PHOTOSYNTHETICA 36 (1-2): 129-138, 1999

Net photosynthetic rate in peanut (*Arachis hypogaea* L.): Influence of leaf position, time of day, and reproductive-sink

P.C. NAUTIYAL*, V. RAVINDRA and Y.C. JOSHI

National Research Centre for Groundnut, Post Bag No. 5, Junagadh, 362 001 Gujarat, India

Abstract

Net photosynthetic rate (P_N) was studied in field-grown peanut cv. GG 2 in relation to leaf position, time of day, reproductive-sink, and phenophase. In general, P_N remained higher in the upper leaves (first from top to the fourth) than in the lower leaves (fifth to eighth). The mean P_N of the leaves situated upper and the leaves lower in the canopy increased from the morning, reached a maximum during noon hours, and decreased thereafter. Between 09:00 to 10:00 h, P_N, stomatal conductance (g_s), and transpiration rate (E) in the upper leaves were higher than in the lower leaves, but between 12:00 and 13:00 h, these activities increased significantly in the lower leaves. Highest P_N was found during pod-development phase. Removal of flowers, and hence of active reproductive-sink, decreased plant height and number of leaves, and initiated accumulation of photosynthates in the leaves. The P_N per unit leaf area in plants with reproductive-sink (WRS) was similar to those without reproductive-sink (WORS). However, leaf area of WORS plants decreased significantly, mainly due to the reduction in number of leaves. No feed-back inhibition of P_N (per unit leaf area) was found despite accumulation of photosynthates in the leaves as a result of removal of the active reproductive-sink.

Additional key words: chlorophyll; dry mass; leaf number and area; peg; pod; saccharides; stomatal conductance; temperature; transpiration.

Received 19 January 1998, *accepted* 11 September 1998.

*Fax: +91-285-51550 , e-mail: nrcg@400.nicgw.nic.in

Abbreviations: c_i = internal CO_2 concentration; Chl = chlorophyll; E = transpiration rate; g_s = stomatal conductance; P_N = net photosynthetic rate; PAR = photosynthetically active radiation; SLA = specific leaf area; WORS = plants without reproductive-sink; WRS = plants with reproductive-sink.

Acknowledgments: Authors are grateful to Mr. S. Srinivas, Manager, Library and Documentation Services, ICRISAT, Asia Region, Patancheru, India for providing current literature on the topic, and Mrs. Vidya Chaudhary and Mr. P.V. Zala for technical assistance during experimentation.

Introduction

The total biomass accumulation of peanut crop is dependent on the integrated net photosynthetic rate (P_N) of single leaves throughout the total canopy. Leaves lower in the conopy have lower photosynthetic potential than the leaves in the upper canopy (Henning *et al.* 1979, for review see Šesták 1985). Though there are several reports on leaf P_N of field-grown peanut (compiled by Ketring *et al.* 1982), some more information is available on the P_N as influenced by the leaf position (Henning *et al.* 1979), leaf age (Trachtenberg and McCloud 1975, Gallaher *et al.* 1976), leaf development (Ram *et al.* 1994), cool night temperatures (Bell *et al.* 1994, Sinclair *et al.* 1994), various irradiances (Sengupta and Jadhav 1988), and soil moisture deficit stress (Sharma *et al.* 1993, Nautiyal *et al.* 1995). Diurnal variation in P_N of peanut has been studied on single seedlings (Pallas and Samish 1974) and single leaves (Nayyar *et al.* 1990, Ravindra *et al.* 1995). Little information is available on how the availability of reproductive-sinks affects the P_N of peanut. The present study aims at understanding the influence of position of leaves in the canopy, time of day, phenophase, and reproductive-sink on P_N of peanut.

