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INHERITANCE OF SHORTDAY INDUCED DWARFING IN PHOTOSENSITIVE COWPEAS

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ABSTRACT

Cowpea [*Vigna unguiculata* (L.) Walp.] is an important source of food and fodder in the dry savanna of West Africa. Traditional cowpea varieties are photosensitive (PS), growing profusely when planted in long days and they flower when days become shorter. However, we have observed that all PS cowpea varieties exhibit dwarf characteristics when planted during short-days. This study was undertaken to confirm this observation and to elucidate the inheritance of shortday induced dwarfing in PS cowpea. Two PS and two Photoinsensitive (PI) cowpea varieties were evaluated at IITA Kano Station, Nigeria (12°03'N latitude and 8°32'E longitude) at 4 planting dates. As expected, PS varieties flowered earlier when planted during short days (<12.5 h., February and October plantings) and later during long days (>13 h., May and July plantings). However, they became extremely dwarf during short days due to lack of internode elongation resulting in a rosette appearance. The mean plant heights of PS varieties were 20.5 cm, 142 cm, 89.0 cm and 15.0 cm, when planted in February, May, July and October, respectively. The corresponding plant heights of the PI varieties were 39.0 cm, 31.5 cm, 26.0 cm and 24.5 cm. The parental, F_1, F_2 and backcross populations derived from a PI variety IT87D-941-1 and a PS variety, Kanannado were evaluated in short day conditions and selected F_3 progenies tested in long-day conditions. The genetic segregation revealed that short-day-induced dwarfing of PS is controlled by a single recessive gene pair which is designated as '*psps* (photosensitive). The complete correspondence between dwarfing under short-day conditions and PS for flowering, indicates that both phenomena are manifestation of the same PS gene pair.

Key Words: Day-length, dwarfing, genetic segregation, photoperiod, *Vigna unguiculata*

RÉSUMÉ

Le niebe [*Vigna unguiculata* (L.) Walp.] est une importante source de nutriture et de fourage dans la savanne seche de l' Afrique de l'Ouest. Les varietes traditionnelles de vigna sont photosensibles, poussant exuberamment quand elles sont plantees en jours longs et elles flourissent quand les jours reccounissent. Cependant, nous avons observe que toutes les varietes de niebe manifesterent des caracteristiques de nanisme quand elles sont plantees en jours courts. Cette etude fut entreprise pour confirmer cette observation et pour elucider l'heritabilite du nanisme induit par les jour courts. Chez les varietes de vigna photosensibles. Deux varietes photosensibles et deux insensibles a la photoperiod furent evaluees a la Station Kano, IITA, Nigeria a 4 dates de semis comme attendu la varietes photosensibles fleurirent plus tot quand elles furent plantees en jours courts (<12,5 h, semis de fevrier et d'Octobre) et plus tard en jours longs (> 13 h semis de Mai et Juillet). Cependant, elles devinrent extremement naines durant les jours courts a cause d'une abscence d'elongation des entrenceuds, resultant a un aspect de rossette. Les hauteurs moyennes des plantes des varietes photosensibles furent 20,5 cm, 142,0 cm, 89,0 cm et 150,0 cm, quand elles sont semees en Fevrier, Mai, Juillet et Octobre respectivement. Les hauteurs de plant correspondantes des varietes non photosensibles furent 39,0 cm 31,5 cm, 26.0 cm et 24.5 cm. Les parents, F_1, F_2 et les populations issues de backcross de la variete non photosensibles IT87D-941-1 et la variete photosensible

Kanannado furent evalues en conditions de jours courts et les descendants F_3 selectionnes testes en conditions de jours longs. Le segregation genetique revela que le nanisme induit par les jours courts des varietes photosensibles est controle par une seule paire de genes recessives qui est designee "psps" (photosensible). La correspondence complete entre nanisme en conditions de jours courts et le photosensibilites pour fleurir indique que les deux phenomenes sont la manifestation de la meme paire de genes de photosensibilite

Mots Clés: Day-length, dwarfing, genetic segregation, photoperiod, *Vigna unguiculata*

