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# Rates of Progress towards Flowering and Podding in Bambara Groundnut (*Vigna subterranea*) as a Function of Temperature and Photoperiod

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The influence of temperature and photoperiod on phenological development of three bambara groundnut (*Vigna subterranea*) selections from Botswana, Zimbabwe and Mali was investigated in a semi-controlled environment experiment with factorial combinations of three constant temperatures (20·9, 23·4 and 26·2 °C) and four constant photoperiods (10·0, 12·5, 13·5 and 16·0 h $d^{-1}$). In all three selections, the onset of flowering was influenced by temperature but not by photoperiod, while the onset of pod-growth ('podding') of all three selections was influenced by both factors. The influence of temperature and photoperiod was quantified by means of photothermal models, linking development rates to temperature and photoperiod with linear equations. The rate of progress from sowing to flowering of the three selections could be described very well ($r^2 > 95$%) as a function of temperature; the rate of progress from flowering to podding was described reasonably well as a function of both temperature and photoperiod by a combination of one to three response planes ($r^2$ for the different selections ranging from 63 to 90%). Model testing with independent data sets showed good agreement between observed and predicted times to flowering and podding.


**Key words:** *Vigna subterranea*, *Voandzeia subterranea*, bambara groundnut, phenology, development, flowering, podding, photoperiod, temperature, modelling.

## INTRODUCTION

The leguminous crop bambara groundnut [*Vigna subterranea* (L.) Verdc., syn. *Voandzeia subterranea* (L.) Thouars] is an important secondary food crop in semi-arid Africa, where it is mainly grown by smallholders (Linnemann and Azam-Ali, 1993). It produces protein-rich seeds which are eaten unripe or ripe. Compared to groundnut (*Arachis hypogaea* L.), bambara groundnut performs relatively well under water stress and is less susceptible to diseases (Linnemann and Azam-Ali, 1993).

To explore the potential production of different bambara groundnut selections in various agro-ecological regions and assess the possibilities of transferring selections to other regions, it is necessary to know how development rates are influenced by environmental factors. In most crops, development rates are mainly determined by temperature and/or photoperiod (Roberts and Summerfield, 1987; Squire, 1990). Multi-locational field trials and/or controlled environment research are needed to identify the influencing factors and to quantify their effects. However, it is easier to separate the effects of photoperiod, temperature and radiation in controlled environments than in field situations.

Quantification of the influence of temperature and photoperiod on development has been done with different types of models (Hodges, 1991; Sinclair *et al*., 1991). A relatively simple method, developed at the University of Reading, uses linear equations to relate the rate of progress from sowing to flowering (calculated as the inverse of the duration from sowing to flowering) to the mean pre-flowering photoperiod and temperature (Hadley, Summerfield and Roberts, 1983*b*; Summerfield *et al*., 1991; Lawn *et al*., 1995). The main advantages of this method are that the responses to photoperiod and temperature become linear and that interactions between temperature and photoperiod influences often disappear (Summerfield *et al*., 1991). The method has been used to describe the flowering response to temperature and photoperiod in various leguminous crops: cowpea [*Vigna unguiculata* (L.) Walp.] (Hadley *et al*., 1983*a*; Ellis *et al*., 1994*a*); soya bean [*Glycine max* (L.) Merr.] (Hadley *et al*., 1984; Summerfield *et al*., 1993); mungbean [*Vigna radiata* (L.) Wilczek] (Ellis *et al*., 1994*b*); chickpea (*Cicer arietinum* L.) (Roberts, Hadley and Summerfield, 1985; Ellis *et al*., 1994*c*); lentil (*Lens culinaris* Medic.) (Summerfield *et al*., 1985; Erskine *et al*., 1994); and faba bean (*Vicia faba* L.) (Ellis, Summerfield and Roberts, 1990).

In the short-day species bambara groundnut, not only the onset of flowering, but also the onset of pod growth ('podding') is affected by photoperiod (Harris and Azam-Ali, 1993; Linnemann, 1993; Linnemann, Westphal and Wessel, 1995). Photoperiod usually has a stronger effect on the onset of podding than on the onset of flowering. Linnemann and Craufurd (1994) applied the Reading method to ascertain the rate of progress towards flowering and podding, but they did not validate their results with independent data sets.

The objectives of the present study were to assess the

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influence of temperature and photoperiod on flowering and podding in bambara groundnut selections from different origins; to quantify the temperature and photoperiod effects by means of photothermal models which relate development rates to photoperiod and temperature by means of linear equations; and to test whether these photothermal models adequately predict development rates in other situations.

## MATERIALS AND METHODS

### *Experiments*

The study involved eight different experiments: a main semi-controlled environment experiment used to construct development models and seven other experiments to test the models.

The main experiment was carried out from 16 May to 2 Nov. 1994 in three identical glasshouses in Wageningen, The Netherlands (51° 58′ N). The experimental design was a split-split-plot with temperature (three levels) as first main factor, photoperiod (four levels) as second main factor, and selection (three selections) as subfactor. The bambara groundnut selections included were 'GabC92' from Botswana, 'NTSC92' from Zimbabwe, and 'Tiga Nicuru' from Mali.