Materials and methods

Experiments were done during the rainy (July-October) and the summer (February-June) seasons of the years 1993, 1994, and 1995 with peanut cultivar GG 2 (*Arachis hypogaea* L. ssp. *fastigiata* var. *vulgaris*, Spanish type). The crop was sown in plots of 3×2 m size with a spacing of 10 cm (plant to plant) and 30 cm (row to row) in three replicates in a complete randomised block design. All recommended agronomical practices including the plant protection measures were followed to maintain a healthy crop. Measurements on P_N, g_s, E, leaf (T_l) and air (T_a) temperature were recorded on peanut leaflet using a *LI-6200* (*Li-Cor*, Lincoln, USA) portable photosynthesis system. Efforts were made to measure P_N in the natural angles of the leaves on the main stem or the cotyledonary branches in the canopy. After the measurements, the leaflets were excised, and leaf area was determined with an area meter (*LI-3000, Li-Cor,* Lincoln, USA).

To study the effect of removal of flowers on P_N, experiment was done during summer 1995, with plants with (WRS) or without (WORS) reproductive-sink. In the second treatment, all the flowers of the plants were removed daily, from the day of first flower (25 d after sowing) until pod-formation phase (85 d after sowing) to avoid active reproductive-sink during the P_N measurements. The P_N, g_s, internal carbon dioxide concentration (c_i), E, T_l, and T_a were recorded on individual leaves, *i.e.*, from the first fully opened top leaf (leaf 1) to the bottom leaf (leaf 8) of the main stem, between 09:00 and 10:00 h during pod-formation phase (75-85 d after sowing, when mean PAR value was 1597 μmol m^{-2} s^{-1}).

Plant height, number of branches, leaf area, and numbers of pegs and pods were recorded on ten plants sampled randomly from each treatment and replicate. Individual leaves from top to bottom (leaves 1 to 8), were analysed for the contents

of total chlorophyll (Chl), total sugars, reducing sugars, fructose, total phenol, and *o*-dihydroxyphenol. Chl content was calculated using the equations of Holm (1954). For the analysis of total sugars, reducing sugars, fructose, total phenols, and *o*-dihydroxyphenols, leaves were sampled and killed immediately in warm 80 % methanol. The leaf samples were refluxed twice in 80 % methanol for 1 h and the methanol extract was used for the determination of total phenol (Bray and Thorpe 1954) and *o*-dihydroxyphenol (Arnow 1937). Total sugar, reducing sugar, and fructose were determined following Ashwell (1957). From the analysis of total sugar, reducing sugar and fructose, contents of saccharose (total sugars *minus* reducing sugars × 0.95) and glucose (reducing sugars *minus* fructose) were calculated. All estimations were replicated thrice and the values were expressed as g kg^{-1}(fresh matter).

Since the total number of leaves on the main stem or cotyledonary branches was reduced because of the removal of flowers in the WORS plant, there were more leaves (8) on WRS than on the WORS plants (6). Thus for statistical analysis the mean of all the observations on the 5th and 6th leaves, and 7th and 8th leaves of WRS was considered as the 5th and 6th leaf, respectively.

Influence of phenophase on P_N was studied during the summer (1993) and the rainy (1994) seasons at: (*a*) flowering (40 d after sowing in both the seasons), (*b*) pegging (60 d after sowing in the rainy, and 70 d after sowing in the summer seasons), (*c*) pod-formation (80 d after sowing in the rainy, and 90 d after sowing in the summer seasons). The P_N was measured on the fully expanded, first or second leaf of three plants between 09:00 and 10:00 h for three consecutive days. In the rainy season, measurements were made on full-sunny-days only. Mean PAR values during the measurements for the rainy and summer seasons were 1501 and 1630 μmol m^{-2} s^{-1}, respectively.

Results

Diurnal variation in P_N: Measurements began at the pod-formation phase (75 d after sowing) during the summer 1994 on the second or the third leaf from the top daily between 09:00 and 10:00, 12:00 and 13:00, 15:00 and 16:00, and 18:00 and 19:00 h for three days (mean PAR between 230 to 1634 μmol m^{-1} s^{-1}), and means of the three leaflets measured at the respective time on a single day were considered one replicate.