INTRODUCTION

Cowpea [*Vigna unguiculata* (L.) Walp.] is an important source of dietary protein and nutritious fodder in the semi-arid tropics, particularly in West and Central Africa. It is normally grown in intercropping with cereals in complex cropping systems and contributes to soil fertility and sustainability of the systems (Mortimore *et al.*, 1997; Singh *et al.*, 1997; Tarawali *et al.*, 1997). The traditional varieties are photosensitive such that when planted in long days (June - July) they grow profusely and remain vegetative until the onset of short days (September) when they begin flowering. They become ready for harvest in October-November taking 120 to 130 days from sowing to maturity. Farmers have consciously selected such varieties because i) they flower and mature after millet has been harvested and therefore no shading during reproductive stage, ii) they mature after the rains ensuring good seed quality, iii) they mature when competition for labour is minimum, and iv) they provide grain as well as fodder (Mortimore *et al.*, 1997). Therefore, current cowpea breeding efforts in the region aim to improve these local photosensitive varieties by incorporating resistance to diseases, insect pests and parasitic weeds such as *Striga gesnerioides* and *Alectra vogelii* in them (Singh, 1994; Singh *et al.*, 1997).

The effects of photoperiod and temperature on reproductive development of cowpea have been studied by several workers (Njoku, 1958; Hadley *et al.*, 1983; Craufurd *et al.*, 1996a, 1996b; Ishiyaku, 1997). However, none of the reports have mentioned the effect of photoperiod on the vegetative growth of photosensitive and photoinsensitive cowpea varieties. In our routine breeding programme we have noticed that when cowpea varieties are grown in shortday conditions (off season) for generation advance or for seed multiplication, the photosensitive varieties flower early as expected, but they also become extremely dwarf in contrast to the photoinsensitive varieties which show near normal growth and maturity. This suggests that photosensitivity affects both vegetative and reproductive stages. This experiment was conducted to confirm the dwarfing phenomenon observed in short days and its inheritance in photosensitive cowpea varieties.

MATERIALS AND METHODS

This study was conducted at the International Institute of Tropical Agriculture (IITA) Kano Station, Kano, Nigeria which is located at 12°: 03' N latitude and 8° : 32' E longitude. The first part of the study was to confirm the dwarfing effect of short daylength on photosensitive cowpeas and the second part dealt with the inheritance of this phenomenon.

Dwarfing due to short days. Two photosensitive cowpea varieties (Kanannado and IAR 1696) and two photoinsensitive cowpea varieties (IT87D-941-1 and IAR-48) were evaluated in pot culture at four planting dates, 12 February 1993, 16 May 1993, 16 July 1993 and 16 October 1993. These dates were chosen so that the vegetative phase of the plants will coincide with short or long days as well as possible commercial planting dates by the farmers in West Africa, representing both rainy season and dry season crops. At each date, three seeds of each variety were sown in 25 cm plastic pots filled with a 90:10 mixture of soil and farmyard manure. Each variety was planted in six pots constituting six replications. The pots were arranged in a completely randomised design on table tops in the screenhouse. After germination, thinning was done to maintain one plant per pot. Pots were regularly watered and kept weed free. Plants were sprayed with Sherpa plus at 1 lt ha^{-1} to protect them against insects. Data recorded were days from sowing to firstflower, days from sowing to first pod maturity, and plant height at first pod maturity. Plant height was measured from soil level to the growing tip on the main stem. Data were subjected to Analysis of Variance using MSTATC programme.

Inheritance study. The photosensitive variety, Kanannado, was crossed with the photoinsensitive early maturing variety, IT87D-941-1 and sufficient F_1, F_2 and backcross seeds were obtained between July 1993 and October 1994. Fifty seeds of each of the two parents, 25 F_1 seeds, 20 seeds of each of the two backcrosses and 150 F_2 seeds were sown on 18 November 1994 in 19 cm plastic pots in the screenhouse when the daylength became less than 12.5 h. One seed was sown in each pot. However, not all the seeds germinated. The pots were arranged in a completely randomised design. The plants were regularly protected against pre-flowering and post-flowering insects using Sherpa plus at 1 lt ha^{-1}. Data were recorded on days from sowing to first flower together with plant height at first flower, for each plant. Plant height was measured from soil level to the tallest growing tip on the main stem. Differences between tall and dwarf plants were quite pronounced and therefore, classification based on plant height was easy. However, genetic classification based on days to flower was difficult because differences with respect to days to first flower were not clear among the two parents and the overall range in F_2 was also not great. This was due to the fact that photosensitive plants flowered earlier due to short days and photoinsensitive plants were not affected by daylength and flowered early. Therefore, genetic classification was restricted to growth habit only. The numbers of tall and dwarf plants in F_1, backcross and F_2 populations were recorded and tested against expected genetic ratios using Chi-square. All the dwarf segregates were progeny tested in the field under long day condition in 1995 to check whether they all represent photosensitive class as expected.

