

# Phenological development in bambara groundnut (*Vigna subterranea*) transferred from 14 to 11 h photoperiods

A. R. LINNEMANN\*

Department of Agronomy, Wageningen Agricultural University, Haarweg 333, 6709 RZ Wageningen, The Netherlands

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## SUMMARY

Aspects of the photoregulation of phenological development in bambara groundnut were studied in a glasshouse experiment in The Netherlands. The influence of a 14 h photoperiod (which retards podding) during a period of variable length prior to an 11 h photoperiod (which induces podding) on flowering, yield and on the position of pods on the plants was determined. The third generation of three plants of genotype 'Ankpa 4' from Nigeria was used as the split-plot factor in a split-plot design with three replicates. The main plots were four daylength treatments: a period of 21, 28, 41 or 54 days under the 14 h photoperiod before transference to the 11 h photoperiod. Plants transferred after 28 or more days started flowering sooner the earlier they were transferred. Plants transferred after 21 and 28 days began flowering at the same time (51 days after sowing), thus indicating juvenility. At harvest, 135 days after sowing, the total seed dry weight per plant was higher for plants transferred after 41 and 54 days than for plants transferred after 21 days. Plants transferred after 28 days gave an intermediate value. Most (79–91 %) pods were produced on branches that developed on nodes 1–4 of the main axis. There were no differences in the fractional distribution of the pods along the main axis in plants transferred after 28 or more days. Pods of plants transferred after 21 and 28 days were more evenly distributed over the nodes of the first two primary branches than pods of plants transferred after 41 and 54 days. Plants of the latter treatments produced their pods more towards the tips of the branches and concentrated on two neighbouring nodes (nodes 5 and 6 for plants transferred after 41 days and nodes 6 and 7 for plants transferred after 54 days). Delaying the induction of podding in this experiment therefore resulted in higher seed yields per plant and a more synchronized development and hence maturity of pods.

## INTRODUCTION

Bambara groundnut (*Vigna subterranea* (L.) Verdc., syn. *Voandzeia subterranea* (L.) Thouars) has been grown for many centuries in the tropical regions of Africa south of the Sahara (Linnemann & Azam-Ali 1993). This leguminous crop is cultivated for its subterranean seeds. These are consumed fresh when semi-ripe, as a pulse when dry and mature, or ground into flour. Bambara groundnut is an indeterminate, annual herb up to 30 cm in height. It has prostrate, much-branched lateral stems just above ground level. The trifoliate leaves are carried on erect, grooved petioles, produced at the nodes of the creeping stems.

Flowers are normally carried in pairs on peduncles at the base of the petioles. After pollination and fertilization, the peduncles lengthen, thus bringing the ovaries underground.

Simultaneous maturity of all the fruits on one plant is a desirable trait in food production systems where harvesting is a single event. Fruits that mature long before the harvest date are more likely to be attacked by pests and diseases, and/or to germinate prematurely. Large yield losses may be the result. In bambara groundnut, for example, yield loss resulting from pod rotting in the humid environment of Ibadan was found to be 1.5 % rotten pods at 115 days after sowing and 37.3 % 35 days later (Goli & Ng 1988). Because of the indeterminate habit of bambara groundnut, pods develop and mature over a long period. The first pods normally develop from early flowers close to the main axis of the plant. During the

\* Present address: Laboratory of Dairying and Food Physics, Department of Food Science, Biotechnion, Bomenweg 2, 6703 HD Wageningen, The Netherlands.



