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Remobilization of nitrogen from senescing leaves of pigeonpea (*Cajanus cajan* (L.) Millsp.): genotypic differences across maturity groups?

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Abstract

Remobilization of leaf nitrogen during the seed filling stage was investigated in relation to patterns of leaf abscission with three pigeonpea genotypes (*Cajanus cajan* L.) of different maturity duration [extra-short (ESD), short (SD), and medium (MD)].

Leaflet abscission (trifoliate leaf) started from the bottom of the plants. The life span of defined leaf layers in the canopy differed among the genotypes and tended to be longer toward the top of the plants. At harvest, the leaf layer close to the pod-bearing top of the plant had a survival rate of 75% and 31% in ESD and SD pigeonpea, respectively, indicating that a large number of leaves in ESD was not entirely exploited for nutrient redistribution to the seed.

Net remobilization of nitrogen from leaves during the reproductive stage was obtained from an above-ground plant budget for N and amounted to 35%, 47%, and 37% of the pod's requirement for N in ESD, SD, and MD, respectively. The amount of nitrogen in the defined leaf layers decreased exponentially with time, and the rate of N loss was calculated from the regressions in terms of half-life. For most of the layers half-life was longest in ESD pigeonpea indicating slower abscission and remobilization compared to both other genotypes.

The present study compares two pigeonpea hybrids (ESD and SD) with a conventional genotype (MD). The results imply (1) that the efficiency to remobilize leaf nitrogen for seed development is related to the pattern of leaf abscission in pigeonpea, and (2) that SD pigeonpea remobilizes leaf N more efficiently than ESD and MD.

Key words: *Cajanus cajan*, nitrogen remobilization, leaf senescence, leaf abscission, leaf life span.

Introduction

The withdrawal of nutrients (particularly nitrogen) from leaves during reproductive development plays an important role in the process of leaf senescence and has been studied intensively with several legume crops in relation to seed nutrient accumulation, to biochemical changes in the leaves, or to whole plant budgeting. Nitrogen economy and redistribution was investigated comprehensively with soybean (Derman *et al.*, 1978; Sesay and Shibles, 1980; Mauk and Noodén, 1992), lupin (Hocking and Pate, 1977; Pate and Herridge, 1978), and pea (Pate and Flinn, 1973; Hocking and Pate, 1977). A few studies are available on chickpea (Hooda *et al.*, 1986; Hooda, 1990), cowpea (Herridge and Pate, 1977, Peoples *et al.*, 1983), and pigeonpea (Rao *et al.*, 1984, Grover *et al.*, 1985).

Pigeonpea, one of the major grain legume crops of the semi-arid tropics, is intrinsically a perennial shrub, but is widely cultivated as an annual crop, particularly in India (Ali, 1990). The development of extra-short (ESD) and short duration (SD) genotypes during the last decade aimed to match the length of the rainy season better with a quick crop growth cycle to escape severe yield reduction in drought-prone regions (Chauhan *et al.*, 1993). However, the incorporation of annuality into the pigeonpea plant through breeding combined with high yielding potential (van der Maesen, 1990) resulted in the need for improved nitrogen uptake and efficient transfer

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of nitrogen from vegetative tissue to the seed (referred to as N remobilization efficiency). Remobilization efficiency represents an important feature during periods of adverse environmental conditions when soil N uptake is restricted or during the time of decreasing N_2-fixation, which is known to occur even before flowering in pigeonpea (Kumar Rao *et al.*, 1996). Remobilization of N from leaves, particularly if excessive, inevitably causes self-destruction to a certain extent by senescence and abscission of the leaves. As commonly observed in annual plants, this may ultimately lead to whole plant death, which is most severely expressed in monocarpic senescence of soybean (Noodén *et al.*, 1978). The extent of N remobilization during the pod filling stage differs among species and cultivars and is an important criterion for breeding programmes. It has been postulated by Sinclair and de Wit (1975) that nitrogen remobilization is a necessary physiological process for legumes (including pigeonpea) in order to meet their high requirements for seed development since uptake alone cannot provide sufficient nitrogen.

Leaf abscission is of considerable interest because nitrogen abscised with prematurely dead leaves is considered to be a loss for seed protein production. Similarly, nitrogen left in the canopy at harvest is considered to be not fully utilized by the plants, unless the assimilate supply of such leaves with delayed leaf senescence supports the maintainance of nodule N_2 fixation (Abu-Shakra *et al.*, 1978). Therefore, nitrogen remobilization in relation to leaf life spans and the age structure of the canopy was investigated. So far only a few investigations have focused on the significance of leaf properties within a canopy (Secor *et al.*, 1984; Harper, 1988; Peoples *et al.*, 1983).

This study compares three pigeonpea genotypes from different maturity groups [extra-short (ESD), short (SD), and medium duration (MD)]. The aim was to relate leaf abscission patterns to differences in N remobilization efficiency and to investigate the cycling of leaf nitrogen in relation to pod development and leaf senescence. For this purpose, leaflet abscission (trifoliate leaf) was monitored precisely and the net remobilization of nitrogen from leaves as well as the loss of leaf N to the soil was quantified.

Materials and methods

Plant material and experimental design

Three cultivars of pigeonpea (*Cajanus cajan* L., cv. ICPLs 84023, 87, 1–6) representing the maturity groups of extra-short duration (ESD), short duration (SD), and medium duration (MD) were grown on an Alfisol at ICRISAT Asia Center, Hyderabad, India, in 1993. The field was prepared by a basal incorporation of diammonium phosphate at 100 kg ha^{-1} and by arranging a row spacing of 0.10 × 0.30 m. Irrigation was applied into furrows twice after sowing for crop establishment and then as required to maintain optimal soil moisture availability. The size of a plot was 43.2 m^2 consisting of 18 rows. Three replications for each genotype were randomly placed.