RESULTS AND DISCUSSION

Significant varietal differences with respect to growth and reproductive development were observed at different dates of planting. The effect of dates and genotype x date interactions were also significant.

Days taken to first flowering. The number of days taken to first flower of different varieties at different dates of planting is presented in Table 1. The mean number of days to flowering was 46.2 for February, 80.0 for May, 52.1 for July and 50.0 for October plantings. However, there was significant variety x planting date interaction which affected the means for different dates of planting. Thus, even though the mean number of days to flowering for February, July and October are similar, the values for the photosensitive and photoinsensitive varieties differed markedly

TABLE 1. Effect of planting date on days taken to first flower in photosensitive and photoinsensitive cowpea varieties

Variety	Phenotype[2]	Days to first flower at different planting dates [1]				Mean	LSD 5%
		12.2.93	16.5.93	16.7.93	16.10.93		
		SD	LD	LD	SD		
IT87D-941-1	PIE	48.5	41.0	39.5	50.0	44.8	3.1
IAR-48	PIE	44.8	44.3	38.8	48.0	43.9	7.4
Mean	46.6	42.6	39.1	49.0	44.3		
Kanannado	PSL	50.0	118	58.0	57.8	70.9	10.4
IAR 1696	PSL	41.5	117	72.3	45.5	69.1	16.1
Mean		45.7	117.5	65.1	51.6	69.9	
Grand Mean		46.2	80.0	52.1	50.0		
LSD 5% between varieties		5.7	14.6	8.1	6.8		
LSD 5% between dates		3.0	Interaction =	9.0			

*SD = short day; LD = long day; PI = Photoinsensitive, PS= Photosensitive; E= Early, L= Late within and between dates (Table 1). In general, photosensitive varieties flowered later in longer days (May and July plantings, 117.5 d and 65.1 d, respectively) compared to shorter days (February and October plantings i.e., 45.7 d and 51.6 d, respectively). The corresponding values for the photoinsensitive varieties were 42.6 and 39.1 d for May and July plantings, and 46.6 and 49.0 days for February and October plantings, respectively.

Days to first pod maturity. The mean time to first pod maturity differed significantly between sowing dates and between varieties. The variety x sowing date interaction was also significant (Table 2) and therefore, the mean days to first pod maturity for different dates of planting were not a true reflection of the effect of dates. For example, even though the mean maturity period for May planting was maximum, this was due more to delayed maturity of photosensitive varieties and not so much due to photoinsensitive varieties. In general, photosensitive varieties matured earlier than photoinsensitive ones in short day sowings and later in long day sowings (Table 2). The mean days to pod maturity for the photosensitive varieties in the short day plantings of February and October were 63.5 days and 79.7 days, respectively and the corresponding values for the same period in the photoinsensitive varieties were 72.5 days and 74.0 days, respectively. The photosensitive varieties matured in 131.0 and 78 days in the long day sowings of May and July, respectively. The photoinsensitive varieties on the other hand took 60.5 and 58.5 days for the same sowing dates.

Plant height. Planting dates had significant effect on plant height and May planting gave the tallest plants. However, the effect of sowing date on plant height varied with varieties, the photosensitive varieties being more affected than photoinsensitive varieties (Table 3). The average plant height of photosensitive varieties for May and July plantings were 142.0 and 89.0 cm, respectively, compared to 31.5 and 26.0 cm for the photoinsensitive varieties (Fig. 1A, 1B, 1C). In short day sowings, the photosensitive varieties became extremely dwarf whereas the photosensitive varieties grew normally (Fig. 1D, 1E, 1F, 1G). The mean heights in the February and October sowings were 20.5 and 15.0 cm for photosensitive and 39.0 and 24.5 cm for photoinsensitive varieties, respectively (Table 3). The decrease in plant height due to change of sowing date from May (long day) to February (short day) is more than 400% (23 cm versus 141 cm in Kanannado). Generally plant height in photoinsensitive varieties was less affected by sowing date (Fig. 1D, 1G). Extreme dwarfing of the photosensitive varieties occurred in the February and October sowings when daylength

