Relationship of Net Photosynthesis to Carbon Dioxide Concentration and Leaf Characteristics in Selected Peanut (**Arachis**) Genotypes[1]

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ABSTRACT

Five genotypes, including two cultivars of **Arachis hypogaea** L. and three wild species of **Arachis,** were tested for their photosynthetic capacity at atmospheric CO_2 concentrations and for photorespiration in CO_2-free air. Photosynthetic response to CO_2 concentrations in the range of 50 to 600 ppm was also tested. Diffusive resistance (DR_{H_2O}) of the adaxial surface of the five genotypes was measured with a diffusive resistance porometer. Several other leaf characteristics related to CO_2 exchange were measured.

There was a linear increase in net photosynthesis (Pn) for four of the five genotypes as CO_2 concentration was increased from 50 to 600 ppm. The increase in Pn of an **A. hypogaea** genotype from Tanganyika appeared to be progressively less at CO_2 concentrations near 600 ppm. The florunner cultivar of **A. hpogaea** had the highest Pn at CO_2 concentrations of 300 ppm and above; **A. pintoi** had the lowest. Photorespiration as measured by CO_2 evolution into CO_2-free air averaged about 4 mg CO_2 dm^{-2} hr^{-1} and did not differ among genotypes. Dark respiration was higher in leaves of wild species than in the two genotypes of **A. hypogaea.**

Diffusive resistance of **A. hypogaea, A. pintoi** and **A.** sp. (**glabrata**?) leaves remained constant from 9 a.m. to 3 p.m. EST and then increased up to the last measurement at 10 p.m. The DR_{H_2O} of **A. hypogaea** and **A. pintoi** were similar during the daytime and ranged from 1.5 to 5.0 sec cm^{-1} between 9 a.m. and 3 p.m. **A. villosulicarpa** and **A.** sp. (**glabrata**?) had higher DR_{H_2O} values during the same time period, ranging from 5 to 12 sec cm^{-1}. At 10 p.m. DR_{H_2O} of **A. hypogaea** was 84 sec cm^{-1} compared to only about 20 sec cm^{-1} for **A. pintoi.** Net photosynthesis of leaves of the five **Arachis** genotypes was not closely related to DR_{H_2O} nor leaf characteristics including chlorophyll content, stomatal frequency, leaf nitrogen content or specific leaf weight.

Key words: **Arachis hypogaea,** photorespiration, chlorophyll, groundnut.

Differences in response of Pn of several plant species to CO_2 concentrations have beeen described (1,2,7,9,20). Linear increases in Pn have been shown for most species studied when CO_2 concentration is increased in the range of 0 to 600 ppm. However, Akita and Tanaka (2) and Akita and Moss (1) have shown that Pn of species with the C_4 cycle of CO_2 fixation approaches saturation at CO_2 levels of about 400 to 600 whereas species exhibiting the C_3 cycle show a linear response through the 0 to 600 ppm range.

Differences in net photosynthesis (Pn) among genotypes of several field crops have been reported (11,12,13,18,20,23). However, efforts to correlate Pn with leaf characteristics have resulted in various conclusions about characteristics involved in control of Pn.

Photosynthesis can be limited by resistances to the movement of CO_2 from air to the photosynthetic site in the leaf (15). An important and variable resistance is imposed by stomata. Decreases in net photosynthesis (Pn) caused by water stress or reduced light intensity have been shown to be accompanied by increased stomatal resistance (4,8,24,27). Differences in Pn among genotypes have not usually been attributed to differences in stomatal number. Low stomatal frequency was associated with high Pn rates in bean (*Phaseolus vulgaris* L.) (18) and maize (*Zea mays* L.) (16). Miskin et al. (22) reported no decrease of Pn in barley (*Hordeum vulgare* L.) lines with low as compared to high stomatal frequency, although transpiration was less in lines with low frequency. El-Sharkawy and Hesketh (14) found no relationship between Pn and stomatal frequency nor between Pn and the product of stomatal length and frequency.

