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GAS EXCHANGE AND WATER STATUS OF PIGEON PEA CULTIVARS IN PUERTO RICO

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ABSTRACT

The photosynthetic and transpiration rates of various cultivars of pigeon pea (Cajanus cajan (L.) Millsp.) were measured using a portable infrared gas analyzer system at the Fortuna Experimental Station in Puerto Rico. The 16 lines studies were long-day determinate types and showed great variability at 4.5 months after planting with respect to plant height (0.85-2.1m), photosynthetic rate ($0.19 - 0.85mg CO_2 m^{-2} sec.^{-1}$) and transpiration rate (263 -556mg H₂O m⁻² sec.⁻¹). Conductances also varied over a 3-fold range. Leaf nitrogen and chlorophyll were also measured for correlation with photosynthesis. The 16 lines have been shown to have distinct physiological attributes.

RESUMEN

La tasa fotosintética y de transpiración de varias variedades de gandúl (Cajanus cajan (L.) Millsp.) fueron medidas, usando un sistema portátil de análisis infrarojo de gas, lo cuál se llevo a cabo en la Estación Experimental La Fortuna en Puerto Rico. Las dieciséis variedades que fueron estudiadas eran de tipo determinado y de día largo y mostrarón gran variabilidad, a los cuarenta y cinco dias despues de haber sido plantadas, en lo referente a: la altura de la planta (0.85-2.1m), tasa fotosintética ($0.19-0.85mg CO_2/m^2/sec$), tasa de transpiración ($263-556mg H_2O/m^2/sec$). La conductancia tambien vario en una escala mayor de tres veces. La cantidad de nitrógeno y de clorofila tambien fueron medidas para poder correlacionarlas con la fotosintésis. La dieciséis variedades mostratón tener atributos fisiológicos diferentes.

Keywords: Gas and water exchange, Cajanus cajan.

Pigeon pea (*Cajanus cajan* (L.) Millsp.) is a significant crop within the Caribbean Basin, noted for its drought resistance, general hardy nature, low nutrient requirements, and N-fixing *Rhizobium* associations. It is a valued food crop and is ubiquitous not only under standard cultivation practices, but also in the wild. or as a doorstop plant. Major selection work of the pigeon pea is underway in many areas to improve its qualities. These efforts are aimed, among others, at dwarfing, enhancing determinant growth, and producing long-day flowering types.

The availability of organized field trials of pigeon pea at several of the Research and Development Centers of the University of Puerto Rico's Agricultural Experimental Station made it feasible for the experiments described below to be performed on many lines under the same field conditions in conjunction with standard screening programmes. This paper only briefly describes the work in progress. The project will continue at other sites in Puerto Rico and with other aspects such as whole plant and crop modeling to determine carbon balance and allocation.

Materials and methods

Plant material

This research was carried out on experimental plots established by investigators of the Horticulture Division, College of Agronomic Sciences, University of Puerto Rico, Mayaguez who are working to screen 16 lines of pigeon pea (Morales 1985, personal communication) for determinant flowering and insensitivity to day length. The planting was done in April 1985 in four replicate blocks made up of 16 plots of the individual pigeon pea lines. Each plot was planted with four 6n1 rows at a 0.9m x 0.3m spacing. The plants were not fertilized, but other normal cultivation practices were followed. Average plant height for each line was measured at the same time as photosynthetic rate.

Gas exchange

Leaf gas exchange was measured using a portable system (LI-6000 Portable Photosynthesis System, LI-COR, Inc., Lincoln, NB). The system allows the simultaneous measurement of the fluxes of carbon dioxide and water vapour from a leaf, leaf and air temperature, and incident quantum flux or photosynthetically active radiation (PAR – solar radiation between 440 and 700 nm). Determinations for a single leaf can be made in less than one minute.

For the automatically collected data and the leaf area, the system calculates photosynthesis, transpiration, leaf conductance, and an internal leaf CO_2 concentration. An integral data storage circuitry allows the accumulation of over 100 single leaf measurements. Data can be dumped onto a printer or computer system.

Measurements were made at the Fortuna Station about 4 months after planting. A single block of the four replicates was chosen at random, and within its 16 plots five replicate leaves from each line were tested with the portable photosynthesis system. After measurement the leaflets were harvested, put on ice, and transported to San Juan for further analysis.

