Post-flowering photoperiodic and temperature effects on phenological development and yield in field-grown bambara groundnut (*Vigna subterranea*) landraces in a sub-tropical environment.

A. Sesay
Department of Biological Sciences, University of Swaziland,
Private Bag 4 Kwaluseni, Swaziland

ABSTRACT

The post-flowering phenological development of two local bambara groundnut (*Vigna subterranea*) landraces was studied at Luyengo, Swaziland using six sowing dates between mid-October 1999 and late January, 2000. The objective was to examine the influence of variation in post-flowering photoperiod and temperature on the phenological development and pod yield of the crop. While the rate of progress from sowing to podding was influenced by both temperature and photoperiod, the rate of progress from flowering to podding (1/ (p-f), with (p-f) being the number of days from 50% flowering to 50% podding) was influenced only by photoperiod between flowering and podding ($r^2 = 0.86$, $p < 0.01$). Pod yield was strongly and positively related to the duration of the pod-filling period ($r^2 = 0.96$, $p < 0.01$), while the duration of the pod-filling period was strongly related to thermal time accumulated during the reproductive period. Photoperiod during the reproductive period influenced pod yield indirectly, through its influence on the onset of podding. The study confirms the photosensitivity of the onset of podding in bambara groundnut, and it was concluded that in bambara groundnut, unlike in other leguminous crops, the duration of the reproductive or pod-filling period, and therefore yield, are largely influenced by environmental factors prevailing at and subsequent to the onset of flowering.

Keywords: Bambara groundnuts, post-flowering, photoperiodicity, phenology

INTRODUCTION

Bambara groundnut is an indigenous African leguminous crop grown by subsistence farmers throughout sub-Saharan Africa, but mainly in the semi-arid regions of the continent (Linnemann and Azam-Ali, 1993). The crop is grown mostly by female subsistence farmers, and mostly for home consumption (Sesay et al., 1999; Brink *et al.*,1996.; Hampson *et al*, 2000).

Reports in the literature indicate that the mature seeds are a rich source of protein (16-25% DM) and carbohydrate (42-60% DM) but, in comparison with groundnut, the lipid content is low (5-6% DM) (Poulter and Caygill 1980; Aykroyd and Doughty, 1982; Brough and Azam-Ali, 1992). Thus, bambara groundnut plays an important role in the food security and, in particular, in meeting the protein requirement of resource-poor farmers in semi-arid Africa. However, yields of bambara groundnut obtained by subsistence farmers are often low and unpredictable.

An important aspect of plant productivity and adaptation is the way reproductive development is influenced by environmental factors. Temperature and daylength are the main environmental factors influencing the development rates of annual crops (Roberts and Summerfield, 1987; Squire, 1990).

The role of photoperiod in controlling reproductive development in the bambara groundnut, a short-day species, is now well established (Linnemann, 1991; 1993; Harris and Azam-Ali, 1993; Brink 1997 and 1999). In the bambara groundnut, depending on the landrace, flowering and/or podding may be delayed or even prevented by photoperiod longer than the optimum. It is also established that within a given bambara groundnut genotype the photoperiodic effect on fruit set is always stronger than the effect on flowering. The stronger photoperiodic effect on pod production relative to flowering appears to be the unique aspect of the photoperiodic response of bambara groundnut. There is evidence in the literature indicating post-flowering photoperiodic responses in other grain legumes, such as groundnut (Wynne et al 1973; Flohr *et al.* 1990), soybean (Morandi *et al.* 1988; Grimm et al. 1994) and cowpea (Wien and Summerfield., 1980; Craufurd et al, 1996).

What is different is that in these other leguminous crops the onset of flowering often determines the entire crop duration. If floral induction occurs, the crop will produce pods, and if it occurs very quickly, yields may be very low because of very short growth duration. Hence, in these crops, the photoperiodic response of fruit set has been considered of secondary importance to flowering.

In the bambara groundnut it would seem that the correct timing of pod initiation is a major component of its environmental adaptation, and therefore, its productivity. Thus any environmental factor that influences pod initiation in the crop should have an effect not only on the phenology of the crop, but also on its yield and yield determining traits. There is little information on the effects of photoperiod and temperature on the post-flowering development and productivity of bambara groundnut in the field.

An understanding of the response of phenological development to environmental factors could help stabilise crop yield. Thus the objective of this study was to examine the influence of variation in post-flowering photoperiod and temperature on the phenology, pod yield and yield components of two bambara groundnut landraces.