Temperature in the three glasshouses was set at 20, 23 and 26 °C, respectively. These temperatures were chosen because preliminary experiments at the Department of Agronomy of Wageningen Agricultural University had indicated that bambara groundnut does not grow well at constant temperatures below 20 °C and that the optimum temperature for podding of some selections was lower than 28 °C (A. R. Linnemann, pers. comm.). It was not possible to keep the temperature in the glasshouses constant at these predetermined levels because of the warm, sunny weather during the experiment. Measured mean daily temperatures were 20·9, 23·4 and 26·2 °C, respectively. Relative air humidity in the glasshouses was kept above 60 %, and the glasshouses transmitted 52 % of the outside photosynthetically active radiation (PAR).

The photoperiod treatments were constant photoperiods of 10, 12·5, 13·5 and 16 h $d^{-1}$. These photoperiod treatments were chosen because earlier research had shown that at an average temperature of around 25 °C, the main photoperiod response of 'Tiga Nicuru' occurs between photoperiods of 12 and 14 h $d^{-1}$ [A. R. Linnemann, pers. comm.; results were later published in Linnemann, Westphal and Wessel (1995)]. A photoperiod of 10 h $d^{-1}$ was expected to be below the critical photoperiod of 'Tiga Nicuru' in the temperature range of the experiment, and a photoperiod of 16 h $d^{-1}$ above the ceiling photoperiod. A tent with lightproof tentcloth (a double layer of LS100 from Ludvig Svensson Ltd Company) with four compartments, each 3·10 m wide, 1·50 m long and 2·05 m high, was erected in each glasshouse. The photoperiod treatments were randomly allocated to compartments. The tents were open from 0800 to 1600 h, and closed from 1600 to 0800 h. The plants in all compartments received natural daylight from 0800 to 1600 h. The photoperiod was prolonged separately in each compartment by means of low intensity artificial light (two Philips TLD 36 W fluorescent tubes (colour no. 84) and two Philips 40 W bulbs in each compartment, together giving around 10 $\mu$mol $m^{-2}$ $s^{-1}$ PAR at plant height). Artificial lighting was supplied from 0700 to 0800 h and from 1600 to 1700 h, 1930 h, 2030 h and 2300 h for the 10, 12·5, 13·5 and 16 h $d^{-1}$ photoperiod treatments respectively. From 1600 to 0800 h, removable metal roofs were put over the glasshouses to exclude daylight and to prevent the temperature inside the tents from becoming too high. Each compartment contained a staging, on which 78 plants (26 plants per selection) were randomly placed. Within each compartment, the plants were circulated weekly.

TABLE 1. *Characteristics of the seven validation experiments*

| | Experiment | | | | | | |
|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 |
| Sowing date | 19 May 1993 | 6 Jul. 1993 | 7 Jul. 1993 | 3 Nov. 1993 | 18 Apr. 1994 | 16 May 1994 | 16 May 1994 |
| Final harvest date | 18 Oct. 1993 | 10 Nov. 1993 | 3 Nov. 1993 | 7 Mar. 1994 | 2 Nov. 1994 | 24 Oct. 1994 | 25 Oct. 1994 |
| Selections | 'GabC92' | 'GabC92' | 'NTSC92' 'Tiga Nicuru' | 'GabC92' | 'GabC92' 'NTSC92' | 'GabC92' 'NTSC92' 'Tiga Nicuru' | 'GabC92' 'NTSC92' 'Tiga Nicuru' |
| Average daily temperature (°C) | 24·8 | 24·5 | 24·4 | 23·9 | 25·7 | 22·1 | 23·4 |
| Average minimum temperature (°C) | 22·2 | 22·3 | n.a. | 21·4 | 22·9 | 21·6 | 23·1 |
| Average maximum temperature (°C) | 27·5 | 27·0 | n.a. | 28·1 | 29·5 | 22·5 | 23·7 |
| Photoperiod treatments (h $d^{-1}$) | 10, 12 | 12, 14 | 11·5 | 12 | 11, 14 | 12·5 | 13·5 |
| Number of replicates | 3 | 2 | 3 | 3 | 1 | 1 | 1 |
| No. of plants per selection per photoperiod treatment per replicate: | | | | | | | |
| flowering observations | 17 | 18 | 4 | 15 | 30–36 | 4 | 26 |
| podding observations | — | — | 4 | 15 | 6 | 4 | 26 |