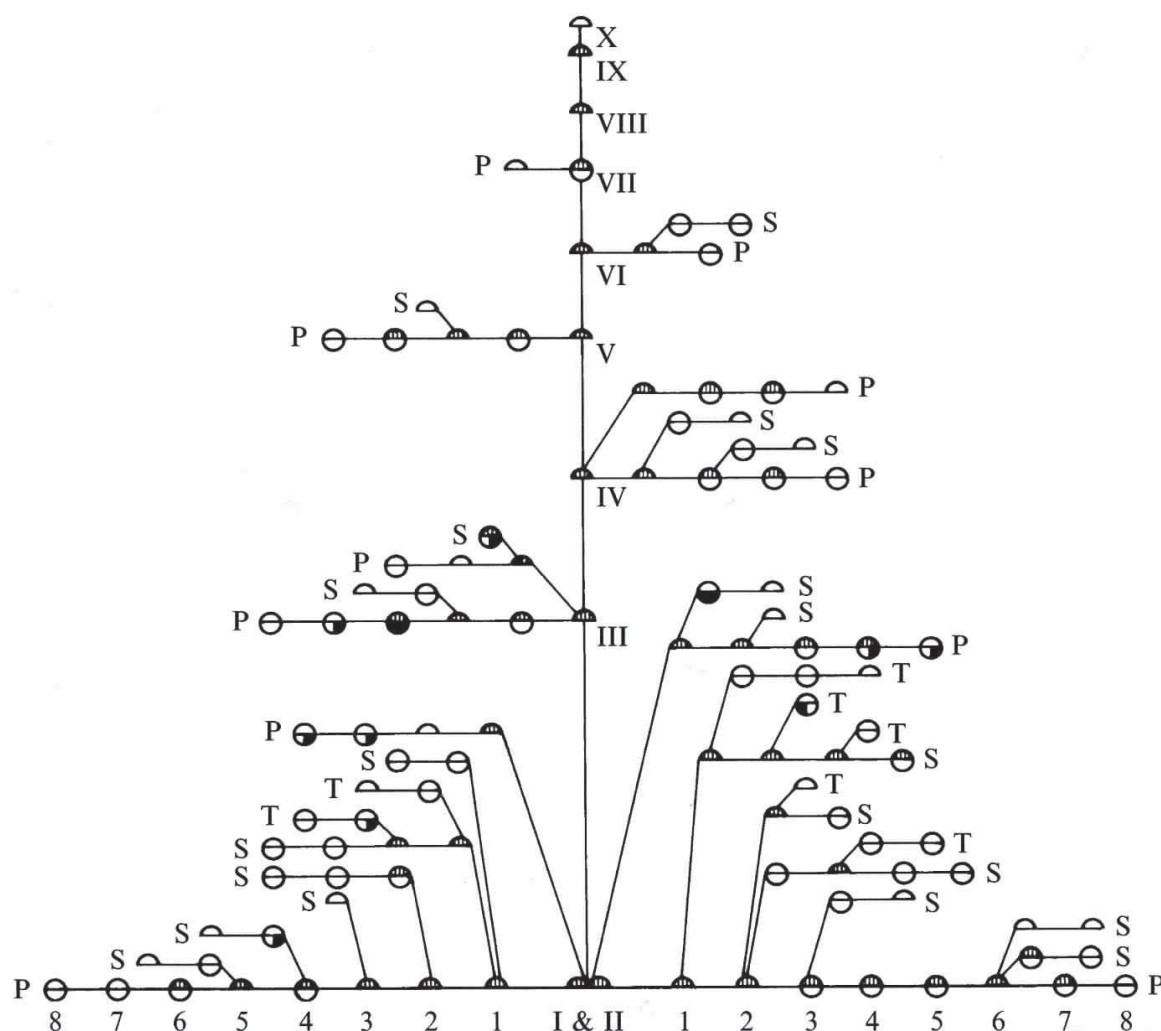


Fig. 1. Example of a schematic drawing of the habit of a bambara groundnut plant (in this case of a plant transferred after 41 days from a 14 h to an 11 h photoperiod). Roman numerals indicate node number on main axis, Arabic numerals indicate node number on the first two primary branches, and letters indicate branch order: primary (P), secondary (S) or tertiary (T). Symbols are used for a node without ( $\circ$ ) or with a leaf ( $\bullet$ ), with ovaries and without ( $\ominus$ ) or with a leaf ( $\oplus$ ), and without a leaf with one ( $\odot$ ) or two full-grown pods ( $\bullet$ ), and with a leaf and one ( $\oplus$ ) or two ( $\bullet$ ) full-grown pods.

growing season the branches develop and flowers and pods continue to be produced. However, small-scale bambara groundnut farmers often solve the problem of uneven maturity by harvesting the pods as they mature (Kay 1979).