Photorespiration in C_3 species has been shown to be 1 to 3 times greater than dark respiration. Photorespiration has been estimated to depress Pn by 25 to 40% and to be detrimental to dry matter production (30). Peanut apparently assimilates CO_2 by the C_3 pathway and exhibits photorespiration on the basis of CO_2 compensation concentrations in the range of 30 to 50 ppm (10) and increased Pn at an O_2 level of 1.5% (23). Attempts to correlate photorespiration with Pn within plant species have produced conflicting results (11,12,13,30).

Specific leaf weight has been found to be related to Pn in soybean (*Glycine max* L.) (13) and alfalfa (*Medicago sativa* L.) (25). However, Watanabe and Tabuchi (28) observed no correlation between Pn of soybean cultivars and specific leaf weight. Net photosynthesis of *Arachis* genotypes was significantly correlated with specific leaf weight in only one out of three earlier experiments (6). The research reported here is a portion of a study of photosynthetic characteristics of five selected *Arachis* genotypes. The puprpose of this experiment was to determine Pn of selected *Arachis* species at several CO_2 concentrations and to relate differences in Pn to other leaf characteristics.

Materials and Methods

Five genotypes which showed a range in photosynthesis in previous studies (6) were grown in the greenhouse. The group consisted of three wild species, **A. pintoi** Krap et Greg (Unpubl.) (P. I. No. 338314), **A.** sp. (**glabrata**? cv. arb.) (P. I. No. 118457) and **A. villosulicarpa** Hoehne (P. I. No. 336984). Florunner, a cultivar from the United States, and a genotype from Tanganyika, Africa,

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(P. I. No. 149268, abbreviated as Tang) were cultivated genotypes (**A. hypogaea** L.).

A. sp. (**glabrata**?) was propagated vegetatively due to failure of seed germination. The other genotypes were started from seed. All plants were grown in pots containing field soil and were fertilized weekly with Hoagland's solution. The day and night temperatures were 29 ± 2 and 22 ± 1 C, respectively. The light intensity varied from 55 to 65 klux at midday.

Net photosynthesis was estimated on attached leaves using a chamber made after the air seal principle of Wolf et al. (29) with some modifications. The two halves of the rectangular chamber were sealed together with plastic spacers facing each other. The upper and lower halves had the spacers removed from one edge to serve as an air outlet and to accommodate the leaf. A lid with a notch for the petiole was fitted on the outlet side of the chamber. Air was introduced through a manifold and passed over the leaf at 1.5 1 min^{-1}. Approximately 0.5 1 min^{-1} were withdrawn through a manifold positioned between the leaf and the chamber outlet. This sample of air was transported to an infrared gas analyzer. The remainder of the air left the chamber through the notch in the lid which accommodated the petiole. The positive pressure of the exiting air provided a seal for the chamber against external CO_2. The lower half of the chamber contained a water jacket to allow for temperature control. Measurements were made on the second or third fully expanded leaves from the stem tip at 30 ± 1 C and 48.4 klux light intensity from 300 w incandescent lamps.

Net photosynthesis was measured on each genotype in two experiments. In the first experiment Pn of each genotype was estimated in four replications by passing atmospheric air through an air sealed leaf chamber described earlier. The air was pumped from a drum placed outside the greenhouse and bubbled through water before entering the leaf chamber. Relative humidity in the chamber air was always greater than 50%. Measurements were made with an infrared gas analyzer calibrated in a differential mode. Carbon dioxide concentration in the air ranged from 300 to 330 ppm.

In the second experiment Pn was measured under conditions similar to those for the first experiment, except that CO_2 concentrations of 50, 100, 295, 398 and 605 ppm were used and five replications of the measurements were made. Leaves were inserted into the chamber and air from compressed gas cylinders containing the desired CO_2 concentrations was passed over the leaf until a steady rate of Pn was obtained. Leaves were subjected to the various CO_2 concentrations in ascending order. For this experiment, the infrared analyzer was calibrated in an absolute mode for CO_2 concentrations from zero to 605 ppm using N_2 as a reference gas.

