Seedling Characteristics and Retention of Current Photosynthates in Leaves in Relation to Initial Growth in Pigeonpea (*Cajanus cajan* L. Millsp.) and Cowpea (*Vigna sinensis* Endl.)

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Improved varieties of pigeonpea (*Cajanus cajan* L. Millsp.) still retain some growth characteristics of perennial types of wild species such as slow seedling growth and ratoonability which are considered to be major yield-restricting characteristics when the growth period is shortened. Studies on the physiological background of slow initial growth may help improve the potential productivity of short-duration pigeonpea. It was found that the low seedling vigor of pigeonpea could be ascribed to the small seed size (Narayanan et al. 1981; Brakke and Gardner 1987), low rate of photosynthetic CO_2 fixation (Rawson and Constable 1981), and low rates of metabolic processes (Huber and Hanson 1992; Ito et al. 1996). However, few authors have related the slow growth to the retention of current photosynthates and leaf respiration during the night. In contrast, seedling growth of cowpea (*Vigna sinensis* Endl.) was reported to be vigorous (Brakke and Gardner 1987).

The objectives of this study were to characterize the initial growth of pigeonpea in comparison with cowpea. Two experiments were carried out, one dealing with growth analysis and the other with O_2 uptake of leaf and retention of current photosynthates during the night.

Materials and methods

Experiment 1. Pigeonpea (*Cajanus cajan* L. Millsp. cv. ICPL 87) and cowpea (*Vigna sinensis* Endl. cv. EC 82-7) plants were grown in a pot containing 3 kg of Alfisol soil in a glasshouse at the ICRISAT Asia Center on November 10, 1993. Urea and single superphosphate were applied at the rate of 1 g and 3 g per pot to these crops, respectively, while potassium was not applied. Seeds of pigeonpea were inoculated with *Rhizobium* strain IC3195 to provide about 10^5 rhizobia per seed, unlike those of cowpea. Seedlings were grown under a 30/25°C day/night temperature regime. The thermoperiod was 12 h. The experimental layout was a completely randomized factorial design with five replications. At 14 d after sowing (DAS), plants were thinned to two plants per pot. For the growth analysis, sampling was carried out at 21 DAS and 28 DAS. The plants were separated into leaves, stems, and roots. Leaf area of each plant was measured using an area meter (LI-3100, Licor).

The dry weight of the samples was determined after oven-drying at 70°C for 3 d. Calculation of the growth parameters followed the method described by Radford (1967). At 24 DAS, the photosynthetic rate of an intact third leaf from the top of each plant was measured outdoors between 10:00 A.M. and 10:30 A.M. with five replications using a portable leaf chamber analyzer (LCA-2, ADC). During the measurements, photosynthetically active radiation, relative humidity, and leaf temperature ranged from 1,124 to 1,201 μmol m^{-2} s^{-1}, 30 to 35%, and 28.1 to 28.7°C, respectively.

   Experiment 2. The two plants species were grown in a glasshouse under the same conditions as those described in Experiment 1 on June 23, 1993. The experiment was set up using a completely randomized factorial design with six replications. Fertilizer application, *Rhizobium* inoculation and thinning were carried out as described in Experiment 1. At 24 DAS, plants were brought into the glasshouse for radioisotope experiment. The third leaf from the top of each crop was fed with 10 μL of $^{14}CO_2$ (370 kBq) gas in a cylindrical glass chamber (ca. 500 mL) sealed with rubber stoppers for several minutes between 10:00 A.M. and 11:00 A.M. The $^{14}CO_2$ gas was released by the addition of an adequate amount of lactic acid to the NaH$^{14}CO_3$ solution in a beaker using a syringe from outside. Six treated leaves were sampled every 2 h during the night from 6:00 P.M. to 6:00 A.M. in the next morning and were incubated at 25°C in a gas-tight syringe for 1 h to measure the O_2 uptake using an oxygen meter (LC700F, TORAY). After the measurements, the leaves were kept in a freezer at -20°C until further analyses. A 0.5 g aliquot of leaf discs of the frozen leaves was ground in a mortar with 5 mL of distilled water and quartz sand, followed by incubation at 60°C for 30 min in a hot water bath for separation into water extract and residues. Furthermore, 5 mL of acetone was put into the residues and the samples were kept in a refrigerator overnight for separation into acetone extract and residues. After centrifugation, the residues were dried on a water bath, weighed, and analyzed for total ^{14}C with a biological oxidizer (R.J. Harvey Instrument Co., Ltd.) and a scintillation counter (LS5801, Beckman). The main components of the residues consisted of starch and structural carbohydrates.