Bambara groundnut genotypes differ in their response to photoperiod (Linnemann 1991). This has implications for breeding locally adapted varieties. In a photoperiod-sensitive genotype from Ankpa in Nigeria, for example, the onset of flowering, progress of flowering, onset of podding and progress in pod growth in plants under photoperiods of 14 h or longer were all retarded compared with plants under photoperiods of 13 h or less (Linnemann 1993). Podding was affected more than flowering: some plants flowered but failed to produce pods under photoperiods of 14 and 16 h. These plants had many undeveloped ovaries, some of which developed into full-grown pods after transference to a 12 h photoperiod regime. Hence the delay or absence of podding under photoperiods of 14 h or longer was attributed to the growth of fertilized ovaries being checked.

Transference from a 14 to a 12 h photoperiod for 16 days or less was insufficient to induce podding in this genotype from Ankpa (Linnemann 1994). Pods were only produced by plants which were not returned from the 12 to the 14 h photoperiod.

This paper presents a further quantification of photoregulation of development in bambara groundnut. In an experiment, the influence of a 14 h photoperiod during a period of variable length was determined on yield and on the position of pods which developed after transference to an 11 h photoperiod. The aim of the trial was to establish the conditions that would induce pods to develop on nodes close to one another, thus resulting in more even development and maturity than when pods develop on nodes scattered over the branches.

## MATERIALS AND METHODS

The experiment was conducted in a glasshouse at Wageningen Agricultural University (51° 58' N), The Netherlands. A genotype collected in a market in



Ankpa (7° 22' N), Nigeria, was used. This genotype, 'Ankpa 4', had been used in previous experiments (Linnemann 1993, 1994). It is photoperiod-sensitive for both flowering and podding. Plants were the third generation of three parent plants randomly selected from material collected in 1988. This planting material was used instead of the original seed lot to create greater genetic homogeneity within treatments and thus to enable the differences between treatments to be expressed more clearly.

The trial was conducted as a split-plot experiment with three replicates. The main plot set-up was a randomized complete block design with 12 units (three sets of four trolleys). The main plot treatments were four daylength treatments: a period of 21, 28, 41 or 54 days under a 14 h photoperiod before transference to an 11 h photoperiod. A main plot consisted of a trolley carrying 30 pots, each containing one plant. Each main plot was split into three for the different progenies. Plants were grown in 5-litre pots filled with a mixture of sand and humus-rich potting compost (1:1 v/v). Seed was sown on 2 April 1991. Eight days later, plants had emerged. Plants received an 8 h period of natural daylight, which was extended in sheds by low-intensity, fluorescent (from Philips TLD 36 W tubes) and incandescent light (from Philips 40 W bulbs) of 10  $\mu\text{mol}/\text{m}^2/\text{s}$  photosynthetically active radiation (PAR; 400–700 nm) at plant height to achieve the desired photoperiod. Thus, the differences in total PAR between treatments were negligible. Average temperatures were between 26 and 30 °C during the day and between 22 and 25 °C at night. Average daily relative humidity was 60 %, or less on sunny days.

The date of the first open flower and the number of leaves per plant on the day of the onset of flowering were recorded for all plants. Five plants per progeny per trolley, randomly chosen at the beginning of the daylength treatments, were used for analysis at the final harvest, 135 days after sowing (DAS). In order to study plant habit and pod development, random samples of three plants (one of each progeny) were taken from the remaining 15 pots per trolley at fortnightly intervals from the time that 50% of the plants of a treatment had started flowering. Thus, the intermediate harvests were: 52, 66, 80, 94 and 108 DAS for plants transferred after 21 and 28 days; 66, 80, 94, 108 and 121 DAS for plants transferred after 41 days; and 80, 94, 108 and 121 DAS for plants transferred after 54 days. At the intermediate and final harvests, plants were drawn schematically, using different symbols for different nodes (Fig. 1). These drawings were used to derive the following quantitative data on certain plant characteristics: the number of primary (P), secondary (S) and tertiary (T) branches; the position of the first open flower on the first two, equally old, primary branches on nodes 1 and 2 of the main axis (only for the intermediate

harvests taken 80, 94 and 108 DAS, when all treatments were sampled); the distribution of the pods over the length of the main axis; and the position of the pods on the branches. In addition, the number of leaves per plant was recorded, as well as total above-ground dry matter after drying for 24 h at 105 °C, and number and dry weight of pods and seeds. Data were submitted to an analysis of variance.