Photorespiration was measured in CO_2-free air by enclosing the leaf in a leaf chamber consisting of two halves which were clamped together. A soft rubber gasket was placed between the two halves of the chamber to prevent damage to petioles. Nylon string was stretched across each half to hold the leaf in place. A water jacket was constructed on the lower half to facilitate temperature control. The CO_2-free air was introduced into one side of the chamber and removed from the opposite side through manifolds. Glass tubing was used where possible to minimize the chance of mixture due to diffusion of external CO_2. The light intensity and temperature were 48.4 klux and 30 ± 1 C, respectively. The air was bubbled twice through 10% KOH solution to remove CO_2. Nitrogen was used as the reference gas in the calibration of the CO_2 infrared analyzer used for the photorespiration measurements. Dark respiration was determined during the day time at 25 ± 1 C by covering the leaf chamber with a black cloth. The air flow rates were 0.8 to 0.9 1 min^{-1} for light and dark respiration measurements.

Diffusive resistance (DR_{H_2O}) (both stomatal and boundry air layer) of the adaxial surface of the leaves was measured in the greenhouse with the diffusive resistance porometer developed by Kanemasu et al. (19) and manufactured by Lambda Instruments Company, Inc., Lincoln, Nebraska. The porometer was calibrated in a growth chamber at 70% relative humidity. Diffusive resistance was measured on the second or third fully expanded leaf from the tip of a stem at 9 a.m., 12 noon, 3, 6 and 10 p.m. for five consecutive days from July 31 to August 4, 1973. The same leaves were used throughout one day. To provide visibility at the 10 p.m. measurement time, dim light of about 1 klux was used. It required 1 hour for measurement of DR_{H_2O} on all plants at each time period. Five measurements were made on each leaf at each measurement time. Five leaves were measured on Florunner, Tang and **A. pintoi** and three leaves in the case of **A. villosulicarpa** and **A.** sp. (**glabrata**?). Chlorophyll was determined by Arnon's (3) procedure. Leaf impressions were made with silicon rubber as suggested by Horanic and Gardner (17). Stomata were counted and length measurements were made on the leaf impressions. Stomatal numbers are presented separately for the adaxial and abaxial surfaces. Leaf area was measured with an automatic area meter.

Results

Florunner had the highest rate of photosynthesis (30.8 mg CO_2 cm^{-2} hr^{-1}) and *A. pintoi* had the lowest (17.5 mg CO_2 dm^{-2} hr^{-1}) under atmospheric CO_2 concentrations (Table 1). Pn for Tang, *A. villosulicarpa* and *A.* sp (*glabrata*?) were intermediate at 26.3, 24.9 and 21.7 mg dm^{-2} hr^{-1}, respectively. These differences among genotypes were similar to those reported earlier (6). Net photosynthesis of peanuts was a linear function of CO_2 concentration and approximately doubled between 300 and 600 ppm (Figure 1), except for Tang which appeared to respond less at high CO_2 levels. Differences in Pn among genotypes were slight at 50 and 100 ppm CO_2. At CO_2 concentrationns of 300 ppm and higher, *A. pintoi* had the lowest and florunner the highest rate of Pn. *A. pintoi* exhibited a Pn rate about 60% of that for Florunner in the range of 300 to 600 ppm CO_2. The other genotypes had intermediate rates of Pn, as indicated in the experiment using atmospheric CO_2 concentrations (Table 1.)

There was no significant difference among the genotypes in photorespiration, as measured in CO_2-free air, the average rate being about 4.0 mg CO_2 dm^{-2} hr^{-1} (Table 1.) The photorespiration rates of *A. pintoi* and Florunner were about 25 and 15% of their respective rates of Pn at 300 ppm CO_2, with values of other genotypes falling in between. The photorespiration rates, estimated by extending the CO_2 response line to zero CO_2 concentration, varied between 2.9 and 4.7 mg CO_2 dm^{-2} hr^{-1}, with an average for all the genotypes of 4.0 mg CO_2 dm^{-2} hr^{-1} (Figure 1). The CO_2 compensation points, interpolated from the zero Pn intercept of the CO_2 response line, were 45 and 84 ppm CO_2 for Tang and *A. pintoi,* respectively, with values for other genotypes occurring between. Dark respiration rates varied from 1.7 to 2.6 mg CO_2 dm^{-2} hr^{-1}, with *A. pintoi* and *A.* sp. (*glabrata*?) having significantly higher respiration rates than *A. hypogaea.*

The DR_{H_2O} of adaxial surfaces of peanut leaves

Table 1. Rates of net photosynthesis and leaf characteristics of selected peanut genotypes.