Leaf area, leaf specific weight and chlorophyll content

The freshly harvested leaflets (5 replicates from 16 lines) were refrigerated until the area was determined with an optical area meter (LI – 3000 with belt conveyor, LI–COR, Inc., Lincoln, NB). A single disk (4.25cm² area) was cut from one leaf of each of the 16 lines for chlorophyll determination. The remaining material was dried to a constant weight at 65°C and the leaf specific weight (g m⁻²)calculated.

The dimethyl sulfoxide (DMSO) chlorophyll extraction technique was used (Hiscox and Israelstam, 1979). This method uses a direct extraction of the chlorphyll from a whole piece of leaf tissue in DMSO at 65°C without any other treatment. After 15 min. to 3h (depending on leaf toughness) the extract is decanted and read directly for optical density on a spectrophotometer at 645 and 663nm. For the purposes of this research, where physiological processes were determined on a leaf area basis, the chlorophyll contents were calculated on both a mg g^{-1} fresh weight and mg dm⁻² basis.

Nitrogen and carbon contents

The dried leaf samples were ground through a 40 mesh sieve in a Wiley mill in preparation for analysis in a Carlos Erbe C-H-N analyzer. This instrument allows the simultaneous determination of C, N and H from a single *circa* 1mg sample. Analytical yield and sensitivity were calculated using standards from the National Bureau of Standards. Calculations were made to allow analysis of the data on both weight and area bases.

Results and discussion

Plant material

The photosynthetic rate measurements were made 4 months into the growth cycle of the 16 lines of pigeon pea, but the lines were clearly at different stages of development at that time. All but two of the lines (206 and 207) had flowered by the measurement date, and most had reached the podding stage, some with dried pods.

This wide variation in phenological state reflects on the range of days needed by the lines to reach flowering, and has been reported in many studies (Abrams *et al.*,1969; Clarke, 1984; Hammerton, 1976). The lines which flower and pod late have more time to allocate photosynthate for growth rather than the strong sink of flowering and pod filling. It is not coincidental that two of the taller lines were those still without flowers. The heights of the 16 lines ranged (Table 1) from 0.85 to 2.13m, with an average of 1.4m. The size range was peaked towards the mean values (Fig. 1).

Table 1. Mean leaf area, leaf specific weight, nitrogen content, photosynthetic rate and transpiration rate of 16 pigeon pea lines in Puerto Rico

Line	Leaf area (cm²)	Leaf specific weight (g/m ²)	Cholorophyll (mg/dm²)	N (%)	Photosynthetic rate (mg/m²/h)	Transpiration rate (mg/m ² /s)
201	13.7	44.6	48.1	5.4	0.62	477.5
202	10.3	55.8	49.7	3.6	0.78	-
203	28.9	50.2	46.4	3.9	0.79	433.8
204	20.6	41.7	46.6	5.7	0.85	458.4
205	21.4	58.5	47.6	3.8	0.28	419.8
206	25.1	49.1	51.1	4.5	0.27	445.4
207	16.0	55.7	48.8	4.6	0.43	469.6
208	27.0	49.0	56.1	5.2	0.64	431.7
209	17.0	40.6	45.0	3.4	0.28	537.9
210	27.9	54.6	45.5	3.8	0.40	434.1
211	29.2	50.4	47.6	-	0.39	378.3
212	27.6	46.5	46.0	-	0.19	386.1
213	26.9	59.7	50.4	3.6	0.27	262.9
214	31.0	57.2	53.0	3.6	0.39	322.0
215	16.6	49.5	49.9	4.5	0.79	556.5
216	20.0	54.7	52.1	4.5	0.48	496.6



Figure 1. Distribution of average heights among 16 pigeon pea lines in Puerto Rico.

Gas exchange

Although leaf photosynthetic rate is not a direct indicator of potential harvest yield (Kramer, 1981), it is an important indicator of the relative carbon acquiring capabilities of plants. The complication of direct correlations between carbon uptake and yield lie in the often neglected sources of carbon loss such as root and stem metabolism, root turnover, chewing and sucking insect predation, and carbohydrate leakage through the roots.