## RESULTS

### *Onset of flowering*

Plants transferred after 21 or 28 days from the 14 to the 11 h photoperiod were the first to flower (Table 1): on average, 49.7 and 51.5 DAS, respectively. Plants transferred after 41 days flowered *c.* 10 days later. Plants transferred after 54 days needed another 10 days more for the onset of flowering. Progenies differed significantly in the onset of flowering ( $P < 0.05$ ; Table 2). There was a 5-day difference between the average date of the onset of flowering for the earliest and the latest progenies. No interaction was found between main plot treatments and progenies for the onset of flowering, nor for any of the other effects studied.

Table 1. *Growth characteristics of bambara groundnut, 'Ankpa 4' from Nigeria (averages per plant of three progenies) for treatments that received 21, 28, 41 or 54 days under a 14 h photoperiod before transference to an 11 h photoperiod*

	Days under a 14 h photoperiod				S.E. (6 D.F.)
	21	28	41	54	
Onset of flowering (days after sowing)	49.7	51.5	61.9	71.3	1.32
Period between transference and onset of flowering (days)	28.7	23.5	20.9	17.3	1.32
No. of leaves at the onset of flowering	23.7	25.6	35.2	40.8	1.39
No. of leaves at harvest	44.2	44.8	45.7	53.1	3.63
No. of pods	4.1	4.7	6.7	7.2	1.60
Total seed dry weight (g)	1.00	1.36	2.50	2.70	0.580
Average seed dry weight (g)	0.24	0.29	0.37	0.38	0.036
Total dry matter, excluding roots (g)	9.5	10.3	11.5	13.0	1.55
Harvest index	0.10	0.13	0.22	0.21	0.036
No. of primary branches	13.7	14.5	12.8	12.4	0.27
No. of secondary branches	18.0	19.1	16.8	18.5	2.73
No. of tertiary branches	2.5	2.3	2.2	2.5	0.72



Table 2. *Growth characteristics of three bambara groundnut progenies from genotype 'Ankpa 4', Nigeria (averages per plant of four daylength treatments)*

	Progeny			S.E. (16 D.F.)
	1	2	3	
Onset of flowering (days after sowing)	55.8	59.0	60.9	0.58
Period between transference and onset of flowering (days)	19.8	23.0	24.9	0.58
No. of leaves at the onset of flowering	30.2	29.6	34.2	0.88
No. of leaves at harvest	48.0	44.6	48.4	1.26
No. of pods	5.2	6.0	5.8	0.48
Total seed dry weight (g)	1.80	2.05	1.83	0.313
Average seed dry weight (g)	0.33	0.33	0.31	0.040
Total dry matter, excluding roots (g)	11.0	10.8	11.4	0.41
Harvest index	0.15	0.18	0.16	0.015
No. of primary branches	14.0	12.4	13.8	0.34
No. of secondary branches	16.3	18.7	19.2	1.02
No. of tertiary branches	1.4	3.2	2.5	0.53

The number of days between the day of transference from the 14 to the 11 h photoperiod and the onset of flowering was inversely related to the duration of the 14 h photoperiod (Table 1). The largest difference between two consecutive treatments (5.2 days) was for plants transferred after 21 days compared with plants transferred after 28 days. Differences between progenies were as for the onset of flowering (Table 2).

#### *Number of leaves*

The number of leaves per plant at the onset of flowering was similar for plants transferred after 21 and 28 days (Table 1). On average, these plants had 25 leaves each. Plants transferred after 41 days had 35 leaves at the onset of flowering, whereas plants transferred after 54 days had 41 leaves. One of the progenies had on average four leaves more at the onset of flowering than the other two progenies ( $P < 0.05$ ; Table 2).

The rate of leaf development was similar for all treatments before the onset of flowering. The following linear relationship, based on counts of leaf numbers on 23, 37 and 51 DAS, describes the rate of leaf development during this period:  $-14.2 + 0.78t$  ( $r^2 = 0.96$ ), in which  $t$  is the period from sowing in days. In other words, 'Ankpa 4' produced three leaves every four days during the first 51 DAS.