Characteristic	A. pintoi	A. sp. (glabrata?)	A. villosulicarpa	A. hypogaea	
				Tang	Florunner
1. Net photosynthesis[1] (mg CO_2 dm^{-2} hr^{-1})	17.5 d*	21.7 c	24.9 bc	26.3 b	30.8 a
2. Photorespiration					
a) CO_2-free air	4.0 a	4.0 a	3.8 a	4.0 a	4.2 a
b) Extrapolation[2]	4.7	3.6	4.5	2.9	4.7
3. CO_2 compensation[3] concentration	84	58	64	45	55
4. Dark respiration (mg CO_2 dm^{-2} hr^{-1})	2.5 a	2.6 a	2.3 ab	1.7 c	1.9 bc
5. Stomatal frequency (mm^{-2})					
a) Adaxial surface	28 d	246 b	464 a	156 c	143 c
b) Abaxial surface	267 b	195 c	387 a	153 d	147 d
6. Stomatal length, μ	4.1 b	6.5 b	5.5 b	10.3 a	9.6 a
7. b x n[4]	1210	2867	4681	3183	2781
8. Specific leaf weight (g dm^{-2})	.33c	.71a	.63ab	.59b	.63ab
9. Percent nitrogen of dry weight	3.3 b	3.4 b	3.8 a	3.3 b	2.8 c
10. Chlorophyll (a+b) (mg g^{-1})	1.2 b	2.4 b	3.2 a	3.0 a	3.0 a

* Numbers marked with the same letters with rows are not significantly different at the 5% level.
1/ Net photosynthesis measurements were made at 30 C, 48.4 klux light intensity and 300-330 ppm CO_2.
2/ Photorespiration estimated from the zero CO_2 concentration intercept of the CO_2 response line.
3/ CO_2 compensation concentration estimated from the zero Pn intercept of CO_2 response line.
4/ The b x n index is the product of the longer axis (b) of the elliptical stomata and the number of stomata per mm^2 of leaf area.

varied from 1.5 to 12.5 sec cm^{-1} at 3 p.m. and from about 20 to 104 sec cm^{-1} at 10 p.m. (Figure 2). The DR_{H_2O} of *A.* sp. (*glabrata*?) and *A. villosulicarpa* leaves was higher than that of other genotypes during the day. At 10 p.m. the DR_{H_2O} of leaves of *A.* sp. (*glabrata*?) was twice that of *A. villosulicarpa* and about five times that of *A. pintoi*. The DR_{H_2O} of the two cultivated genotypes was similar, varying from 1.5 to 5.0 sec cm 1 between 9 a.m. and 6 p.m. and being about 84.0 sec cm^{-1} at 10 p.m. *A. pintoi* exhibited DR_{H_2O} similar to that of cultivated genotypes during the day but at 10 p.m. DR_{H_2O} of *A. pintoi* was only 25% of the values for Tang and Florunner.

A. villosulicarpa and *A.* sp. (*glabrata*?) had significantly higher stomatal frequency than other genotypes (Table 1). Stomatal frequency of the two cultivated genotypes was similar to values already reported for these genotypes (6). The stomatal frequency of adaxial surface of *A. pintoi* was much lower in this experiment compared to previous experiments conducted outside the greenhouse (6) and consequently total stomatal frequency is much lower for this species than for the other two wild species. The maximum light inten-