The mean P_N, g_s, and E of top to bottom leaves (leaf 1 to leaf 8) on the main stem or cotyledonary branches increased through the morning hours (between 09:00 and 10:00 h) to a maximum at noon (between 12:00 and 13:00 h) and decreased thereafter (Fig. 1). The difference of leaf and air temperatures (T_l - T_a) increased till 15:00 h and decreased only in the late evening hours (between 18:00 and 19:00 h), when T_l was below T_a (Fig. 2*D*). P_N of the upper leaves (1 to 4) remained higher than of the lower leaves (5 to 8) throughout the day, but in the upper leaves P_N was maximum during the morning hours (between 09:00 and 10:00 h), while the P_N of the lower leaves was maximum during the noon hours (between 12:00 and 13:00 h).

Between 09:00 and 10:00 h, P_N, g_s, and E in the upper leaves were higher than in the lower leaves, but decreased between 12:00 and 13:00 h. There was a significant increase in the P_N of lower leaves between 12:00 and 13:00 h over that during 09:00 and 10:00 h (Fig. 2*A,B,C*). The P_N of upper and lower leaves ranged from 15.49 to 2.31 μmol m^{-2} s^{-1} between 09:00 and 10:00 h, and from 9.93 to 5.81 μmol m^{-2} s^{-1} between 12:00 and 13:00 h. The P_N and E of the lowest leaf 8 increased almost two-fold from 09:00 and 10:00 h to the interval between 12:00 and 13:00 h. T_l remained higher than T_a throughout the day, irrespective of leaf position, except during the evening. At 12:00 h the difference in T_l and T_a was maximum in the lower leaves (Fig. 2*D*).

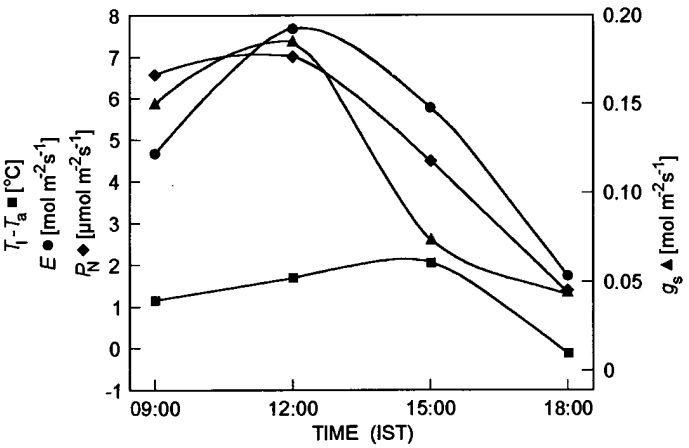

Fig. 1. Diurnal variation in net photosynthetic rate, P_N (SEm ± 0.20, CD = 0.57), stomatal conductance, g_s (SEm ± 0.01, CD = 0.03), transpiration rate, E (SEm ± 0.16, CD = 0.45), and leaf-air temperature difference, T_l -T_a (SEm ± 0.16, CD = 0.44) of peanut leaves situated on the main stem or cotyledonary branches (values are means of observations recorded on leaves 1 to 8 during summer season).

P_N of the leaves on main and cotyledonary branches: P_N was measured in the upper and lower leaves on main stem and cotyledonary branches between 09:00 and 10:00 h (mean PAR 1640 μmol m^{-2} s^{-1}) on three randomly selected plants from each replicate. In general, leaf area decreased from the uppermost fully expanded leaf to the lowermost leaf, and was higher in the main stem than the cotyledonary branches. The mean P_N and E of the individual leaves were higher in the leaves situated on main stem than in those on the cotyledonary branches. The P_N and E decreased from upper fully expanded leaf to lower leaves on both main stem and cotyledonary branches with an increase in c_i concentration (Table 1).