At the final harvest, similar numbers of leaves per plant were found for all treatments (Table 1). On average, a plant had 47 leaves. Therefore the plants which spent 21 or 28 days in the 14 h photoperiod produced more leaves per plant in the period between the onset of flowering and harvest than the plants

which spent 41 or 54 days in the 14 h photoperiod. The number of days used for the production of one leaf in the period between flowering and harvest were: 4.2, 4.3, 7.0 and 5.2 days for plants which were transferred after 21, 38, 41 and 54 respectively.

One of the progenies had significantly fewer leaves than the two other progenies (Table 2).

#### *Yield characteristics*

The total seed dry weight per plant was significantly higher for plants transferred after 41 and 54 days than for plants transferred after 21 days ( $P < 0.05$ ; Table 1). Plants transferred after 28 days gave an intermediate value. There was a trend for number of pods to increase, but not significantly, with the number of days under the 14 h photoperiod. The average seed dry weight was again significantly higher for plants transferred after 41 and 54 days than for plants transferred after 21 days. The average seed dry weight for plants transferred after 28 days was intermediate. No differences were found between progenies for total seed dry weight and number of pods per plant, nor for the average seed dry weight (Table 2).

#### *Dry matter production and harvest index*

There was no difference between treatments for the total above-ground dry matter (DM) per plant although the total above-ground DM per plant tended to increase with the period that plants were under the 14 h photoperiod before transference to the 11 h photoperiod (Table 1). The harvest index (seed dry weight/total DM) of plants transferred after 41 and 54 days was more than twice the value obtained for plants transferred after 21 days. An intermediate value was found for plants transferred after 28 days.

Progenies did not differ in total above-ground DM nor in harvest index (Table 2).

#### *Number of primary, secondary and tertiary branches*

The number of primary branches per plant differed significantly between treatments ( $P < 0.05$ ; Table 1). The highest number was found for plants transferred after 28 days. The lowest values for plants transferred after 41 and 54 days. Plants transferred after 21 days had an intermediate number of primary branches per plant. No differences between treatments were found for the number of secondary and tertiary branches per plant. On average, plants had *c.* 18 secondary and 2.5 tertiary branches each.

Progenies differed in the number of primary, secondary and tertiary branches per plant (Table 2). Progeny three had relatively high numbers in all three classes of branches. Progeny one combined a high number of primary branches with low numbers of secondary and tertiary branches, whereas progeny



Table 3. Average node number on which the first open flower developed on the first two branches on the main axis of bambara groundnut plants (averages of three progenies) that received 21, 28, 41 and 54 days under a 14 h photoperiod before transference to an 11 h photoperiod

	Days under a 14 h photoperiod				S.E. (6 D.F.)
	21	28	41	54	
Average node number	2.9	3.3	4.3	5.7	0.30

two had the opposite; a low number of primary branches with high numbers of secondary and tertiary branches.

#### *Position of the first flowers*

Seedlings have two leaves: one on the first and one on the second node of the main axis. These nodes are so close that their order cannot be determined macroscopically. Soon after germination, the first two primary branches develop simultaneously in the axils of the two leaves on the main axis. The position of the first open flower on each of these two, equally old, primary branches was determined at the three intermediate harvests when plants of all treatments were sampled (i.e. 80, 94 and 108 DAS). The position of the first flower was expressed as the node number on which the flower developed, counting from the main axis. There were no differences between plants transferred after 21 or 28 days (Table 3): on average, the first flowers developed on node 2.9 from the main axis in plants transferred after 21 days and on node 3.3 in plants transferred after 28 days. Plants transferred later produced their first open flower on a higher node number ( $P < 0.05$ ), i.e. further from the main axis: transferring plants after 41 and 54 days caused differences of 1.0 and 2.4 nodes, respectively, in the position of the first flower, compared with plants transferred after 28 days. There were no differences between progenies in the position of the first open flower.

Once flowering had started, plants produced a pedunculus with two flowers at every node that subsequently developed. Thus, all plants produced many ovaries.