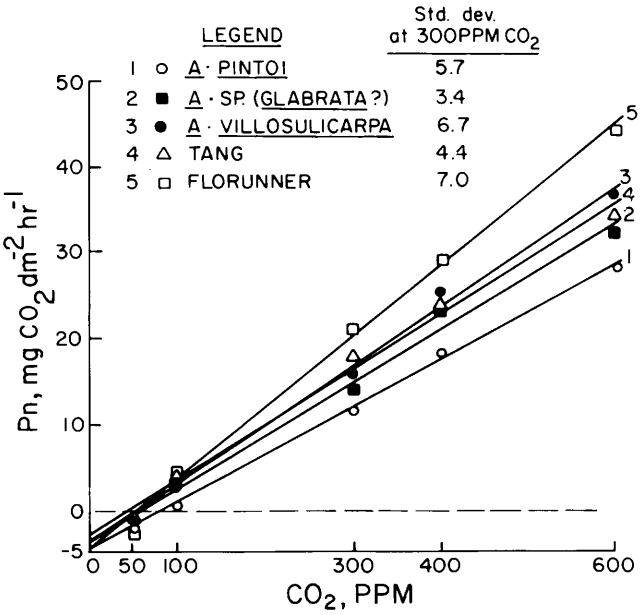

Fig. 1. Photosynthetic response to CO_2 concentrations of selected peanut genotypes. Each point is an average of 5 measurements.

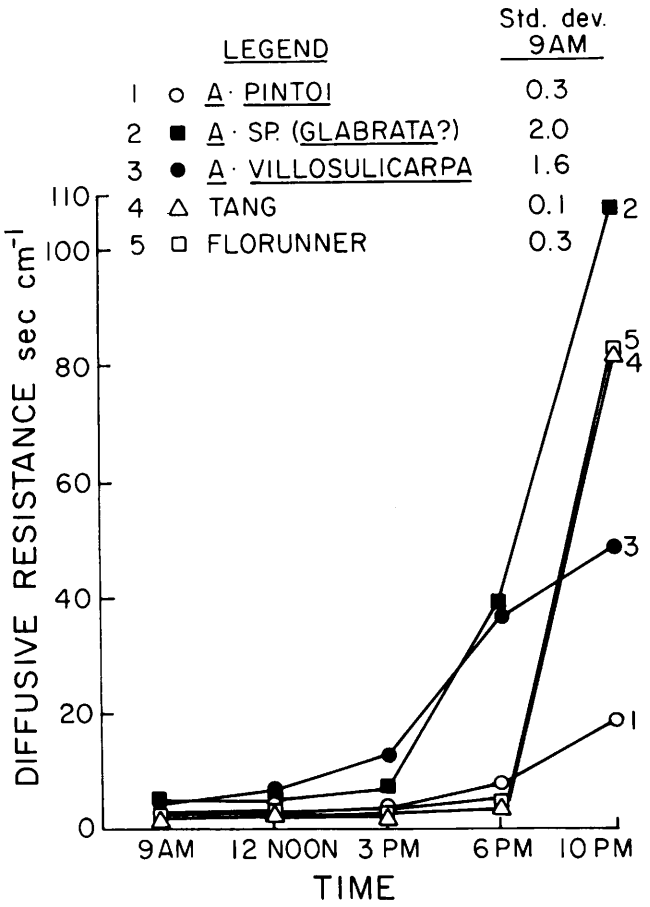

Fig. 2. Diffusive resistance of peanut genotypes. Each point is the average of 25 measurements over 5 days except for A. sp. (glabrata?) and A. villosulicarpa for each of which 15 measurements are averaged.

sity in the greenhouse during the middle of the day was 55 to 65 klux, while for previous studies plants were grown in full sunlight. Decreased light intensity might have decreased the stomatal frequency in *A. pintoi* as reported by Salisbury for woodland species (26). The stomatal length for *A. hypogaea* was significantly higher than for the wild species, being over double that for *A. pintoi*. Therefore, total stomatal area as indicated by stomatal length x frequency (b x n, Table 1) does not vary as much among genotypes as does stomatal frequency.

A. pintoi and *A.* sp. (*glabrata*?) had significantly lower chlorophyll content than other genotypes. The chlorophyll a to b ratio varied from 1.9 to 2.2 for all the genotypes. The percentage leaf nitrogen of peanut genotypes varied from 2.8 to 3.8 with *A. villosulicarpa* having significantly higher leaf nitrogen than other genotypes, and Florunner having the lowest.