MATERIALS AND METHODS

The results presented in this paper come from a serial sowing date study conducted at the Department of Crop Production Research Farm, at the Luyengo campus of the University of Swaziland, Swaziland (26° 41_ S, 31° 12_ E, and 750 m. a.s.l.) in 1999-2000. The soil of the experimental site was the Malkerns series deep red loam (Murdock and Baillie, 1966). Two local bambara groundnut landraces, a maroon- seeded and a cream-seeded, were sown at 3-week intervals from 13 October 1999 to 26 January 2000. The different sowing dates were used to produce a range of natural photoperiods and temperature regimes. Variation of sowing date has proved to be a simple and effective means of investigating the effects of environmental factors on phenological development of legumes in the tropics (Lawn and Byth, 1973; Akinola and Whiteman, 1974; Lawn, 1979; Harris and Azam-Ali, 1993; Verghis *et al.* 1999).

The experimental design was a single split plot with the six sowing dates in the main plots and the two landraces in the subplots, replicated four times. Each plot comprised 6 rows, 0.6 m apart and 6 m long with 0.15 m between plants in the row. A basal application of single superphosphate at the rate of 25kg P_2O_5 ha^{-1} was made at planting. Two seeds were sown per station, and seedlings were thinned to the desired population (11 plants m^{-2}) at 26 days after sowing (DAS). Plots were weeded by hand, as necessary, but no pesticides were applied to control pests and diseases. Earthing-up was done after 100 % flowering. The crop was rain-fed and no supplementary irrigation was given. Twelve randomly selected plants were tagged at emergence for developmental measurements.

The number of days to flowering was recorded as the date each of the tagged plants had at least one open flower. The date of 50 % flowering was determined from the daily observations. Starting 10 days after 50% flowering and at 5-day intervals, 5 plants per plot were dug up to determine the onset of podding. At maturity, estimated from visual observations of the onset of senescence characterized by the yellowing of leaves, plants were harvested from an undisturbed net plot area of 4.8 m^2. The number of pods per plant was determined from a sample of five randomly selected harvested plants per plot. Harvest index (HI) was computed, from a sample of 5 plants per plot at physiological maturity, as the proportion of seed weight to total above-ground dry matter. Plants were oven dried at 80 °C for 48 h before weighing. Pods were air-dried and weighed.

Environmental factors:

Meteorological data were kindly provided by the National Meteorological Services, Ministry of Public Works and Transport (Mbabane, Swaziland). Means were calculated from daily values. Mean photoperiod and mean-daily air temperatures were calculated for the period 50% flowering to 50% podding for each of the sowing dates. The duration of the post-flowering developmental phases was measured in calendar days and thermal time (°C d), which was calculated by subtracting the base temperature (10°C) from the mean daily temperatures and summing for the particular developmental phase. The rate of development during these phases was calculated as 1/d, where d was the duration, in days, of each respective developmental phase.

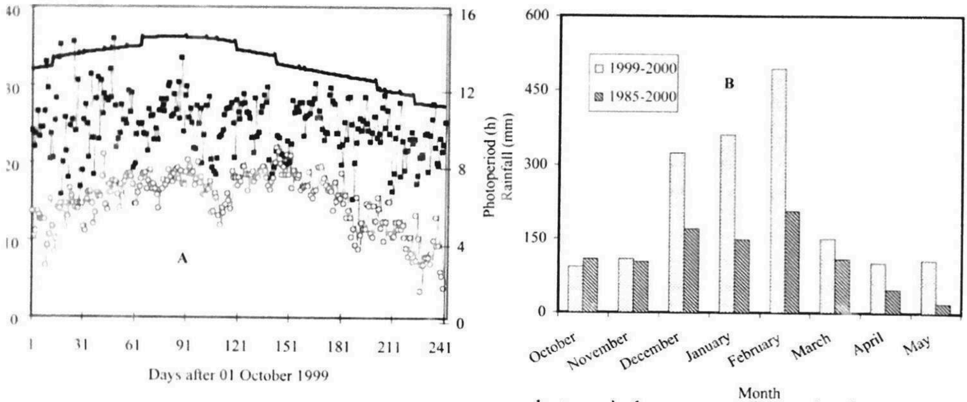
Analysis of variance, correlations, regression analysis and other statistical procedures were performed on the data using STATISTIX 8 for windows (Analytical Software, Tallahassee, Florida. USA). Linear and multiple regression analyses were used to relate phenology and yield, to daylength and temperature.