Effect of removal of flowers on P_N: Plant height, leaf area, specific leaf area (SLA), and number of leaves on the main stem and cotyledonary branches decreased significantly in WORS plants (Table 2). The mean P_N, g_s, and E of the leaves 1 to 6 in WRS and WORS plants did not differ significantly, but c_i was higher in the leaves

Table 1. Leaf area, LA [cm^2], net photosynthetic rate, P_N [$\mu mol\ m^{-2}\ s^{-1}$], stomatal conductance, g_s [$mol\ m^{-2}\ s^{-1}$], transpiration rate, E [$mol\ m^{-2}\ s^{-1}$], and leaf temperature *minus* air temperature, $T_l - T_a$ [°C] in the leaves from top to bottom on the main stem and cotyledonary branches, during summer 1994. Values are means of the observations recorded between 09:00 and 10:00, 12:00 and 13:00, and 15:00 and 16:00 h.

Leaf position	LA	P_N	g_s	E	$T_l - T_a$	c_i
Main stem						
1	31.00	8.60	0.120	6.53	1.85	183
2	36.30	6.68	0.100	6.42	2.39	175
3	30.91	10.82	0.280	8.64	0.48	182
4	29.39	5.64	0.162	5.94	1.80	179
5	30.50	4.66	0.083	5.21	2.03	213
6	27.16	5.81	0.116	6.65	1.33	203
7	24.52	3.96	0.078	5.70	0.08	218
8	23.77	2.22	0.073	4.73	1.81	223
mean	29.19	6.05	0.127	6.23	1.47	197
Cotyledonary branches						
1	22.64	6.57	0.131	6.25	1.14	207
2	30.76	6.74	0.182	6.84	1.46	184
3	20.78	8.66	0.127	5.92	1.30	183
4	22.62	6.76	0.142	7.26	2.01	169
5	25.94	5.26	0.132	6.42	1.34	211
6	24.43	4.10	0.140	3.50	2.08	233
7	18.40	4.56	0.084	5.92	1.30	226
8	15.56	1.84	0.092	4.50	-0.24	274
mean	22.64	5.56	0.129	5.83	1.30	221
Interaction (leaf position × treatment)						
SEm ±	NS	0.47	0.003	0.12	0.08	8.27
CD ($p = 0.0\ 5$)		1.29	0.002	0.34	0.23	22.92
Treatment						
SEm ±	1.23	0.16	NS	0.04	0.03	2.92
CD ($p = 0.05$)	3.55	0.46		0.12	0.83	8.10

of WORS plants (Table 3). In general, contents of Chl (Table 3) and the measured chemical constituents (Table 4) were higher in the leaves of WORS than WRS. The amounts of glucose, saccharose, fructose, and total phenols tended to decrease from the upper fully expanded leaf 2 to lower leaves (Table 4).

P_N during different phenophases: During both the rainy and summer seasons P_N increased from vegetative to pegging phase, was maximum during pod development, and decreased during maturity (Fig. 3). In general, T_l remained above T_a, and their difference was lower during the rainy season (Fig. 3). The values (n = 140) of P_N, g_s, and E of different experiments were used to work out pairwise correlations

