^{-2}.

‡ Three counts were made on 1 leaf per genotype.

§ Standard used for calculating Duncan's multiple range values.

ments. SLW showed a significant positive correlation with photosynthesis in the 1971 experiment, but not in 1972. Stomatal numbers and photosynthetic rates were negatively correlated in the 1972 experiments.

Table 3. Correlations (r) of photosynthesis and leaf characteristics of peanut (Arachis) genotypes.

Correlations	1971 pot exp.	1972 pot exp.	1972 field exp.
1. Chlorophyll versus photosynthetic rate	+0.425*	+0.321	+0.432*
2. % leaf nitrogen versus photosynthetic rate	+0.531*	+0.374*	+0.083
3. SLW versus photosynthetic rate	+0.593**	+0.211	+0.170
4. Stomatal numbers versus photosynthetic rate	---	-0.483**	-0.425*

* Significant at .05 probability level

** Significant at .01 probability level

Discussion

Statistically significant positive correlations, though weak, existed between chlorophyll concentration and Pn and between percentage N and Pn of peanut leaves. The low coefficients for correlations between these two characteristics and Pn indicate that neither was strongly influencing photosynthesis in peanut genotypes. SLW and Pn of peanut genotypes were not highly correlated; in the 1972 experiments they were not correlated at all. SLW has been found to be correlated with Pn of soybean (6), oats (*Avena* spp.) (4) and alfalfa (26). In the experiments reported in this paper SLW was determined at the time Pn was measured, which means leaves were collected from 9 a.m. to 6 p.m. and diurnal fluctuations in SLW probably reduced the correlation with Pn.

Pn was not increased by large numbers of stomata on peanut leaves. In the 1972 experiments a negative correlation existed between Pn rates and stomatal frequency per unit leaf area. This

correlation was due mostly to the lower Pn and higher stomatal frequency of wild species, other than *A. monticola,* compared to *A. hypogaea.* Among genotypes of *A. hypogaea* and *A. monticola* there appeared to be no relationship between Pn and stomatal frequency. Inverse relationships between stomatal frequency and Pn rates were observed for *Phaseolus vulgaris* L. (21) and maize (15). In sugarcane, no correlation between Pn and stomatal number was found (19). Miskin et al. (24) reported that 25% reduction in stomatal frequency in barley (*Hordeum vulgare* L.) resulted in a 24% decrease in the rate of transpiration without affecting the rate of Pn. Therefore, it appears from our data and data in the literature that Pn, particularly under favorable environmental conditions, is not limited by stomatal number.

The effect of ploidy level on Pn is inconsistent in this study as well as in some others. The cultivated genotypes of *A. hypogaea* are tetraploids and have higher photosynthetic rates as compared with most of the wild species. *A. monticola* and *A. sp.* (glabrata?), however, are both wild tetraploids. The former had a high Pn rate, similar to cultivated genotypes, whereas the latter had a low rate of Pn. The other wild species used in our experiments were diploids. Photosynthetic capacity in artificially produced tetraploids of *Brassica oleracea* var. gongylodes was higher at high light intensities as compared with diploids but the reverse was true under low light conditions (9). The Pn rates of barley (*Hordeum vulgare* L.) (2), wheat (7,9), and *Datura stramonium* (L) (5), however, were higher in diploids than at higher ploidy levels.

The smilarity between *A. monticola* and *A. hypogaea* in most of the leaf characteristics studied may stem from their close genetic relationship. These two species belong to the Amphiploides series of the Axonomorphae section of *Arachis* (12). *A. duranensis* and *A. villosa* also belong to the Axonomorphae section, but to the Annuae and Perennes series, respectively. Other wild species in these experiments are less closely related to *A. hypogaea. A. monticola* and *A. hypogaea* are both tetraploids and crosses between the two result in fertile progeny. One recently released cultivar was developed from a cross between *A. hypogaea* and *A. monticola* (13,25).

Genotypes of *A. hypogaea* showed variation in Pn from 24 to 37 mg CO_2 dm^{-2} hr^{-1}. The wild genotypes had a greater relative variation in their rates of Pn but with decreased lower and upper limits compared to *A. hypogaea* (15-28 mg CO_2 dm^{-2} hr^{-1}. The wild species also had fewer and smaller pods and consequently low total weight of pods. This reduced yield of pods may mean that sink size was less and if so reduced sink size for photosynthate of the wild species could have been partly responsible for the decreased Pn.

Differences in Pn rates of genotypes and their association with leaf characteristics in these experiments are similar to observations by various authors (6, 14, 19). The correlations existing between photosynthesis and leaf characteristics in peanut genotypes were not strong; however, the possibility of selection for higher photosynthetic rates in *A. hypogaea* exists, as indicated by the variation in photosynthetic rates. Only three cultivars developed in the United States were used in this experiment, Florigiant, Florunner and Starr. Florunner, a high yielding cultivar, had the highest photosynthesis rate of all the cultivars tested. This indicates a selection, although indirectly, for high photosynthetic capacity in present breeding programs.

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