Sampling

Above-ground plant samples were taken at 10 d intervals during the vegetative stage and then weekly starting from budding stage. At regular sampling, 5 plants and at a later stage 10 plants were harvested from 0.5 and 1.0 m of a ridge. The samples were divided into various organs and used to measure leaf area as well as dry weight and N content of each plant organ after being oven-dried at 60 °C to constant weight. Fallen material was collected weekly from cages of 1 m^2 size located in all plots and then separated into plant organs for dry matter and N content measurements.

Critical phenological stages of the field (budding, flowering, seed development, physiological maturity) were determined at 50% of occurrence. The appearance of leaves (counted from full expansion) at the main axis was continuously recorded for the estimation of leaf life spans. As part of the regular sampling, 5 leaf fractions representing different age groups of leaves (leaf layers) were obtained as follows (Fig. 1): The main axis was divided into 5 segments according to the total number of nodes counted when the sampling of leaf fractions started (budding stage). In MD, a large basal stem segment selected proportional to the upper stem was excluded from the determination of leaf fractions because the leaves of this section were already abscised at budding. Therefore, only the upper stem segment was used to obtain the 5 leaf fractions. The number of leaf nodes determined per fraction was 4, 6, and 6 in the ESD, SD, and MD cultivars, respectively. The fractions are referred to as L1 (bottom) to L4 (in the upper canopy) and their determination was continued throughout the samplings regardless of scars of abscised leaves. The fifth leaf fraction covered the growing top zone of the plants (top) and had, therefore, a variable number of leaves. The main axis of ESD and SD terminated at

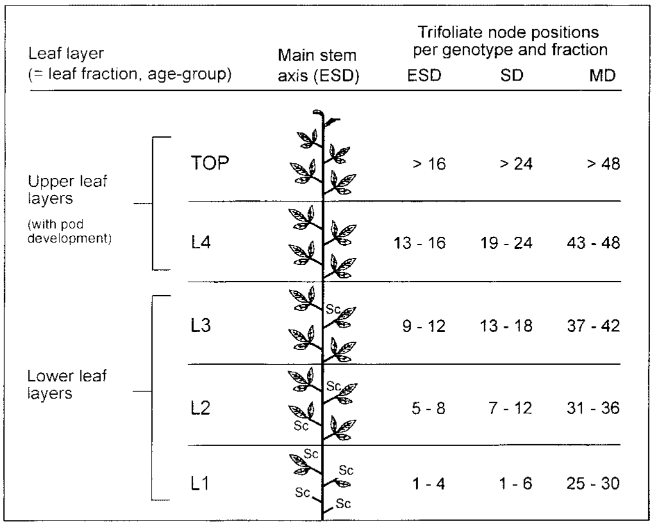

Fig. 1. Terminology and sampling of the leaf fractions representing leaf layers of defined sizes (node positions) in three pigeonpea genotypes, and precise registration of the number of attached leaflets per fraction. Sc, Scar(s) caused by abscission of 1–2 leaflets or whole leaf (3 leaflets). Each abscised leaflet counted as a scar. Sampling started when the plants were at budding stage (illustrated axis). The main axis of ESD and SD terminated at flowering. ESD, extra-short duration; SD, short duration; MD, medium duration.

flowering, while that of MD continued growing. Pod development occurred almost entirely in the top layer of the plants. The scars of abscised leaves and leaflets (trifoliate leaf) were precisely recorded throughout the reproductive stage.

Chemical analysis

Plant samples were ground to a fine powder after being dried. A portion of the powder was digested with a mixture of sulphuric acid and hydrogen peroxide. Ammonium in the digest was analysed with an indophenol colorimetric method (Chaykin, 1969).

Statistical analysis

Statistical analysis was done with SAS (SAS Institute Inc., Cary, USA, 1996). Non-linear regressions were calculated by using the DUD method, and analysis of variance was carried out with the GLM procedure followed by a Tukey test.

Results

Leaf life span

Leaf yellowing and abscission were observed to spread from the bottom to the top of the plants indicating that the senescence process was related to leaf age. The life span of five defined leaf layers in the canopy was obtained from precise records of leaf appearance and abscission at the main axis as explained earlier (Fig. 1). The youngest leaf node of each layer was used to estimate the life span of the respective layer. Only the top layer of MD could not be age-determined due to continuous growth of the main axis during the reproductive stage.

The proportion of attached leaflets decreased with time following a negative-logistic function (Fig. 2) derived from Landsberg (1977). The 'abruptness' of leaf abscission, expressed by the fit parameter n shown in Table 1, was steepest in the bottom layer L1 and less steep in the top layer. The life span of the leaves was longest in layer L4 in each of the genotypes and was extremely long in ESD, which is indicated by the high fit parameter c (72.9) representing the switch point of the time course of leaf abscission. There was a significant difference for c in the layer L4 between ESD and the other two genotypes proved by the Tukey test at the level of 1%. Start and end of leaflet abscission during the crop growth cycle was calculated from the fit equation for the first and the last leaflet abscised. At harvest, the leaf layer L4 close to the pod-bearing top of the plant had a survival rate of 75% in ESD and only 31% in SD (Fig. 2).