TABLE 2. Effect of planting date on days taken to first pod maturity in photosensitive and photoinsensitive cowpea varieties

Variety	Phenotype[2]	Days to first pod maturity at different planting dates[1]				Mean	LSD 5%
		12.2.93	16.5.93	16.7.93	16.10.93		
		SD	LD	LD	SD		
IT87D-941-1	PIE	67	60	58	79	66	3.6
IAR-48	PIE	78	61	59	69	67	18
Mean	72.5	60.5	58.5	74.0	66.5		
Kanannado	PSL	68	134	75	94	93	8.3
IAR 1696	PSL	59	128	81	77	86	11
Mean		63.5	131.0	78.0	79.7	89.5	
Grand Mean		68.0	95.7	68.2	85.5		
LSD 5% between varieties			9.7	15.6	8.4	10.3	
LSD 5% between dates		5.0	Interaction =11.0				

[1]SD = short day; LD = long day; [2]PI = Photoinsensitive, PS= Photosensitive; E= Early, L= Late

was shorter than 12.5 h. The effect of temperature was ruled out by the results of an experiment conducted concurrently by growing selected photosensitive and photoinsensitive varieties under short day condition (February 4 planting) with ambient temperatures (33.8/17.5 °C) in the screenhouse and under heated conditions (37.4/22.1 °C), in a glasshouse. The dwarfing effect of the shortday sowing date (4 February) on the photosensitive varieties was not significantly different in the heated glasshouse from that of the relatively cooler ambient temperatures in the screenhouse. This indicates that the phenomenon of dwarfing exhibited in the photosensitive varieties is due to the effect of the short days. Also, since this response is common to all photosensitive varieties, it must be related to differential expression of photosensitive and photoinsensitive gene(s) during short and long days.

Inheritance of shortday induced dwarfing. The segregation patterns for dwarfing in different populations derived from the cross between a photoinsensitive variety, IT87D-941-1 and photosensitive variety Kanannado grown under shortday condition are presented in Table 4. All the 12 plants of Kanannado were dwarf while all the 14 plants of IT87D-941-1 were tall. The mean plant height of Kanannado was 11.9 cm while the mean plant height of the variety IT87D-941-1 was 28.6 cm. The F_1 plants were as tall as the tall parent, with a mean plant height of 26.6 cm indicating complete dominance of photo-insensitivity in respect of growth in short days. The F_2 population segregated into 95 tall to 33 dwarf plants giving a close fit to a 3 tall : 1 dwarf ratio. The backcross F_1 plants involving Kanannado segregated into 2 tall to 4 dwarf which fits closely to 1:1 ratio, even though population size is small. All the 6 plants of the backcross involving IT87D-941-1 were tall with mean plant height of 26.9 cm. Thus, even though the backcross population size is small the results show that the dwarfing of photosensitive genotypes grown under short day is controlled by a single recessive gene pair.

In order to test whether the same gene governing photoperiod sensitivity for flowering is responsible for the control of dwarfing under short day conditions, seeds from all the dwarf F_2 plants were planted in the field in 1995 in long day conditions. All the progenies had profuse growth like the photosensitive parent Kanannado and flowered when the days became shorter. This suggests that the photosensitivity and dwarfing due to short days may be a pleiotropic effect of the same gene, which is being designated '*psps*' (photosensitive).

The earlier studies on inheritance of photosensitivity in cowpea in cowpea were made by growing the segregating populations under

TABLE 3. Effect of planting date on plant height at first pod maturity in photosensitive and photoinsensitive cowpea varieties

Variety	Phenotype²	Plant height (cm) at first pod maturity at different planting dates¹				Mean	LSD 5%
		12.2.93	16.5.93	16.7.93	16.10.93		
		SD	LD	LD	SD		
IT87D-941-1	NPSE²	40	32	27	29	32	11
IAR-48	NPSE	28	31	25	20	26	8.1
Mean		39.0	31.5	26.0	24.5	29.0	
Kanannado	PSL	23	141	68	17	62	29
IAR 1696	PSL	18	143	110	13	71	4.3
Mean		20.5	142.0	89.0	15.0	66.5	
Grand Mean		29.7	86.7	57.5	19.7		
LSD 5% between varieties		7	16	20	3		
LSD 5% between dates			4	Interaction =	13.0		

¹SD = short day; LD = long day; ²PI = Photoinsensitive, PS= Photosensitive; E= Early, L= Late