The maximum photosynthetic rates observed

under ambient conditions among the 16 lines of pigeon pea at Fortuna ranged from 0.19 to 0.85mg $CO_2 \text{ m}^{-2} \text{ sec.}^{-1}$, the average value was 0.49mg CO_2 $\text{m}^{-2} \text{ sec.}^{-1}$. Ambient air temperatures were $35 - 39 \,^{\circ}\text{C}$ and light levels 1000–1900 micromols quanta m^{-2} sec.⁻¹ (PAR). Transpiration rates ranged from 262.9 to 556.5 mg H₂O m⁻² sec.⁻¹ with an average of 434.0mg H₂O m⁻² sec.⁻¹. The lowest photosynthetic rates and warmest leaves were generally associated with the low transpiration rates due to stomatal closure (lower conductance to water vapour) and reduced evaporative cooling (Figs. 2 and 3).



Figure 2. Correlation of observed transpiration with leaf photosynthesis of 16 pigeon pea lines.



Figure 3. Relationship of conductance of leaf photosynthesis for 16 pigeon pea lines.

Chlorophyll

Although appearing uniformly green, the total chlorophyll content of the leaves ranged from 1.91 to 2.38 mg g⁻¹ fresh weight (45.0 to 56.1 mg per dm²), there being a 25 percent difference between the extremes (Table 1). Given unlimited resources (nutrients, water, light), a plant within a single species should present higher photosynthetic rates with a higher chlorophyll content (Fig. 4). The DMSO chlorophyll extraction method proved very useful; the leaves were a translucent white at the end of the extraction, indicating complete removal of chlorophyll.

Leaf area

Leaf area index is not too reliable for precise comparisons since only the youngest age class of fully expanded levels was used. The leaf size depends to a great extent on the environment during leaf expansion. Also, the sample size was small. Nonetheless, a wide range of individual leaf areas was recorded. The smallest leaf area was only 7.75 cm², the largest 38.7 cm². The overall average for the 80 samples was 22.4 cm². Leaf size has considerable effect on leaf energy budget and temperature. The only observation of leaf temperatures below air temperature was made in the two plants with the smallest leaves (lines 202, 217). Leaves are cooled by re-radiation of infrared radiation, evaporation of water from transpiration and convection. A small leaf is a more efficient shape for convective heat transfer (Gates, 1980).

Leaf specific weight (LSW)

Leaf densities of single leaves ranged from 40.6 to 66.90g m⁻², however, the average LSW was 52.2g m⁻². The range of average LSW between lines (five leaves per line) was 40.6 to 59.7g m⁻² (Table 1).

Nitrogen and carbon contents

Nitrogen is a critical element involved in many physiological processes, especially photosynthesis and protection against herbivory via secondary metabolic compounds. In both agricultural and native plants, photosynthesis is positively correlated with leaf N level. Pigeon pea presents a special case,



Figure 4. Relationship of chlorophyll content on an area basis with photosynthesis of 16 pigeon pea lines.

as with other legumes, in that it can acquire N through the fixative capabilities of the *Rhizobium* sp. bacteria associated with its roots.

The plantings used in this trial were unfertilized, although soil available N levels may have been high due to residual nitrogenous fertilizers on site from previous field trials. Irregardless of previous treatments, the leaf N levels were higher than in non-N fixing plants, and greater than other reports for pigeon pea (Sheldrake and Narayanan, 1979). The minimum leaf nitrogen level was 3.4 per cent, the maximum 5.7 per cent – a 2.3 per cent range, or 67 per cent increase from the lowest to the highest value. When nitrogen is adjusted with the leaf specific weight from a percent to an area basis, much of the difference between the lines is eliminated (Figs. 5 and 6). Carbon content of the leaves reflects on both the structural carbon (cellulose, lignin) and the nonstructural carbohydrates (starch, sucrose, other photosynthetic products). In itself the C content is not too useful, but C:N ratios can be calculated which give an idea of the potential attractiveness of leaf material to herbivores. The higher the C:N, the more intractable and less 'attractive' the material to a chewing insect. They select leaves by N content. The C:N ratios ranged between 9.6 and 16.4; the mean was 12.9.

Conclusions

Photosynthesis was highly variable between the 16 lines of pigean pea tested. There were marked differences in chlorophyll content, nitrogen content,



Figure 5. Per cent leaf nitrogen versus leaf photosynthesis for 16 pigeon pea lines.



Figure 6. Leaf-N (g/m^2) versus observed leaf photosynthesis for 16 pigeon pea lines.

area and specific weight of the leaves, but water related factors such as transpiration and conductance seem to have the greatest effect on gas exchange. This is not surprising in a planting of such variety of leaf area index, plant height, and phenological state. It will be interesting to pursue future projects with an element of modelling to study the carbon balance and allocation effects on yield and growth parameters.

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