Growth and dry matter accumulation in plant parts

Dry matter distribution among plant parts was studied up to crop maturity which took 98, 124 and 200 d after sowing for ESD, SD and MD, respectively (Fig. 3). The length of the vegetative period was the major difference between the genotypes. The time to 50% flowering was 52 and 69 d in ESD and SD, and 118 d in MD. The plants accumulated 10%, 17% and 25% of their total dry matter (TDM) before flowering in ESD, SD and MD, respectively. When the crops entered the reproductive stage, the short-duration types shifted the investment of dry matter from leaves and stems to the pods, whilst MD

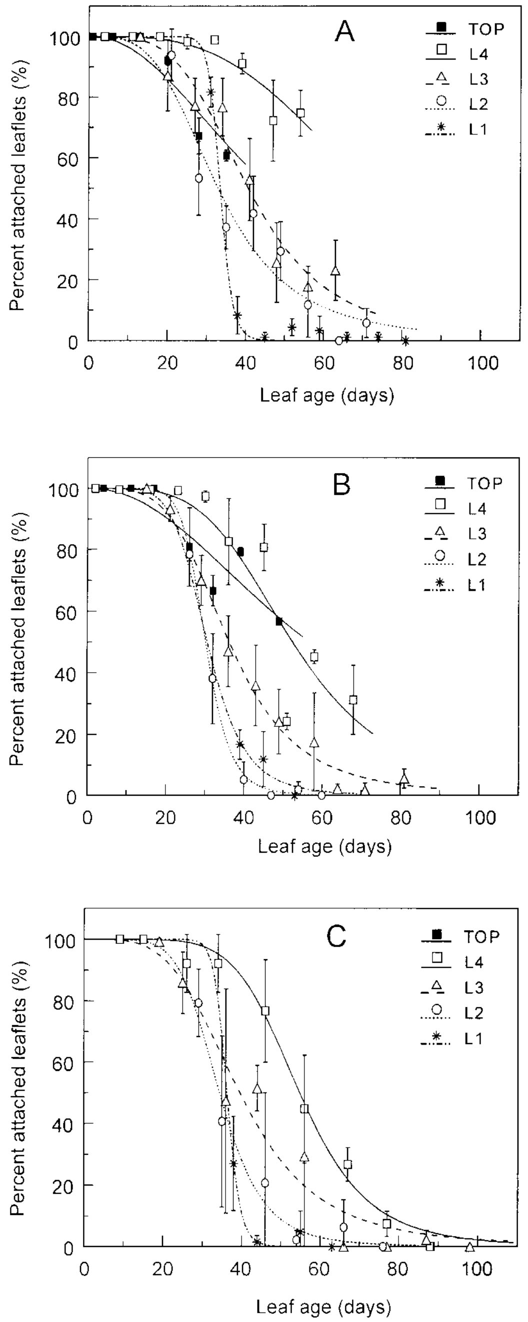

Fig. 2. Life span of various defined leaf layers at the main stem of three pigeonpea genotypes, ESD, extra-short duration (A), SD, short duration (B), and MD, medium duration (C) during one crop growth cycle. The day of full expansion of the last (youngest) developed leaf of each layer was used as starting day for the age determination. In MD, the life span of the top fraction could not be estimated due to continuous growth of the main axis. Error bars indicate standard deviation of means. Fit equation and parameters are shown in Table 1.

Table 1. *Fit parameters for the percentage of attached leaflets shown in Fig. 2 and start and end of leaflet abscission of the different leaf layers at the main stem in ESD (extra-short duration), SD (short duration), and MD (medium duration)*

Leaf layer and genotype		Fit parameters		Leaf abscission (days after full leaf expansion)	
		c	*n*	Start	End
Top	ESD	45.4	2.14	7	—
	SD	56.7	2.16	7	—
	MD	—	—	—	—
L4	ESD	72.9	3.12	20	—
	SD	52.4	4.13	18	—
	MD	54.8	6.32	27	111
L3	ESD	40.6	3.91	14	—
	SD	36.2	4.15	12	—
	MD	39.5	4.02	13	121
L2	ESD	33.0	3.48	10	—
	SD	30.2	9.14	19	49
	MD	34.4	6.20	17	71
L1	ESD	33.5	19.04	27	42
	SD	30.6	6.30	15	62
	MD	36.3	21.38	29	45

Fit equation derived from Landsberg (1977): $y = y_{\max}/1 + (x/c)^n$ with c: switch point of curve ($y_{\max}/2$), n: slope of curve. Start and end of leaflet abscission was calculated from the fit for the first and the last leaflet abscised.

continued to accumulate large amounts of dry matter in the stem. Leaf dry matter reached a maximum at early pod development and then decreased rapidly in ESD and SD due to leaf abscission and carbon translocation (data not shown) during seed filling. In MD, there was no clear decrease indicating that the formation of new leaves continued even at a later growth stage. MD accumulated a relatively small proportion of TDM in pods resulting in a low harvest index. This is a major disadvantage for the use of this type as an annual seed crop.

Nitrogen partitioning to plant parts

Nitrogen partitioning among plant parts was closely related to dry matter accumulation, but differed greatly in the proportion allocated to leaves and stem (Fig. 4). Since fallen biomass was included in the investigation, it was possible to compile an above-ground plant budget for N and calculate the net remobilization of nitrogen from the canopy leaves during reproductive development. ESD remobilized 0.057 g N per plant during the time period of 69–98 DAS (days after sowing). Provided that all the remobilized nitrogen is entirely received by the pods, it would have supplied about 35% of the pod's requirement for nitrogen measured at final harvest. SD remobilized 0.19 g N during the interval of 81–103 DAS which corresponded with the time period from early seed development to physiological maturity of the pods recorded in the field plots. This amount could provide about 47% of the pod nitrogen. Even before the final harvest, new leaf growth took place in SD which was probably due to the inherent perennial growth habit. In MD, an amount of 0.13 g N was mobilized from the leaves during 130–163 DAS. This would meet about 37% of pod nitrogen. ESD, SD and MD remobilized N at rates of 2.0 mg d^{-1}, 8.6 mg d^{-1} and 3.9 mg d^{-1}, respectively. Nitrogen uptake rates during the periods of remobilization increased with crop duration and amounted to 3.40 mg d^{-1} and 7.23 mg d^{-1} in ESD and SD, and to 9.85 mg d^{-1} in MD on a plant basis.