#### *Distribution of pods along the main axis*

Most (79–91 %) pods were produced on branches that developed on nodes 1–4 of the main axis (Table 4). The fractional distribution of pods along the main axis (expressed as the total number of pods produced on the branches of a node on the main axis divided by the total number of pods per plant) indicated no

Table 4. Distribution of pods along the main axis (expressed as the total number of pods produced on the branches of a node on the main axis divided by the total number of pods per plant) for bambara groundnut plants (averages of three progenies) that received 21, 28, 41 or 54 days under a 14 h photoperiod before transference to an 11 h photoperiod

Node number on main axis	Days under a 14 h photoperiod				S.E. (6 D.F.)
	21	28	41	54	
1 and 2*	0.63	0.50	0.61	0.55	0.050
3	0.08	0.22	0.18	0.22	0.034
4	0.08	0.14	0.12	0.13	0.039
5	0.14	0.09	0.07	0.06	0.048
6	0.05	0.03	0.02	0.03	0.024
7 and up	0.02	0.02	0.01	0.01	0.010

\* No distinction between branches from nodes 1 and 2 was possible, because they developed simultaneously.

differences for plants transferred after 28 or more days. Only plants that were transferred after 21 days had a different pod distribution: they had a higher fraction of pods on nodes 1 and 2 than plants transferred after 28 days, whereas the fraction on node 3 was less than that of all other treatments ( $P < 0.05$ ). In general, the fraction of pods decreased as the node number on the main axis increased, except in plants that were transferred after 21 days.

Significant differences between progenies were found in two instances: the fraction of pods of progeny 1 on node 3 (0.12) was smaller than that of progenies 2 and 3 (0.20 and 0.21, respectively), and the fraction of pods of progeny 2 on node 5 (0.03) was smaller than that of progenies 1 and 3 (0.14 and 0.11, respectively).

#### *Position of pods on the branches*

Branches that developed on nodes 1 and 2 of the main axis could be divided into five groups: (1) the first two primary branches of similar age, (2) their secondary branches, (3) 1–4 primary branches that formed later, (4) their secondary branches and (5) a few tertiary branches. All treatments and progenies had a similar fraction of pods in each of these five groups of branches. On average, 0.16 of the pods that developed on the branches of nodes 1 and 2 on the main axis occurred on the first two primary branches, 0.41 on their secondary branches, 0.22 on the later-formed primary branches, 0.14 on their secondary branches and 0.07 on tertiary branches.

The distribution of the pods on the first two primary branches was calculated as the number of pods on a node divided by the total number of pods