Results and discussion

   Seedling growth and growth parameters. Pigeonpea showed a significantly low total dry matter (TDM) and small leaf area (LA) in comparison with cowpea at 21 and 28 DAS (Table 1). Brakke and Gardner (1987) also reported that TDM accumulation of pigeonpea was lower than that of cowpea due to the limited leaf development during the 49-d growth period. Pigeonpea displayed small unifoliolate and trifoliolate leaves at 21 and 28 DAS. The LA of pigeonpea at 28 DAS was 30.1% of that of cowpea. Relative growth rate (RGR) of pigeonpea between 21 and 28 DAS was significantly lower than that of cowpea (Table 2). At this stage, the net assimilation rate (NAR) in pigeonpea was significantly lower

Table 1. Total dry matter (TDM$_1$ and TDM$_2$) and leaf area (LA$_1$ and LA$_2$) per plant in pigeonpea and cowpea at 21 and 28 d after sowing, respectively.

| | TDM$_1$ | TDM$_2$ | LA$_1$ | LA$_2$ |
	g	g	cm^2	cm^2
Pigeonpea	0.568 b*	0.890 b	74 b	99 b
Cowpea	1.470 a	3.038 a	186 a	330 a
LSD (5%)	0.196	0.538	35	117

* Means followed by a common letter are not different at 5% level.

than in cowpea, unlike the leaf area ratio (LAR). Low initial growth vigor in pigeonpea could be attributed to the low NAR as well as leaf development. The values of the photosynthetic rate, which is considered to be the main component of NAR, are shown in Table 2. The photosynthetic rate of the third leaf from the top in pigeonpea was significantly lower than that in cowpea. It was reported that the values of the leaf photosynthetic rate in cowpea and pigeonpea ranged from 11.0 to 33.8 and from 12.0 to 19.0 μmol m^{-2} s^{-1}, respectively (Lush and Rawson 1979; Rawson and Constable 1981; Lopez et al. 1987). In our experiment, the values of the leaf photosynthetic rate in pigeonpea were slightly high, while those in cowpea were within this range. Atkinson and Farrar (1983) reported that the small RGR in *Festuca ovinal* L. and *Nardus stricta* L. resulted from the low photosynthetic rates. Therefore, the low photosynthetic rate may be related to the low RGR in pigeonpea.

Leaf respiration.   Averages of O_2 uptake rate of the two crops during the night are shown in Table 2. The O_2 uptake rate of pigeonpea was not significantly higher than that of cowpea at this stage. The ratio of $p_0 : r$ of pigeonpea was lower than that of cowpea. It appears that the C economy of pigeonpea is inefficient. Rao et al. (1984) reported that 28% of carbon as net photosynthesis in pigeonpea was allocated to shoot respiration at the vegetative stage. High dark respiration rate can be associated with the increase in the proportion of assimilates respired for maintenance and poorly controlled metabolism (Azcon-Bieto 1984). Further studies on the estimation of respiratory losses should be carried out for improving the C economy of pigeonpea.