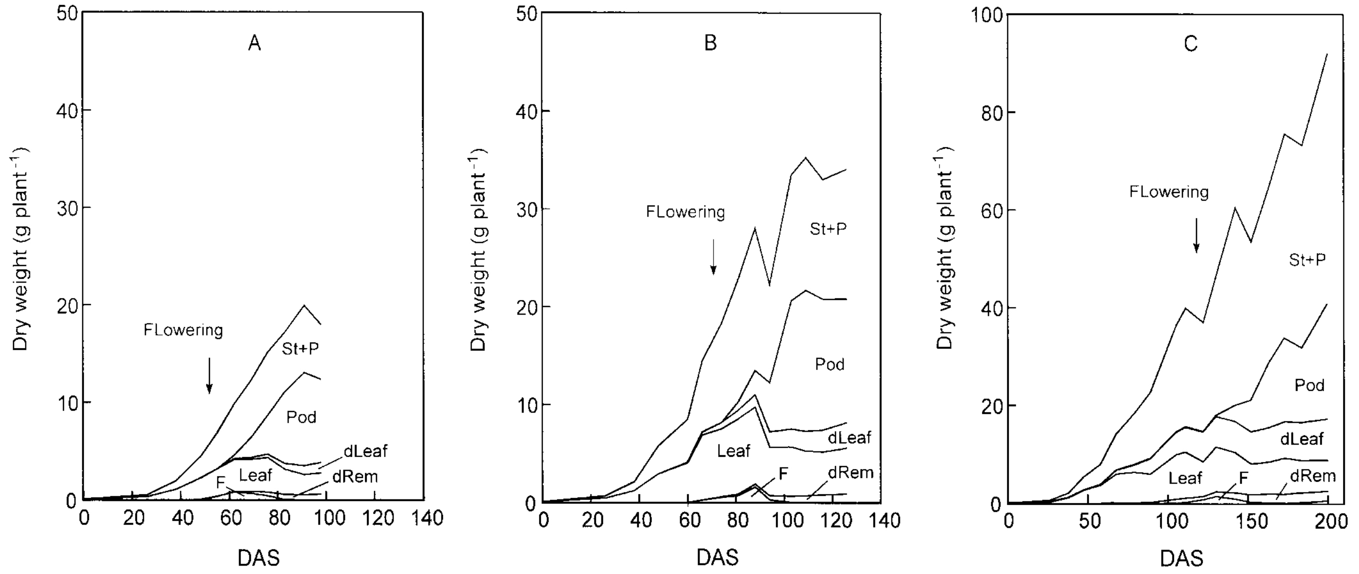

Fig. 3. Changes in total dry matter of three pigeonpea genotypes, ESD (A), SD (B), and MD (C). The dry weight of various plant organs were totalled, so that their quantities are represented by vertical distances between the lines. (Note the different scales.) The time of 50% flowering is indicated by an arrow. Flow, flowers; dLeaf, abscised leaves; dRem, abscised remaining biomass (except leaves); St + P, stem and petioles; DAS, days after sowing.

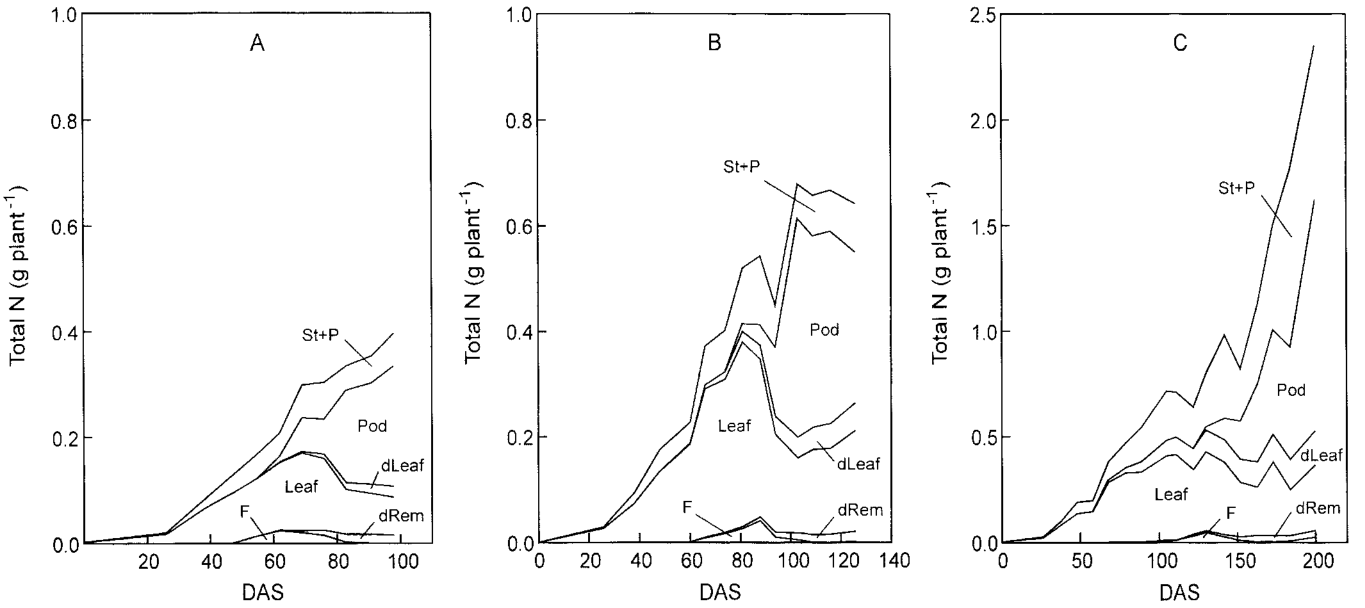

Fig. 4. Changes in total nitrogen content of ESD (A), SD (B), and MD (C) during one crop growth cycle obtained by adding up the N content of various plant organs. Quantities are represented by vertical distances between the lines. (Note the different scales.) Flow, flowers; dLeaf, abscised leaves; dRem, abscised remaining biomass (except leaves); St+P, stem and petioles; DAS, days after sowing.