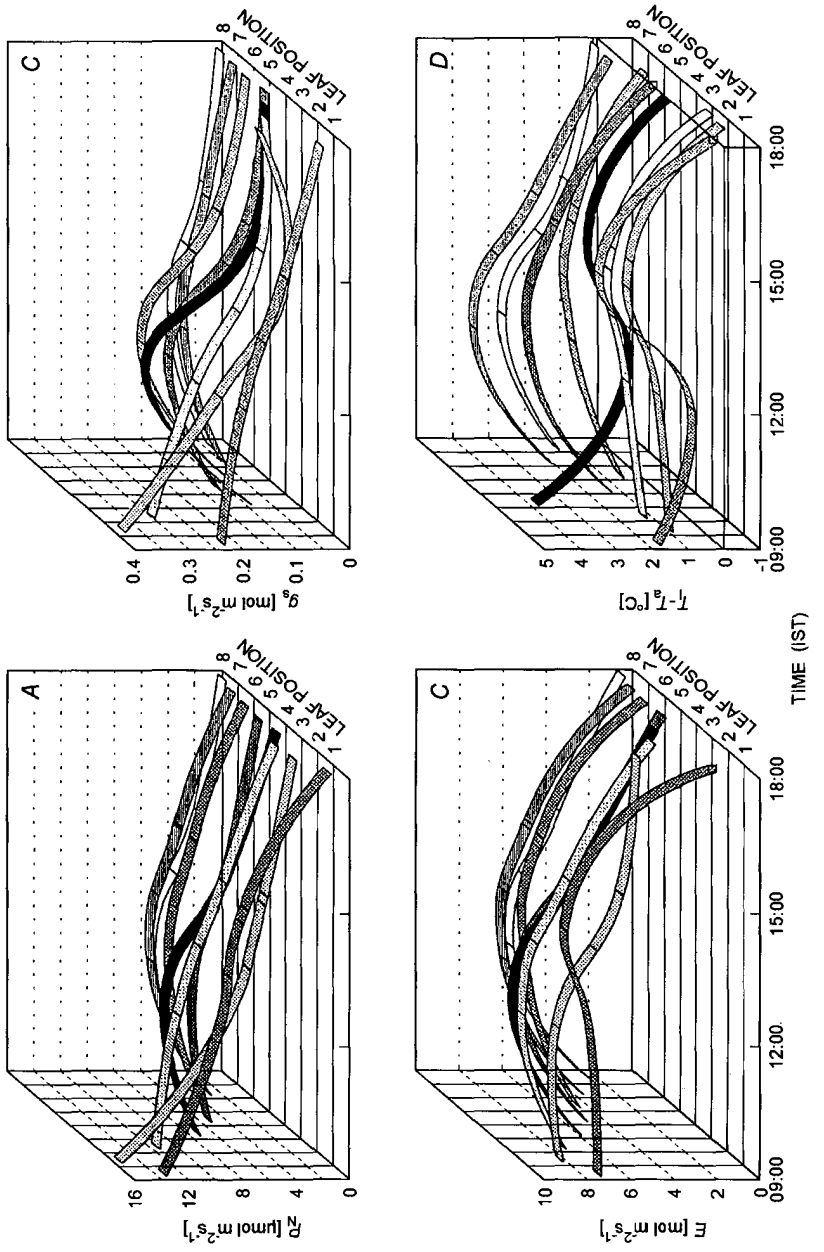

Fig. 2. Diurnal variation in net photosynthetic rate, P_N (SEm ± 0.65, CD = 1.79), stomatal conductance, g_s (SEm ± 0.03, CD = 0.09), transpiration rate, E (SEm ± 0.51, CD = 1.41), and leaf and air temperature difference, T_l - T_a (SEm ± 0.51, CD = 1.41) of peanut leaves situated on the main stem or cotyledonary branches (numbered from top to bottom) during the summer season.

Table 2. Plant height [cm], leaf area, LA [cm^2 $plant^{-1}$], specific leaf area, SLA [cm^2 $plant^{-1}$], leaf dry mass [$plant^{-1}$], stem dry mass [$plant^{-1}$], number of pegs [$plant^{-1}$], number of pods [$plant^{-1}$], and number of leaves on the main stem or cotyledonary branches [$plant^{-1}$] at 85 d after sowing, in plants with (WRS) and without (WORS) reproductive-sink during summer 1995.