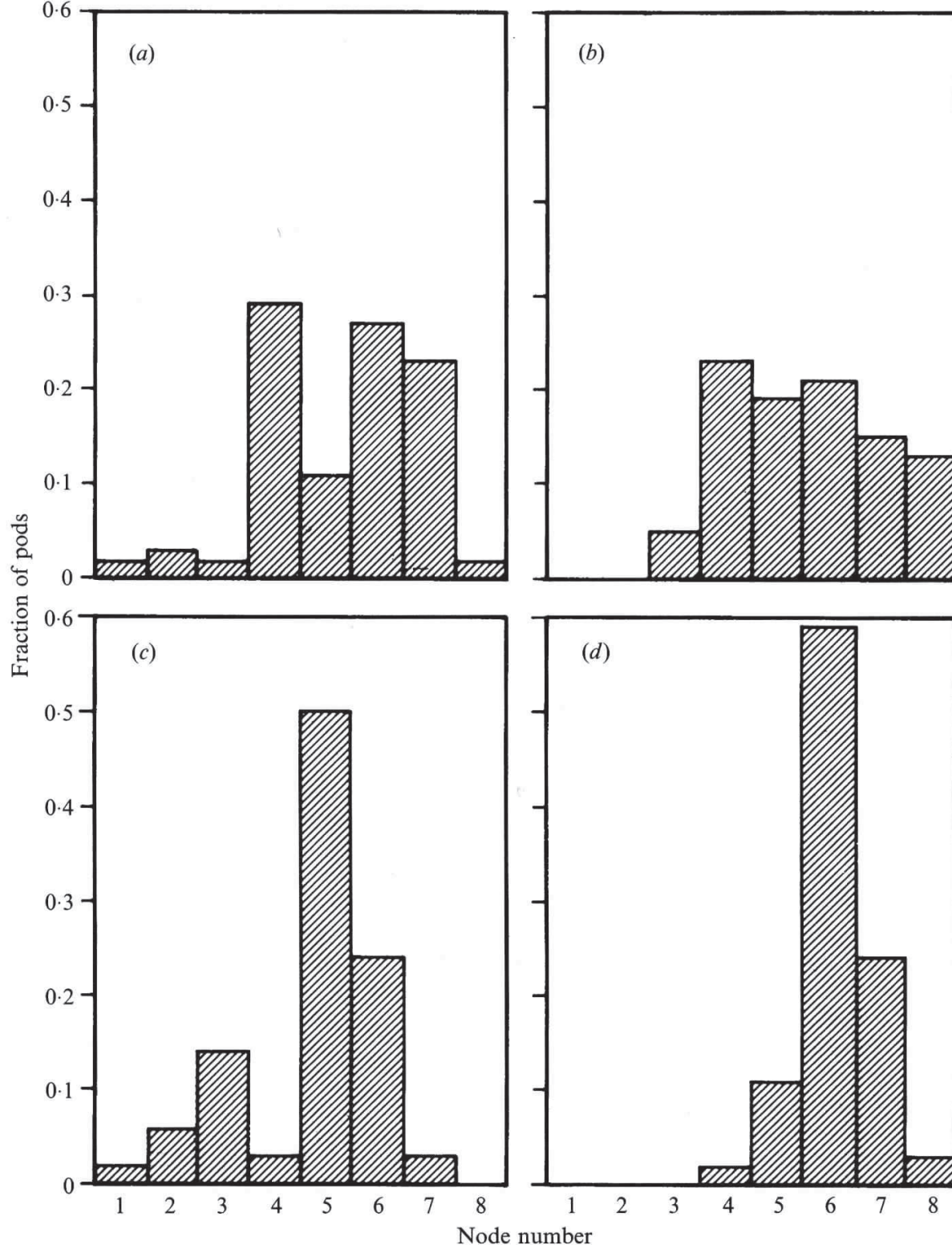


Fig. 2. Fractional distribution of the pods over the nodes of the first two primary branches that developed on nodes 1 and 2 of the main axis for plants that were transferred from a 14 to an 11 h photoperiod after (a) 21, (b) 28, (c) 41 and (d) 54 days.

on these two primary branches (Fig. 2). Treatment effects were found for the fraction of pods on nodes 4 and 7 ( $P < 0.05$ ). Plants transferred after 21 and 28 days had a larger fraction of pods on node 4 than plants transferred after 41 and 54 days. A greater fraction of pods on node 7 was found in plants transferred after 21 and 54 days than in plants transferred after 41 days. Plants transferred after 28 days had an intermediate value.

Differences appeared in the way that the pods were distributed over the first two primary branches. The pod distribution pattern for plants transferred after 21 days showed two peaks: the first on node 4 and the second on nodes 6 and 7 (Fig. 2a). Plants transferred after 28 days had a fairly even pod distribution with similar fractions on nodes 4–8 (Fig. 2b). The pod distribution patterns of plants transferred after 41 and 54 days peaked sharply: on nodes 5 and 6 for



plants transferred after 41 days and on nodes 6 and 7 for plants transferred after 54 days (Fig. 2c, d).

The comparisons of positions of pods on other primary branches and on the secondary branches gave no unambiguous pod distribution patterns.

## DISCUSSION AND CONCLUSIONS

The finding that photoperiod delayed the onset of flowering in plants transferred after 28 or more days, but caused no difference in the onset of flowering between plants that had received 21 or 28 days under the 14 h photoperiod before transference suggests that the progenies in this experiment have a juvenile phase during which flowering cannot be induced by an 11 h photoperiod. However, Summerfield & Wien (1980) contend that most tropical grain legumes have no pre-inductive (juvenile) phase for flowering. The bambara groundnut progenies in this experiment would therefore be exceptions, such as, for example, the four soyabean cultivars investigated by Collinson *et al.* (1993), which had a juvenile phase varying from 11 to 33 days.