Total nitrogen concentration in leaf fractions

The total nitrogen (TN) concentration of the upper canopy layers L4 and top showed similar patterns within each genotype (Fig. 5). In the short-duration types, the TN concentration of those layers decreased by about 2% N (on dry weight basis) between 20 and 40 DAF (days after flowering), while in MD it decreased with a much slower rate. The lower canopy layers (L2 and L3) showed a rapid decline between flowering and 20 DAF in both short-duration types. After that they were either abscised or maintained the TN concentration at about 3.0–3.5% N. Abscised leaves had a lower TN concentration than attached leaves, which was about 2% N. In MD, the TN concentration of abscised leaves increased toward maturity indicating that later senescing leaves were less efficiently depleted.

Total nitrogen content in leaf fractions

The amount of nitrogen decreased exponentially in the leaf layers with delay of upper leaf positions (Fig. 6). In MD, the nitrogen content of the top layer increased almost until harvest due to continuous growth of the main axis, but decreased rapidly after its cessation. The TN content of the different leaf layers was closely related to their dry weight (data not shown). In ESD and SD, the leaf layers were continuously investigated even after harvest, which is indicated by an arrow in the graphs. The layers L4 and top survived far beyond pod maturity.

In each layer, the loss of nitrogen must be due to either leaf abscission or redistribution to other plant parts. Since leaf abscission followed a negative-logistic function with a slow onset (particularly in L4) as described earlier, the exponential decrease of TN, which was measured at the same leaf samples, would be created by redistribution. In order to obtain the rate of N loss from the different canopy layers the half-life of nitrogen in each leaf layer was calculated from the exponential fits shown in Fig. 6 (Table 2). There was a clear tendency that the half-life increased from the bottom to the upper leaf layers. This implies that nitrogen in the lower leaf layers is more readily available for redistribution than nitrogen in the upper layers. For the leaf layers L2, L3, and L4, the half-life of N was significantly longest in ESD. It was shortest in SD, though significant only for L4, suggesting the most efficient N remobilization from leaves in this genotype.

Dry matter and nitrogen content in abscised leaves

The amount of dry matter and nitrogen abscised as dead biomass increased with crop duration as shown in Table 3. More than 60% of the total fallen dry matter was represented by leaves (64% in ESD, 74% in SD and 81% in MD). The proportion of nitrogen abscised with the leaves was similarly high (55% in ESD, 74% in SD and 84% in MD). Both short-duration cultivars lost around 22% of their total canopy N accumulated through leaf abscission, whilst MD lost 34%.

On a plant basis, the amount of nitrogen lost with the leaves during the crop growth cycle was 0.02 g N and 0.053 g N for ESD and SD, respectively. This was less than the net amount remobilized by those genotypes within the reproductive phase (approximately one-third). In MD, it was 0.162 g N per plant, which was more than the plant was able to mobilize for pod development.

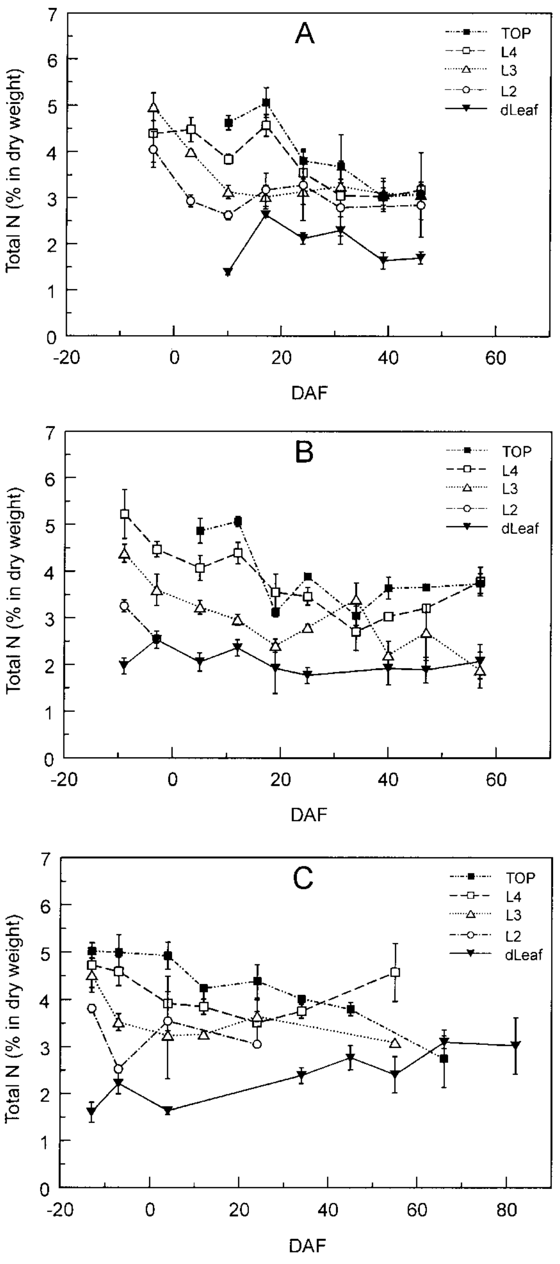

Fig. 5. Seasonal changes in total nitrogen concentration of five different leaf fractions including main stem groups and abscised leaves in ESD (A), SD (B), and MD (C). Error bars indicate the standard deviation of means. dLeaf, abscised leaves; DAF, days after flowering.