RESULTS

Environmental factors

Temperature and daylength changes during the study period are shown in Fig.1A. Maximum and minimum air temperatures ranged between 35.2 and 15.3, and 21.6 and 7.9 YC respectively. Mean daily air temperature declined consistently after March, dropping from 20.6 to 15.9 YC. Mean photoperiod varied between 14.8 h (in December) and 11.35 h d^{-1} (in May). The total rainfall received during the growing season was 1748 mm, 805.2 mm (85%) greater than the long-term average (Fig. 1B). Thus the plants were subjected to rainfall of high intensity and consequently to varying periods of flooding at various developmental stages. The two bambara groundnut landraces responded similarly, therefore only the effects of photoperiod and temperature are presented.

Fig. 1 Variation in environmental factors at Luyengo, Swaziland 1999-2000 cropping season: (A) daily maximum (-•-) and minimum (-o-) temperature, and photoperiod (_), (B) monthly rainfall during the1999-2000 growing season and long term.



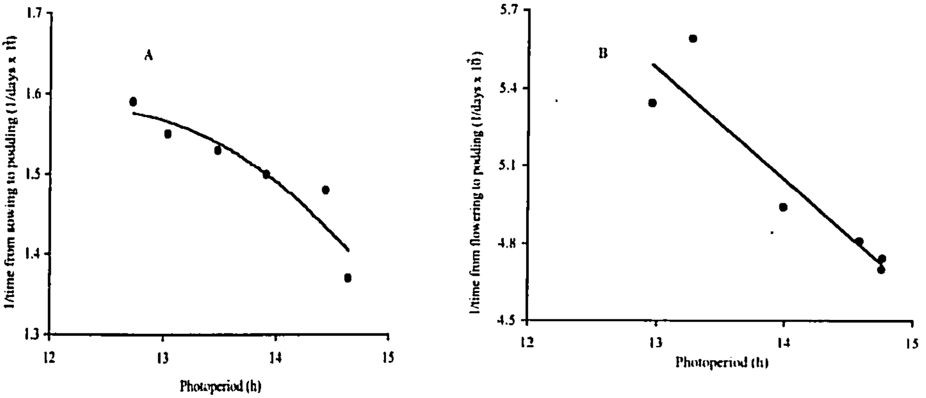
The duration from 50% flowering to 50% podding, flowering to maturity (reproductive period), and from pod initiation to maturity (pod-filling period), expressed either as calendar time or thermal time, varied significantly (p<0.001) with sowing date (Table 1). The rate of progress from sowing to 50 % podding (1/d) (Table 1) and from flowering to podding (1/ (p-f), with (p-f) being the number of days from 50% flowering to 50% podding) also varied significantly (p < 0.001) with sowing date.

Mean photoperiod had a highly significant (p<0.01) influence on the rate of progress from sowing to podding and from flowering to podding (Fig. 2), decreasing with increase in mean daylength from 12 to 15 h per day, suggesting that in the two landraces used in this study, the onset of podding was photoperiod-sensitive. However, the relationship between the rate of progress from sowing to podding and photoperiod during the reproductive period was non-linear (Fig. 2A), perhaps suggesting that photoperiod was not the only factor inducing the observed variation. Table 2 shows the standard partial regression coefficients for regression of rate of progress from sowing to podding on mean photoperiod and temperature during the reproductive period. The relative contribution of photoperiod and temperature in explaining the observed shows the standard partial regression coefficients for regression of rate of progress from sowing to podding on mean photoperiod and temperature during the reproductive period. The relative contribution of photoperiod and temperature in explaining the observed shows the standard partial regression coefficients for regression of rate of progress from sowing to podding on mean photoperiod and temperature during the reproductive period. The relative contribution of photoperiod and temperature in explaining the observed variation in rate to podding from sowing is reflected in the relative sizes of the respective standard partial regression coefficients. Comparison of the partial regression coefficients indicates that the contribution of photoperiod and temperature were approximately equal

Table 1. Rate (1/d) of progress from sowing to podding, and duration of three physiological growth phases (50 % flowering to 50 % podding (F-P), flowering to maturity (F-M), pod initiation to maturity (Pod-filling)) expressed in days and thermal time (°C d) for bambara groundnut sown at six dates at Luyengo, Swaziland, 1999-2000 cropping season.