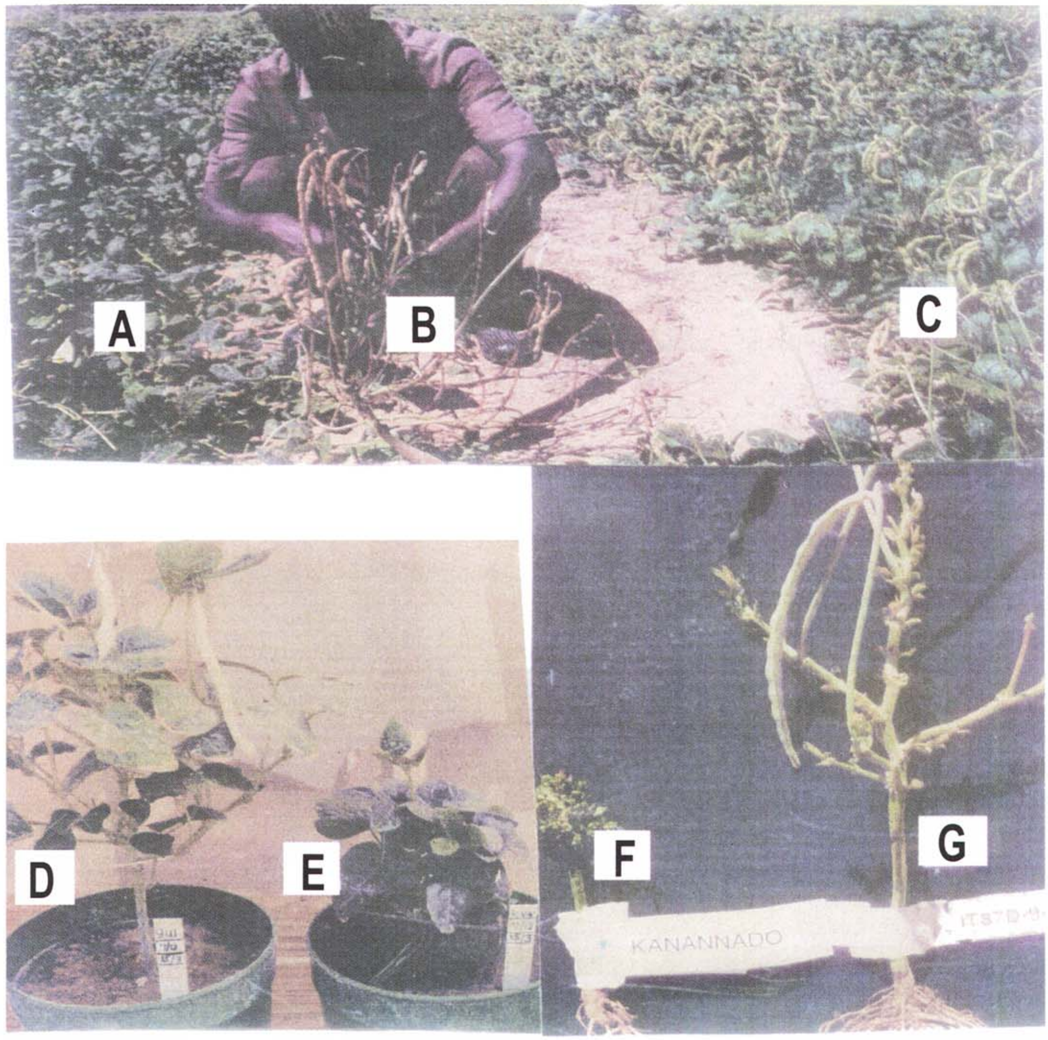

Figure 1. Growth behaviour of Kanannado (1A); IT87D-941-1 (1B); F_1 plants between Kanannado and IT87D-941-1 (1C) in the field under long days (>13 h d^{-1}); and growth behaviour of IT87D-941-1 (1D, 1G); Kanannado (1E, 1F) under short days (<12 hd^{-1}) in the screen house.