Retention of current photosynthates.   The retention of current photosynthates in the treated leaves was expressed by the ^{14}C activity in insoluble materials of the leaves at each sampling time relative to that at 6:00 P.M. (Fig. 1). At 4:00 and 6:00 A.M., the relative value of ^{14}C was significantly higher in pigeonpea than in cowpea, suggesting that the rate of carbon depletion of pigeonpea was lower than that of cowpea in this experiment. The rate of ^{14}C photosynthate depletion from the treated leaves can be compared more accurately with the half-life of ^{14}C calculated from the exponential curve fitting of the data presented in Fig. 1. The time course of the depletion of ^{14}C photosynthates from leaves has been fitted to the exponential equation by Moorby and Jarman (1975) and Gordon et al. (1980). The half-life is a useful indicator for turnover rates of metabolites. The half-life was longer in pigeonpea (Table 2), suggesting that a larger amount of ^{14}C was retained in the treated leaves. Ito et al. (1996) concluded that starch was a major carbon source of translocation to other parts of plants in pigeonpea leaves at night. In the current experiment, ^{14}C export rate may be associated with the rate of starch mobilization, since the residues of leaves consisted of starch and structural carbohydrates. The starch metabolism related to the level of sucrose is regulated indirectly through the environmental and endogenous regulation of export

Table 2.   Growth parameters, photosynthetic rate, respiration rate, and half-life of ^{14}C in treated leaves of two crops.

	RGR g g^{-1} d^{-1}	NAR mg cm^{-2} d^{-1}	LAR cm^2 g^{-1}	p_0 μmol CO$_2$ m^{-2} s^{-1}	r μmol O$_2$ m^{-2} s^{-1}	HL h
Pigeonpea	0.069 b*	0.561 b	123 a	19.8 b	1.74 a	6.7
Cowpea	0.090 a	0.882 a	102 a	21.8 a	1.58 a	5.2
LSD (5%)	0.012	0.187	19	0.8	0.29	

*Means followed by a common letter are not different at 5% level. RGR=relative growth rate, NAR=net assimilation rate, LAR=leaf area ratio, p_0=photosynthetic rate, r=O$_2$ uptake rate, HL=half-life of ^{14}C depletion from the treated leaves calculated from an exponential curve fitting of data presented in Fig. 1.
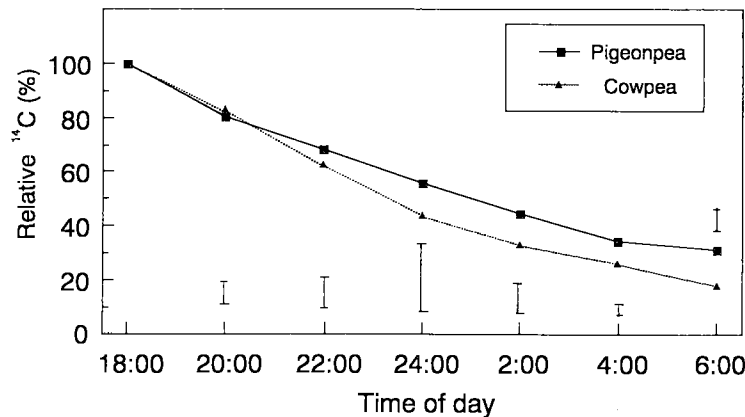
Fig. 1. Changes in retention of residual ^{14}C in leaves of pigeonpea and cowpea during the night. Relative ^{14}C is expressed as the percentage of insoluble ^{14}C in leaves at each sampling time when compared with insoluble ^{14}C in the leaves at 6:00 P.M. Vertical bars indicate the least significant difference at 5% level at each sampling time.

capacity or through the sink demand. The higher retention of current photosynthates in the leaves of pigeonpea may be associated with a weak demand for sucrose in the sink organs as well as low rates of metabolic processes (Huber and Hanson 1992; Ito et al. 1996). However, this assumption should be further examined quantitatively in relation to the soluble components translocated to leaves, stems, roots, and nodules during the night.

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