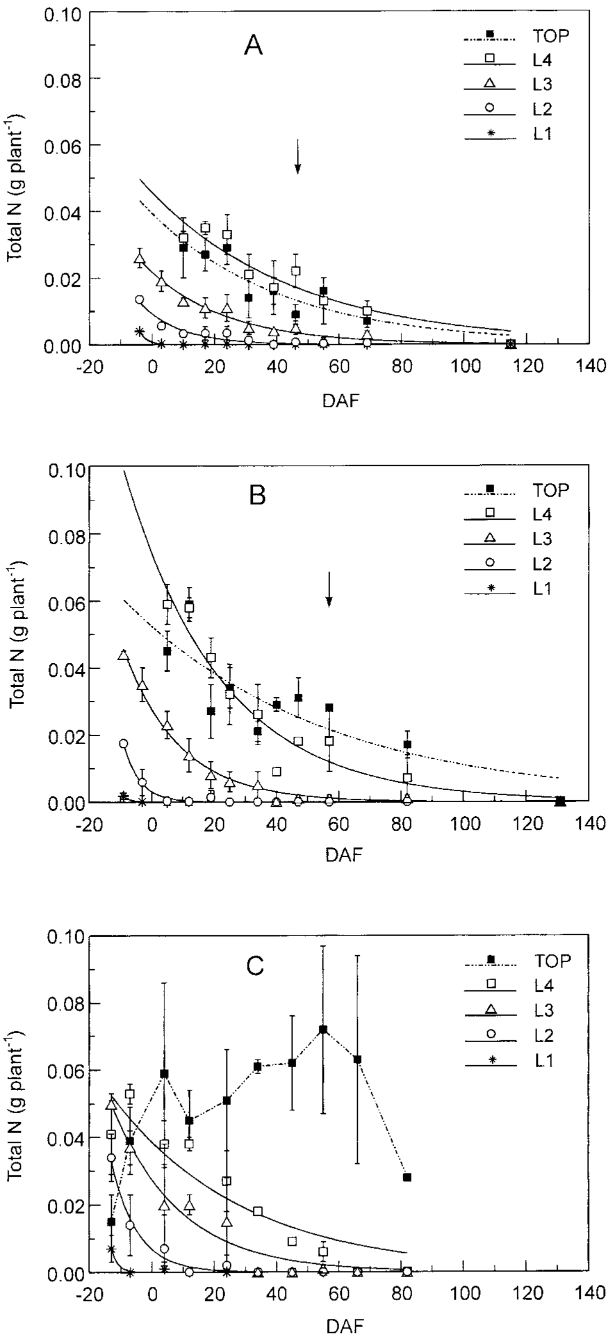

Fig. 6. Changes in the total nitrogen content of five defined leaf layers at the main stem in ESD (A), SD (B), and MD (C). The leaf layers were investigated beyond harvest in ESD and SD. The time of harvest is indicated by an arrow in the middle of the graph. Error bars indicate the standard deviation of means. Fit statistics are shown in Table 2. DAF, days after flowering.

Discussion

Leaf abscission

The process of leaf abscission in pigeonpea was expected to follow one of three options: (1) leaf abscission is mainly a function of leaf age: later developed leaves at upper positions are abscised later than earlier developed ones while leaf age is almost the same among the leaves; (2) upper leaves have a shorter life span due to destructive drainage of N from the developing pods and this pattern has been descibed for a cowpea cultivar by Pate *et al.* (1983); and (3) upper leaves have longer life spans than leaves at low positions in the canopy due to shading in the bottom area or to stay-green behaviour (and prolonged photosynthetic activity) in the upper canopy. This study shows that the third option applies to pigeonpea.

Table 2. *Fit statistics for the changes in TN content of leaf layers at the main stem in three pigeonpea genotypes shown in Fig. 6 and half-life of N calculated from the fit*

Leaf layer and genotype		R^2	a	b	Half-life of N (d)	
TOP	ESD	0.85	0.04	−0.02 a	29.4	±8.3
	SD	0.71	0.05	−0.02 b	44.3	±19.7
	MD	—	—	—	—	—
L4	ESD	0.90	0.05	−0.02 a	32.6	±7.0
	SD	0.93	0.07	−0.03 b	21.7	±3.4
	MD	0.87	0.04	−0.02 a	29.1	±6.9
L3	ESD	0.97	0.02	−0.04 a	17.4	±1.4
	SD	0.99	0.03	−0.06 b	12.5	±0.7
	MD	0.96	0.03	−0.05 b	14.9	±0.6
L2	ESD	0.93	0.01	−0.08 a	8.8	±1.5
	SD	0.99	0.00	−0.19 b	3.6	±0.2
	MD	0.99	0.01	−0.12 b	5.7	±0.6
L1	ESD	0.99	0.00	−0.40 a	1.8	±0.2
	SD	0.99	0.00	−0.45 ab	1.5	±0.0
	MD	0.97	0.00	−0.50 b	1.4	±0.0

Fit equation: $y = a \times e^{bx}$; R^2: coefficient of determination; a: intercept at the Y axis; b: slope. Values with same letters do not significantly differ at $P = 0.01$ by Tukey test. ±: Standard error. ESD, extra-short duration; SD, short duration; MD, medium duration.