Sowing date	1/d	F-P (days)	F-P (°C d)	F-M (days)	F-M (°C d)	Pod-filling (days)	Pod-filling (°C d)
13 October	0.0137	21.4	224.9	58.9	679.7	37.5	435.11
3 November	0.0148	21.2	260.5	62.1	749.0	40.9	466.5
24 November	0.0150	20.9	249.2	64.0	771.7	43.1	525.6
15 December	0.0153	20.2	262.1	55.9	714.0	35.6	447.0
5 January	0.0155	18.1	184.7	49.1	628.6	31.0	344.2
26 January	0.0159	17	157.8	41.8	525.6	24.8	231.8
Mean	0.0150	19.8	223.2	55.3	678.1	35.5	408.4
s.e.	0.0001	0.57	6.3	1.1	19.5	0.96	11.7

Fig. 2. Relationship between rate of progress from: (A), sowing to podding and photoperiod during reproductive period, and (B), flowering to podding and photoperiod between



However, multiple linear regression analyses, relating rate of progress from flowering to podding to climatic factors, indicated that a large proportion of the variation in the rate of development and the duration between flowering and pod initiation in response to sowing date could be accounted for by variation in photoperiod between flowering and podding. The responses were well described by the following relationships:

$y = 0.111 - 0.004x$ ($r^2 = 0.86$, $p < 0.01$)
where y = rate of development between flowering and podding; x = mean photoperiod between 50% flowering and 50% podding.

$y = -12.391 + 2.291x$ ($r^2 = 0.97$, $p < 0.01$),
where y = days between flowering and pod initiation; x = mean photoperiod between 50%
lowering and 50% podding., flowering and podding, for bambara groundnut in Swaziland. Equations of fitted lines: A. $y = -0.0346x^2 + 0.8568x - 3.7258$, $r^2 = 0.87$, $p < 0.01$; B. $y = -0.4298x + 11.063$, $r^2 = 0.86$, $p < 0.01$

Table 2. Standard partial regression coefficients for regression of rate of progress from sowing to podding (1/p) on mean photoperiod and mean daily temperature during the reproductive period.

Variables	Coefficients	Standard errors	P value
Constant	0.0022	0.001	
Photoperiod	- 0.0013	0.00003	0.0000
Mean temperature	0.0014	0.00007	0.0003

Pod yield and yield components

Pod yield was strongly and positively related to photoperiod between flowering and podding (Fig. 3A), duration of the pod-filling period (Fig. 3B), time from sowing to podding, time between flowering and podding, duration of the reproductive period, and thermal time during the reproductive period (Fig. 4A).

Fig. 3 Relationship between pod yield of bambara groundnut and: (A), photoperiod between flowering and podding, and (B), pod-filling period, in Swaziland, 1999-2000. Equations of fitted lines: A. y = -0.132x2 + 3.9475x – 28.955; $r^2 = 0.91$, $p < 0.01$; B. $y = 0.0337x + -0.8066$. $r^2 = 0.96$. $p < 0.01$.

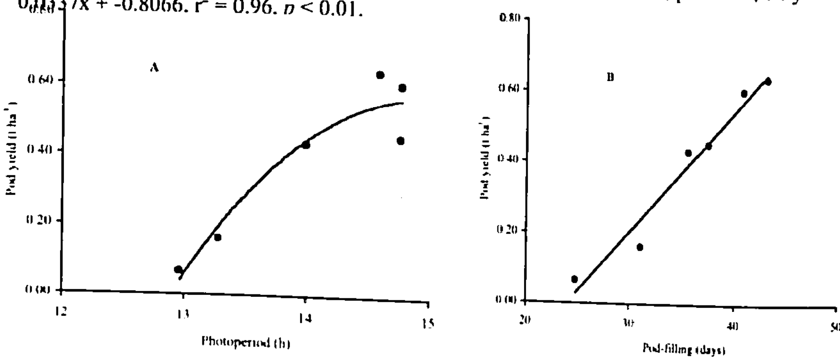
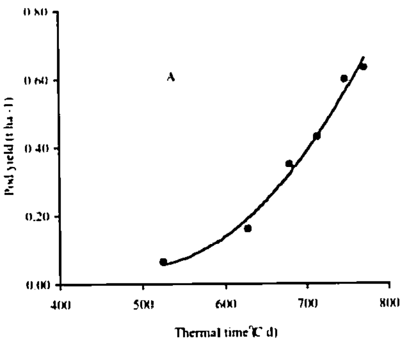
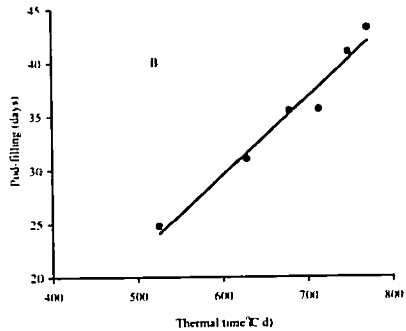