	Plant height	LA	SLA	Dry mass of leaves	Dry mass of stem	Number of pegs	Number of pods	Number of leaves
WRS	15.00	779	130	6.87	6.47	23	5.0	8
WORS	9.00	433	123	3.10	2.89	1	0.33	6
SEm ±	0.82	27.16	0.95	0.28	0.41	2.46	0.62	0.24
CD ($p = 0.05$)	4.97	165.3	5.79	1.69	2.52	14.97	3.79	1.44

among these parameters. Relationship between P_N and g_s ($r = 0.79$), P_N and E ($r = 0.62$), and g_s and E ($r = 0.68$) were positive and significant.

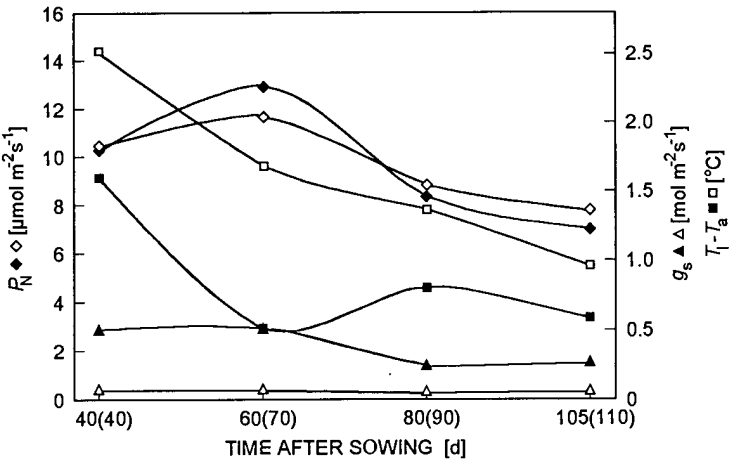

Fig. 3. Net photosynthetic rate, P_N (SEm ± 0.59, CD = 1.65), stomatal conductance, g_s (SEm ± 0.04, CD = 0.11), and leaf and air temperature difference, T_l - T_a (SEm ± NS) during different phenophases of peanut in the rainy (*full symbols*) and summer (*open symbols*) seasons. Figures out of parenthesis are for the days after sowing for the rainy season, and inside parenthesis for the days for the summer season.

Discussion

The highest P_N (15.45 µmol m^{-2} s^{-1}) observed in this study was similar to the rates previously reported for peanut (Gallaher *et al.* 1976, Henning *et al.* 1979). P_N was maximum in the upper leaves in the morning, whereas the mean P_N of the upper and lower leaves was maximum during noon. This is mainly the result of the spurt

Table 3. Mean photosynthetic rate, P_N [μmol m^{-2} s^{-1}], stomatal conductance, g_s [mol m^{-2} s^{-1}], transpiration rate, E [mol m^{-2} s^{-1}], leaf *minus* air temperature, $T_l - T_a$ [°C], internal carbon dioxide, c_i [cm^3 m^{-3}] and chlorophyll, Chl [g kg^{-1}(fr. m.)] concentrations during pod-development phase in the plants with (WRS) and without (WORS) reproductive-sink during summer 1995.

Leaf position	P_N	g_s	E	$T_l - T_a$	c_i	Chl
WRS						
1	9.83	0.217	6.88	0.96	160	1.92
2	9.39	0.228	5.96	1.20	151	2.07
3	8.90	0.242	6.08	0.67	155	1.79
4	8.50	0.192	5.81	1.24	160	2.02
5	5.94	0.140	5.07	1.81	187	1.89
6	4.59	0.124	5.58	2.12	210	1.77
mean	7.85	0.190	5.90	1.33	170	1.91
WORS						
1	10.75	0.164	5.78	1.38	162	1.86
2	10.07	0.212	6.27	1.14	168	2.38
3	8.36	0.175	5.83	2.21	168	1.80
4	6.70	0.147	5.42	1.04	186	1.49
5	8.02	0.175	6.24	0.92	184	1.31
6	4.38	0.104	5.34	1.60	210	1.52
mean	8.03	0.162	5.81	1.38	180	1.73
Interaction						
SEm ±	0.21	0.003	0.09	0.24	2.39	0.04
CD ($p = 0.05$)	0.59	0.010	0.24	0.66	6.62	0.12
Treatment						
SEm ±	NS	0.002	NS	NS	0.97	0.02
CD ($p = 0.05$)		0.004			2.69	0.05

in the P_N of the lower leaves during noon hours. This increase in P_N of lower leaves during noon may be ascribed to increased solar radiation interception by the leaves situated lower in the canopy.