The time-course of leaf abscission was a gradual process from the bottom to the top of the plants as was the decrease of TN in the five defined leaf layers.

The pattern of N translocation related to that of leaf abscission can be constructed: while lower leaves became more and more shaded, the sink demand of upper young leaves increased still before flowering. The decrease of TN concentration in leaf layers L1, L2, and L3 before the beginning of seed development as well as the lower TN concentration of abscised leaves (Fig. 5) indicate the redistribution of N to other sink organs than the seed which would be L4 and top. Thus, early accumulated N may be cycled through several organs and finally to the pods as shown for field pea by Pate and Flinn (1973). In this study, the leaf layers L4 and top represent the major canopy sources for N mobilization to the pods developing almost entirely in the top layer. However, highly efficient recycling of available leaf N for seed protein is apparently not inherited by the annually cropped ESD, where 75% leaflets of layer L4 were still attached to the plant at the time of harvest. Those leaves were able to survive more than 40 d beyond harvest (Fig. 6) despite an increasing risk of death. Even the top layer of both ESD and SD consisted of more than 50% leaflets at harvest. Furthermore, the TN concentration of abscised leaves was fairly high, which was also observed by Kumar Rao and Dart (1987) for different pigeonpea genotypes.

If an annually grown crop can afford not to claim its own leaf N resources for seed protein, it has to utilize other N sources to produce quality seed and satisfactory yield. Biological nitrogen fixation (BNF) is the obvious N source for legumes. Thus, prolonged photosynthetic capacity of the upper canopy leaves combined with maintained nodule functioning (enabled by proper assimilate supply) would result in higher N_2 fixation available for seed protein synthesis. Based on such considerations Sheehy (1983) estimated that, contrary to the self-destruct hypothesis of Sinclair and de Wit (1975), seed production of a legume does not depend on N remobilized from own plant organs, but would greatly benefit from prolonged N_2 fixation. So-called delayed leaf senescence (DLS) can indeed lead to significantly higher yields as reported for soybean (Abu-Shakra *et al.*, 1978), though DLS need not necessarily represent an advantage. A negative correlation between DLS and seed yield in certain DLS phenotypes of soybean has been reported by Phillips *et al.* (1984). However, the studies available on BNF in pigeonpea agree that nodule number and N_2 fixation decrease well before flowering in all maturity groups and particularly ESD has been reported to fix very little N, while SD performs only slightly better (Kumar Rao and Dart, 1987; Kumar Rao *et al.*, 1996). ESD apparently relies almost entirely on soil N, while a considerable amount of N is retained in the leaves at the time of harvest. This could be a limitation for the ESD type when soil N availability is restricted.

Nitrogen flow

The data obtained for net remobilization of N during pod filling can be used to construct a diagram illustrating the semi-quantitative N flow in the three pigeonpea genotypes (Fig. 7). Emphasis was laid on relative contributions to pod N received from the canopy, from other plant parts, and through N intake by roots and nodules. Among the three genotypes, SD was the most efficient one in remobilizing canopy N (Fig. 7B). More than 50% was transferred to the pods and only a relatively small

Table 3. *Dry matter and nitrogen abscised with leaves and other plant parts during the crop growth cycle in three pigeonpea genotypes*

Genotype	Dry matter (kg ha^{-1})		Nitrogen (kg ha^{-1})		% Nitrogen[a] loss
	Leaves	Total	Leaves	Total	
ESD	358±54.3	557±44.3	6.8±1.16	12.3±1.3	22.3
SD	866±61.3	1172±91.2	17.7±2.82	23.9±3.0	21.7
MD	2807±74.3	3455±223.1	54.0±1.03	64.3±1.8	34.4

[a] Proportion of N abscised with dead leaves over nitrogen remaining in attached leaves.

±: Standard deviation of means. ESD, extra-short duration; SD, short duration; MD, medium duration.

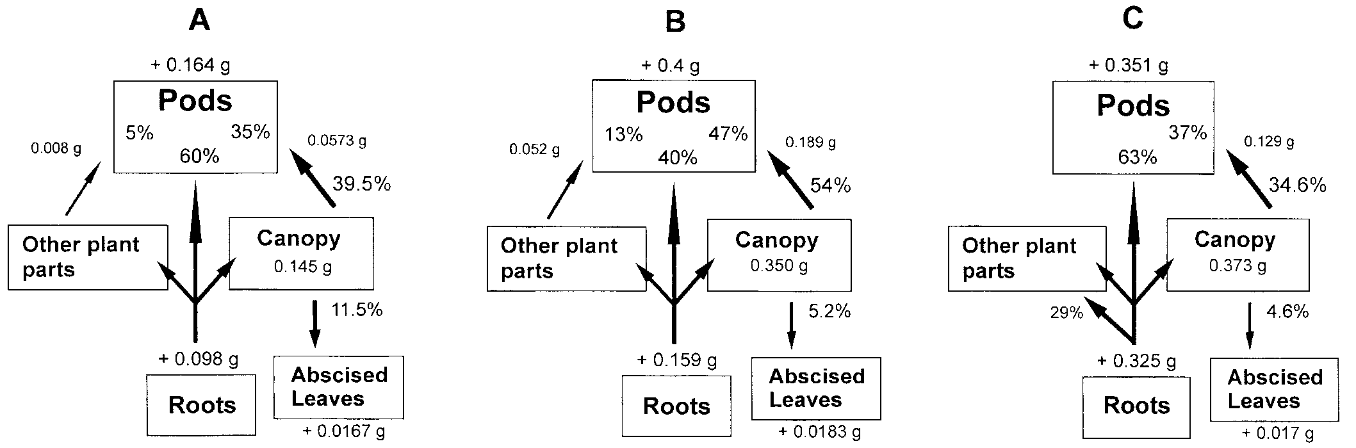

Fig. 7. Nitrogen flow diagrams drawn for the time of estimated net remobilization from canopy leaves in ESD (A), SD (B), and MD (C) matching the main period of seed filling. Amounts of nitrogen are given in g N plant^{-1}. Time periods: ESD (69–98 DAS), SD (81–103 DAS) and MD (130–163 DAS). Nitrogen uptake via roots was assumed to be cycled through vegetative plant parts before entering the pods.