TABLE 4. Segregation pattern for plant height in different populations derived from a cross involving photosensitive and photoinsensitive cowpea varieties under shortday conditions

Generations	Number of plants		Ratio	-2	
	Tall (>15cm)	Dwarf(<14.5cm)		Value	Probability
Kananannado (PS)*	0	12	-	-	-
IT87D-941-1 (PI)*	14	0	-	-	-
F_1	14	0	-	-	-
F_1 x Kanannado	2	4	1:1	0.666	>0.5
F_1 x IT87D-941-1	6	0	-	-	-
F_2	95	33	1:3	0.041	>0.5

* PS = Photosensitive, PI = Photoinsensitive

long day conditions (Sene, 1967) and the results indicated a dominant gene inheritance. This may be due to late flowering of photosensitive segregates and difficulty in separating them from the medium/late photosensitive segregates, giving an appearance of dominant inheritance. The evaluation of segregating populations in the short day conditions makes the classification more discreet due to extreme reduction in height of photosensitive plants giving a clear monogenic recessive inheritance. It is earlier believed that in cowpea, daylength affect only the rate of reproductive development. However, this study show that short daylength not only causes early flowering in photosensitive cowpea varieties but it also induces dwarfing.

The simple inheritance and extreme dwarfing of the photosensitive plants under shortday conditions makes it a useful marker for selection of photosensitive plants in the dry season (short days) because during the main rainy season (long days), photosensitive genotypes grow profusely (Fig. 1A) and must be planted in very wide spacing to permit genetic studies or individual plant selection.

The seeds of parental material used in this study are being maintained at IITA Kano Station and are available to researchers on request.

REFERENCES

Craufurd, P.Q., Aiming, Q., Ellis, R.H., Summerfield, R.J. and Roberts, E.H. 1996a. Development in cowpea (*Vigna unguiculata*). II. Effect of temperature and saturation deficit on time to flowering in photoperiod-insensitive varieties. *Experimental Agriculture* 32:13-28.

Craufurd, P.Q., Aiming, Q., Summerfield, R.J., Ellis, R.H. and Roberts, E.H. 1996b. Development in cowpea (*Vigna unguiculata*). III. Effects of temperature and photoperiod on time to flowering in photoperiod-sensitive genotypes and screening for photothermal responses. *Experimental Agriculture* 32:29-40.

Hadley, P., Roberts, E.H., Summerfield, R.J. and Minchin, F.R. 1983. A quantitative model of reproductive development in cowpea [*Vigna unguiculata* (L.) Walp] in relation to photoperiod and temperature and implications for screening germplasm. *Annals of Botany* 51: 531-543.

Ishiyaku, M.F. 1997. Inheritance of time to flowering in cowpea [*Vigna unguiculata* (L.) Walp.]. Ph D Thesis, University of Reading, U.K.

Mortimore, M.J., Singh, B.B., Harris, F. and Blade, S.F. 1997. Cowpea in traditional cropping systems. In: *Advances in Cowpea Research*. Singh, B.B., Mohan Raj, D.R., Dashiell, K.E. and Jackai, L.E.N. (Eds.), pp. 99-113. International Institute of Tropical Agriculture and Japan International Research Center for Agricultural Sciences, IITA Ibadan, Nigeria.

Njoku, E. 1958. Photoperiodic responses of some Nigerian plants. *Journal of West African Science Association* 4:99-111.

Sene, O. 1967. Determinisme genetique de la precocite' chez *Vigna unguiculata* (L.) Walp. *Agronomie Tropicale* 22:309-318.

Singh, B.B. 1994. Breeding suitable cowpea varieties for West and Central African Savannah. In: *Progress in Food Grain Research and Production in Semi-Arid Africa*. Menyonga, J. M., Bezuneh, T.B., Yayock, J. Y. and Soumana, I. (Eds.), pp. 77-85. OAU/ STRC-SAFGRAD, Ouagadougou, Burkina Faso.

Singh, B.B., Chambliss, O. L. and Sharma, B. 1997. Advances in cowpea breeding. In: *Advances in Cowpea Research*. Singh, B.B., Mohan Raj, D.R., Dashiell, K.E. and Jackai, L.E.N. (Eds.), pp. 30-49. International Institute of Tropical Agriculture and Japan International Research Center for Agricultural Sciences. IITA, Ibadan, Nigeria.

Tarawali, S.A., Singh, B.B., Peters, M. and Blade, S.F. 1997. Cowpea haulms as fodder. In: *Advances in Cowpea Research*. Singh, B.B., Mohan Raj, D.R., Dashiell, K.E. and Jackai, L.E.N. (Eds.), pp. 313-325. International Institute of Tropical Agriculture and Japan International Research Center for Agricultural Sciences. IITA, Ibadan, Nigeria.