Partitioning of photosynthates to pods is the most important physiological factor in yield formation, besides pod number and duration of pod-filling (Duncan *et al.* 1978). Maximum P_N during the pod-formation phase shows that reproductive-sink and its relative strength have an innate effect on photosynthesis (Ravindra *et al.* 1995), however, peanut is of indeterminate growth habit, and vegetative and reproductive-sinks operate simultaneously. In this study the WORS plants tended to produce more flowers than the WRS plants (values not shown), this process might have consumed the photosynthates.

Concentration of photosynthates such as saccharose and fructose in the leaves of WORS was higher than in the leaves of WRS, but it did not modify the P_N per unit leaf area in both plant types. The sink-controlled photosynthesis in peanut seedlings

Table 4. Contents [g kg^{-1}(fr. m.)] of fructose (Fru), saccharose (Sac), glucose (Glu), total phenols (TP), and *o*-dihydroxyphenol (ODP) in the leaves of plants with (WRS) and without (WORS) reproductive-sink at pod-development phase during summer 1995.

Leaf position	Fru	Sac	Glu	TP	ODP
WRS					
1	3.51	1.10	3.32	8.16	5.81
2	7.14	1.07	4.76	5.57	3.73
3	6.03	3.59	3.53	6.30	4.11
4	4.41	4.77	3.83	6.81	4.90
5	5.74	3.95	2.35	8.35	5.99
6	2.46	2.99	2.12	6.01	3.74
mean	4.88	2.91	3.32	6.87	4.71
WORS					
1	4.76	2.47	2.92	6.30	4.78
2	6.75	4.94	3.51	6.28	4.47
3	7.39	7.75	2.40	7.38	5.32
4	6.81	6.39	1.71	7.07	5.43
5	5.87	3.09	2.37	7.21	5.11
6	5.24	2.02	1.31	5.25	5.03
mean	6.14	4.44	2.37	6.58	5.02
Interaction					
SEm ±	0.17	0.55	0.21	0.16	0.09
CD ($p = 0.05$)	0.51	1.62	0.61	0.46	0.27
Treatment					
SEm ±	0.07	0.22	0.84	0.06	0.04
CD ($p = 0.05$)	0.20	0.66	0.25	0.18	0.10

was studied by Bagnall *et al.* (1988): under low-temperature, in association with reduced growth, assimilates accumulate in peanut leaves, and reduce P_N. We did not find a feed-back inhibition of photosynthesis (per unit leaf area) despite accumulation of photosynthates in the leaves as a result of removal of active reproductive-sink.

The decrease in P_N due to diurnal variation and leaf position was concurrent with decreases in g_s and E. Strong relationship between P_N and g_s (r = 0.79) indicated that P_N in peanut is highly related to g_s, which also regulates transpiration (Nautiyal *et al.* 1995).

Improved canopy architecture enabling the lower leaves to receive more solar radiation may be a useful tool to increase the P_N in the Spanish type peanut, thus resulting in higher biomass production. However, peanut needs further detailed investigations to understand the mechanism of control of photosynthesis by the reproductive-sink.

References

Arnow, L.E.: Colorimetric determination of the compounds of 2-4-dihydroxy phenylalanine-tyrosine mixtures. - J. biol. Chem. **118**: 531-37, 1937.

Ashwell, G.: Colorimetric analysis of sugar. - In: Colowick, S.P., Kaplan, N.O. (ed.): Methods of Enzymology. Vol. 3. Pp. 73-105. Academic Press, New York 1957.