proportion was abscised with dead leaves. The proportion contributed to pod N from other organs, which may be mainly the stem, was also highest in SD (13%). The ESD genotype remobilized less canopy N (39.5%) and lost a relatively high percentage by leaf abscission (11.5%), which was mainly an effect of canopy width and plant hight. The small ESD plants with only 3–4 branches contained relatively fewer younger leaves in their small canopy at the beginning of seed filling than SD with six branches.

In MD and ESD, a large proportion of pod N was received from underground plant parts (63% and 60%, respectively) which could be inorganic N uptake, N_2 fixation, and remobilized N from roots and nodules. In MD, this intake via the roots consisted of less N fixed towards maturity, which can be assumed from a study conducted by Kumar Rao and Dart (1987) showing that N_2 fixation decreases after 60 DAS across all maturity groups of pigeonpea. In ESD, nitrogen intake via roots consisted of less N fixed altogether (Kumar Rao *et al.*, 1996). Remobilization from nodulated roots may play a role in MD. This is known to meet about 33% of the seed's requirement for N in chickpea (Hooda *et al.*, 1986), but only 11% in cowpea (Peoples *et al.*, 1983). In MD, above-ground remobilization came only from leaves, while a considerable amount of N taken up by the roots was stored in other plant parts, primarily in the stem. The flow diagrams reveal that remobilization of canopy N and contributions to pod N are almost similar in the hybrid ESD and the conventional MD in relative terms though ESD is expected to be superior. ESD is designed to be cropped in high-yielding monocultures, while MD is normally used in intercropping systems where it provides a considerable amount of N to the soil through litter (Table 3).

The efficiency of leaves to remobilize N for seed filling was generally higher in this study than that reported earlier by Rao *et al.* (1984) for pigeonpea (23%). Seed and podwall were not separated here, but if so, values for seed N percentage would consequently be even higher than those for complete pods. For other legumes like chickpea, Hooda *et al.* (1986) and Hooda (1990) reported values around 25%. Cowpea leaflets remobilized with an efficiency of 31% amounting to 25% of seed N (Herridge and Pate, 1977). An extremely high efficiency of around 63% N from leaflets of a cowpea cultivar was reported by Peoples *et al.* (1983) amounting to 34% of seed N. In the present study, SD pigeonpea showed a very high remobilization efficiency meeting almost 50% of the seed's requirement for N if entirely transferred to the seed compared to only 35–37% in ESD and MD. The podwall is known to provide only negligible amounts to seed N in pigeonpea (Rao *et al.*, 1984).

Remobilization efficiency seems to be closely related to the capability of N intake through roots (soil N) and nodules (BNF). It has already been mentioned that BNF is low in SD and even less in ESD (Kumar Rao *et al.*, 1996). Sinclair and de Wit (1975) showed that the high N demand for seed production in several legumes cannot be met by N intake alone. Therefore, the remaining N has to be obtained from vegetative tissue. It was proposed that a low intake rate should result in an increased translocation from vegetative organs to the seed (Sinclair and de Wit, 1975). In the present study, the N intake rate did not seem to be related to net remobilization, but simply increased with maturity duration and, therefore, may not be directly comparable to each other among the genotypes. However, in relative terms, the N intake amounted to about 4.6% d^{-1} (% of total N taken up during the net remobilization phase) in SD and to 3.5% and 3.0% d^{-1} in ESD and MD, respectively. The phase of net remobilization was 7–10 d longer in ESD and MD compared with SD. This indicates that the N intake rate was relatively higher in SD compared to the other genotypes though SD also provided a relatively high input to seed N by remobilization.

Net remobilization occurred over a period of 22–33 d during seed filling matching the rapid decrease in TN concentration of the upper leaf layers (L4 and top) in the short-duration genotypes. After completion of net N remobilization, the attached leaflets maintained a TN concentration at about 3.0–3.5% N in the short-duration genotypes and slightly higher in MD indicating that this was the required amount of N for leaves to continue metabolic processes. A second translocation phase occurred apparently shortly before abscission. This can be concluded from the lower TN concentration of abscised leaves compared to attached leaves.

In this study, both the data for net remobilization obtained from the above-ground budget for nitrogen as well as the half-life estimated for the TN decrease from the five defined leaf layers suggest that pigeonpea genotypes differ in their efficiency to use own N resources for pod production. These differences are partly reflected by the pattern of leaf abscission. It is not known whether these are typical features inherited by the maturity groups or whether there are also significant differences within the groups. Studies on the effect of water or N deficit on remobilization and leaf senescence would be of valuable impact on the potential to improve the N economy of pigeonpea. The advantage of delayed leaf senescence in the upper canopy of ESD is not clear. It does apparently not help to maintain N_2 fixation. If it is true that the N economy of ESD relies almost entirely on inorganic soil N, than there is a need to improve the N_2 fixation pattern and the redistribution of N from leaves to design an extra-short duration pigenopea for more sustainable cropping. It remains to be proved, and depends on the extent of BNF improvement, whether DLS or self-destruction would present the better option for the ESD genotype.

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