Fig. 4 Relationship A. between pod yield and thermal time during reproductive period, B. between pod-filling period and thermal time during the reproductive period for bambara groundnut, in Swaziland, 1999-2000. Equations of fitted lines: A. y = 8E-06x2 – 00079x + 2.0108, $r^2 = 0.99$, $p < 0.01$; B. y = 00726x – 14.084, $r^2 = 0.97$, $p < 0.01$





A significant relationship was also observed between harvest index and seed mass with photoperiod during the reproductive period (data not presented.)

DISCUSSION

In this study all the sowings fell within the mean photoperiod range of 12.6 and 14.8 h. Mean daily air temperatures declined consistently late in the season, dropping from 20.6 to 15.9 C. Variation in post-flowering photoperiod across sowing dates induced significant differences in the rate of progress to podding. Thus, for the landraces used in this study, the onset of podding was photoperiod-sensitive. The declining rate of progress to podding with increasing photoperiod agrees with results reported from glasshouse experiments (Linnemann, 1991; Linnemann and Craufurd, 1994; Brink, 1997; 1999), and field experiment (Harris and Azam-Ali, 1993). The rate of progress from sowing to podding was influenced by both temperature and photoperiod. Brink (1997) reported a similar observation under controlled environment conditions. This is a pattern of response that has been found in most of the bambara groundnut landraces included in experiments to date, although some landraces have been found in which not only podding, but flowering also is influenced by both temperature and photoperiod. In this study the rate of progress from flowering to podding was considered separately from the rate of progress from sowing to podding. This approach separates the time to flowering from the podding analysis (Brink, 1997).

While the rate of progress from sowing to podding was influenced by both temperature and photoperiod, the rate of progress from flowering to podding was influenced only by photoperiod between flowering and podding, which is in contrast with earlier findings by Brink (1997). The actual mechanism of photoperiodic control of pod set in bambara groundnut is unknown. However, Linnemann (1991 b) demonstrated that embryo development was independent of photoperiod until 18 days after flowering when growth ceased under long photoperiods.

The crop growth period was progressively shortened as sowing was delayed after November. The reduction in the crop growth period with delay in sowing after November reflected a substantial reduction in the reproductive period, the period from flowering to maturity (Table 1). Duration of the reproductive period has a major impact on the productivity of bambara groundnut since pod-filling is dependent on current rather than stored assimilates (Norman and Chongo, 1992; Brink 1999). Thus any environmental factor(s) that restrict the reproductive period of the crop can have adverse consequences with respect to yield. This would explain the relationship between pod yield and the duration of the pod-filling period and reproductive periods.

On the other hand, the duration of the pod-filling period was strongly related to thermal time during the reproductive period. The reduction in the reproductive period and hence the pod-filling period, in the later sowings, is attributable to premature senescence caused by the declining temperatures late in the season. Furthermore, the declining temperatures late in the season would have reduced leaf production and dry matter production resulting in declining harvest index, smaller seeds and reduced yield for later sowing dates.

The strong relationship between pod yield and both time from sowing to podding and time between flowering and podding confirms the findings of Brink (1998; 1999), who found that seed yield in bambara groundnut was strongly related to the time to podding. Pod yield was strongly related to photoperiod between flowering and podding. However, considering the observed relationship between pod yield and time between flowering and podding, and the duration of the pod-filling period (Fig 4B), the observed relationship between pod yield and daylength is likely to be an indirect effect of the influence of photoperiod on time to podding.

The implication of the results of this study is that the duration of the reproductive phase or pod-filling period, and therefore yields in bambara groundnut, largely depend on environmental factors prevailing at and subsequent to the onset of flowering.

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