Bagnall, D.J., King, R.W., Farquhar, G.D.: Temperature-dependent feedback inhibition of photosynthesis in peanut. - Planta **175**: 348-354, 1988.

Bell, M.J., Roy, R.C., Tollenaar, M., Michaels, T.E.: Importance of variation in chilling tolerance for peanut genotypic adaptation to cool, short-season environment. - Crop Sci. **34**: 1030-1039, 1994.

Bray, H.G., Thorpe, W.V.: Analysis of phenolic compounds of interest in metabolism. - In: Glick, D. (ed.): Methods of Biochemical Analysis. Vol. 1. Pp. 27-52. Interscience Publishers, New York 1954.

Duncan, W.G., McCloud, D.E., McGraw, R.L., Boote, K.J.: Physiological aspects of peanut yield improvement. - Crop Sci. **18**: 1015-1020, 1978.

Gallaher, R.N., Brown, R.H., Ashley, D.A., Jones, J.B., Jr.: Photosynthesis of, and $^{14}CO_2$ photosynthate translocation from, calcium-deficient leaves of crops. - Crop Sci. **16**: 116-119, 1976.

Henning, R.J., Brown, R.H., Ashley, D.A.: Effect of leaf position and plant age on photosynthesis and translocation in peanut. I. Apparent photosynthesis and ^{14}C translocation. - Peanut Sci. **6**: 46-50, 1979.

Holm, G.: Chlorophyll mutations in barley. - Acta Agr. scand. **4**: 457-471, 1954.

Ketring, D.L., Brown, R.H., Sullivan, G.A., Johnson, B.B.: Growth physiology. - In: Pattee, H.E., Young, C.T. (ed.): Peanut Science and Technology. Pp. 411-457. Amer. Peanut Res. Educ. Soc. Texas 1982.

Nautiyal, P.C., Ravindra, V., Joshi, Y.C.: Gas exchange and leaf water relations in two peanut cultivars of different drought tolerance. - Biol. Plant. **37**: 371-374, 1995.

Nayyar, H., Malik, C.P., Singh, P., Parmar, U., Grewal, M., Kaur, S.: Diurnal variations in photosynthetic parameters in peanut. - Photosynthetica **24**: 276-279, 1990.

Pallas, J.E., Jr., Samish, Y.B.: Photosynthetic response of peanut. - Crop Sci. **14**: 478-482, 1974.

Ram, S., Sharma, A., Sengupta, U.K.: Photosynthesis and carbon import in developing leaves of groundnut (*Arachis hypogaea* L.). - Photosynthetica **30**: 53-38, 1994.

Ravindra, V., Nautiyal, P.C., Joshi, Y.C. : Ontogenetic changes in growth and net photosynthetic rate of two peanut (*Arachis hypogaea* L.) cultivars. - Biol. Plant. **37**: 225-232, 1995.

Sengupta, U.K., Jadhav, B.B.: Effect of low light intensity on photosynthesis and translocation of photosynthates in groundnut. - Indian J. Plant Physiol. **31**: 270-275, 1988.

Šesták, Z. (ed.): Photosynthesis During Leaf Development. - Academia, Praha; Dr W. Junk Publ., Dordrecht - Boston - Lancaster 1985.

Sharma, P., Nisha, Malik, C.P.: Photosynthetic responses of groundnut to moisture stress. - Photosynthetica **29**: 157-160, 1993.

Sinclair, T.R., Bennett, J.M., Drake, G.M.: Cool night temperature and peanut leaf photosynthetic activity. - Soil Crop Sci. Soc. Florida Proc. **53**: 74-76, 1994.

Trachtenberg, C.H., McCloud, D.E.: Net photosynthesis of peanut leaves at varying light intensities and leaf ages. - Soil Crop Sci. Soc. Florida Proc. **35**: 54-55, 1975.