As Table 1 shows, the 14 h photoperiod had a slight inductive effect: a longer sojourn in that regime shortened the subsequent period required in the 11 h photoperiod to induce flowering. This corroborates the contention of Roberts & Summerfield (1987) that in short-day plants, any photoperiod longer than the base photoperiod can have some inductive effect, at least up to the ceiling photoperiod.

Plants whose onset of flowering was delayed by the photoperiod treatment had more leaves and a larger leaf area at the beginning of flowering. They therefore had a greater capacity to produce assimilates which could be used for reproductive and continued vegetative growth. This hypothesis is supported by the observation that the total above-ground DM per plant tended to increase with the length of the period that plants were in the 14 h photoperiod before transference. Number of pods per plant also tended to increase with the number of days under the 14 h photoperiod. A similar increase was found for the total seed dry weight per plant and the average seed dry weight. In combination with the findings on treatment-induced differences in leaf numbers at flowering and total above-ground DM, these results lead to the conclusion that early induction causes plants to use assimilates for early reproductive growth, at the expense of continued vegetative growth and of total seed yields per plant. An early start of reproductive growth is therefore only a sound strategy in areas where the duration of the growing season is limited, e.g. by water shortage.

In a comparable experiment, soyabean plants were subjected to 30, 45 and 60 days under a 16 h photoperiod before transference to the normal, short photoperiod (Pookpakdi *et al.* 1987). There was a

positive correlation between the amount of vegetative growth before floral induction and the yield, the number of pods per plant, and the number of seeds per pod. From this the authors concluded that vegetative growth before flowering is an important factor influencing the yield of soyabean. The results presented above imply that in bambara groundnut vegetative growth before the onset of podding is of similar importance.

The absence of a difference in the position of the first open flower on the first two primary branches for plants transferred after 21 and 28 days suggests that this position, at about node number 3, is the minimal distance between the main axis and the first node to flower. The position of the first open flower shifted towards the tips of the branches at the rate of about one node per additional fortnight under the 14 h photoperiod. This shift is in accordance with Wallace (1985) who states that one of the ways temperature and/or photoperiod can modulate time to flowering is by causing a different node to flower.

Since no differences in the fractional distribution of pods along the main axis were found between plants transferred after 28 or more days (see Table 4), it can be inferred that differences in the total number of pods per plant were evenly distributed over the branches that developed on the different nodes of the main axis. Furthermore, no evidence was found of yield reductions caused by reduced branch development similar to those reported by Settini & Board (1988) in late-planted (i.e. early-induced) soyabean. Nor was it possible to correlate seed yield with the number of secondary branches (a correlation established by Chhina *et al.* (1991) in chickpea), because in our experiment there were no differences between treatments in this morphological trait.

The pods on the primary branches were not only located nearer the tips of the branches in plants that were transferred late, i.e. after 41 or 54 days (Fig. 2), but they were also more concentrated on a small number of nodes than pods of plants transferred after 21 and 28 days. Consequently, pods develop and mature more evenly if plants are transferred late to the inductive 11 h photoperiod, than if plants are transferred early.

In a future experiment to investigate the position of pods it would be preferable to use an accession that produces more pods per plant. However, when selecting this accession it must be taken into account that number of pods per plant is probably correlated with sensitivity to photoperiod: personal observations indicate that the more photoperiod-sensitive genotypes tend to have fewer large pods, whereas photoperiod-insensitive genotypes have many small pods.

The results obtained with the three progenies in this experiment are probably not representative for the genotype 'Ankpa 4' was a whole. For instance, the



three progenies flowered later than genotype 'Ankpa 4' did in previous experiments (Linnemann 1993, 1994). However, the fact that the results from the three progenies are not typical of genotype 'Ankpa 4', does not invalidate the conclusion from this experiment that early induction of photoperiod-sensitive bambara groundnut accessions leads to lower total seed yields per plant and more uneven maturity than late induction. This conclusion has a practical implication for the selection of adapted genotypes.

Photoperiod-induced podding should be as late as the local growing conditions permit, to maximize the time available for vegetative growth before the onset of podding.

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