A. pintoi had the lowest specific leaf weight of all genotypes. Specific leaf weight of *A. pintoi* was less by about 20% in this experiment compared with previous studies (6), possibly because of lower light intensities in this experiment.

Discussion

The slope of the photosynthetic response curve to CO_2 at saturating light intensity is a reciprocal measure of the resistance to CO_2 diffusion from atmosphere to the photosynthetic site in the leaf (7). The slope of the CO_2 response line of Florunner was greater than for *A. pintoi* and thus it offered less resistance to CO_2 diffusion than *A. pintoi*. However, measurements of stomatal plus boundary layer resistances (DR_{H_2O}) showed that there was no difference between *A. pintoi* and Florunner during the daytime. Thus differences between Florunner and *A. pintoi* in Pn are probably due to differences in resistance to CO_2 movement in the mesophyll tissue. Such differences in resistance could be due to several causes, including physical resistances or carboxylation resistance.

Net photosynthesis did not appear to be related to DR_{H_2O} or stomatal frequency. Florunner had half the number of stomata as compared with *A. villosulicarpa* but the former had higher rates of photosynthesis and lower DR_{H_2O} than the latter species. Although *A. pintoi* had fewer stomata and a lower rate of photosynthesis than *A. villosulicarpa* and *A.* sp. (*glabrata*?), the DR_{H_2O} of *A. pintoi* was lower than for the latter two species throughout the day. The DR_{H_2O} of *A. pintoi* was similar to that of cultivated genotypes even though the Pn of *A. pintoi* was only about 60% of the Pn of the cultivated genotypes.

The use of the b x n index (stomatal length, b x stomatal frequency, n) does little to clarify the relationships among genotypes with respect to Pn, DR_{H_2O} and stomatal area. The b x n index is similar for *A. hypogaea* and *A.* sp. (*glabrata*?), but Pn is lower in the latter species. Diffusive resistance is similar in *A. pintoi* and *A. hypogaea*, but b x n is less than one-half as great in *A. pintoi*. These data strongly indicate that diffusive resistance is not a main factor in the differences in Pn among these *Arachis* genotypes.

Bertsch and Domes (5) found that quantities of CO_2 transported through upper and lower leaf surfaces of maize and *Primula palinuri* Pet. were not independent of each other. If CO_2-uptake were possible only through one surface of the leaf, the CO_2 influx on that side increased. The stomatal frequency of *A. pintoi* was low in the greenhouse compared to field grown plants, but photosynthetic rate was similar under both conditions (6). *A. pintoi* may have maintained its photosynthetic rate, with reduced adaxial stomatal frequency, by a compensating mechanism of CO_2-uptake like that observed by Bertsch and Domes (5). However, there is no indication that stomatal frequency or DR_{H_2O} limit Pn of *A. pintoi*.

Photorespiration has been suggested as the cause for variations in Pn (30) but some authors (11,12, 13) have not attributed such variations to photorespiration. There appears to be no relationship between Pn and photorespiration in peanut genotypes in this study, even though Pn differed by

as much as 100% between the two genotypes having the highest and lowest rates. Neither of the methods of estimating photorespiration are considered to be very accurate because of the refixation of respired CO_2 in the light. The extrapolation of the CO_2 response curve to zero CO_2 may not give an accurate measure of CO_2 exchange because of possible non-linearity of the response at low CO_2 concentrations (21). The similarity of photorespiration by the two methods of estimation and among genotypes in this study indicates that it was not a major determinant of Pn rate.

None of the measured leaf characteristics correlated well with Pn of the five genotypes studied; several factors are probably involved in control of Pn of these genotypes. Of the factors considered in this study specific leaf weight is probably the one which has received the most attention in correlating leaf characteristics with Pn of various genotypes. Several authors have reported a positive correlation between specific leaf weight and Pn (13,25) while others have failed to find a relationship (28). In previous studies with 31 *Arachis* genotypes we found a weak correlation ($r=0.59$) in one of three experiments and none in the other two (6). In the genetically diverse plant material used in this experiment it is possible that tissue components not directly involved in photosynthesis, such as, cell wall material and starch contributed to differences in specific leaf weight.

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