Seeds were pre-germinated at 30 °C in a germination cabinet. When the root tips were visible, the seedlings were put singly in white plastic pots (upper diameter 20 cm; lower diameter 15 cm; height 20 cm; capacity 4·8 l), filled with a 1:1 v/v mixture of sand and potting compost ('potting compost no. 4' from Lentse potgrond b.v., consisting of 85 % peat and 15 % clay). A water extract of the sand/compost mixture (1:2 v/v soil and water) contained 66 mg $l^{-1}$ N, 11 mg $l^{-1}$ P and 35 mg $l^{-1}$ K. At transplanting, the seedlings were inoculated with *Rhizobium* spp. strain CB 756, obtained from the Department of Microbiology, Wageningen Agricultural University. Fertilization was carried out using a standard complete nutrient solution which had been proven to give good results in bambara research at Wageningen Agricultural University (A. R. Linnemann, pers. comm.). The standard solution was obtained by mixing 0·833 g 'Nutriflora-t' (supplied by Windmill Holland b.v.) and 1 g calcium nitrate in 1 l water, resulting in a nutrient content of 172 mg $l^{-1}$ N, 39 mg $l^{-1}$ P, and 263 mg $l^{-1}$ K. Nutrient solution was given at 28 (100 ml per plant), 39 (200 ml), 58 (200 ml) and 96 (200 ml) d after sowing. Water was applied manually when necessary. Predators were introduced preventively at regular intervals: *Amblyseius cucumeris* and *Orius insidiosus* against thrips (*Frankliniella occidentalis* and *Thrips tabaci*), and *Phytoseiulus persimilis* against spider mites (*Tetranychus urticae*).

Observations included dates of first flowering and onset of podding of each plant. The start of podding was defined as the moment the plant had a pod at least 0·5 cm long. Direct podding observations were possible because the selections included in the experiment form pods on the soil surface and not below. Podding observations in a treatment combination were stopped when 50 % of the plants in that treatment combination had started podding. The time to flowering in a treatment was defined as the time between the sowing date and the date when 50 % of the plants in that treatment had started to flower ('50 % flowering'). Similarly, the time from flowering to podding was defined as the time from the date of 50 % flowering to the date when 50 % of the plants had started podding ('50 % podding').

Data sets from seven other experiments, carried out in Wageningen in 1993 and 1994 were used to test the models (Table 1). Experiments 1–5 were carried out in glasshouses, expt 6 in a Heraeus growth cabinet and expt 7 in a growth chamber. In expts 1, 2 and 5, the photoperiod treatments were established as described for the main trial (8 h $d^{-1}$ natural daylight, extended by low intensity artificial light). In the other experiments, there was no photoperiod extension by means of low intensity light, but high intensity natural and/or artificial light throughout the light period. Experiment 3 received natural daylight; expt 4 natural daylight with supplementary lighting (Philips SON-T lamps giving 130 $\mu$mol $m^{-2}$ $s^{-1}$ PAR at plant height); expt 6 received light from 16 fluorescent tubes (Philips TLD 58 W, colour no. 84) and two Philips 100 W incandescent bulbs (total PAR at plant height: 230 $\mu$mol $m^{-2}$ $s^{-1}$); and expt 7 light from Philips HPI and SON-T lamps, fluorescent tubes and incandescent bulbs (total PAR at plant height: 210 $\mu$mol $m^{-2}$ $s^{-1}$). In all test experiments plants were grown in white 5 l pots with a mixture of sand and potting compost, and crop management was as described for the main trial. The onset of flowering and podding was determined directly for individual plants in the same way as in the main experiment. For expts 1 and 2 only flowering data were available.

### *Modelling*

The influence of temperature and photoperiod on the rate of progress from sowing to flowering and the rate of progress from flowering to podding of the three bambara groundnut selections was modelled according to the photothermal approach developed at the University of Reading (Hadley *et al*., 1984; Summerfield *et al*., 1991). In this approach, the rate of progress to flowering ($1/f$; with $f$ being the number of days from sowing to flowering) is related quantitatively to photoperiod ($P$) and/or temperature ($T$) by means of one to three linear equations, assuming that temperatures are between the base and optimum temperatures for flowering. In the most complex situation, three separate but intersecting planes, characterized by six parameters ($a_1$, $b_1$, $a_2$, $b_2$, $c_2$ and $a_3$), can be distinguished (Fig. 1):

A: a thermal plane, characterized by the equation:

$$1/f = a_1 + b_1 T \qquad (1)$$

B: a photothermal plane:

$$1/f = a_2 + b_2 T + c_2 P \qquad (2)$$

C: a plane of minimum development rate:

$$1/f = a_3. \qquad (3)$$

Interactions between temperature and photoperiod effects only occur when plane boundaries are transgressed. Within the planes, there is no interaction. The boundary line between plane A and plane B gives the critical photoperiod ($P_{cr}$) as a function of temperature:

$$P_{cr} = [(a_1 - a_2) + (b_1 - b_2)\,T]/c_2. \qquad (4)$$

The boundary line of plane B and plane C represents the ceiling photoperiod ($P_{ce}$):

$$P_{ce} = (a_3 - a_2 - b_2 T)/c_2. \qquad (5)$$

When the actual photoperiod is shorter than $P_{cr}$, the development rate is influenced solely by temperature. At a photoperiod between $P_{cr}$ and $P_{ce}$, $1/f$ is determined by $P$ and $T$, and above $P_{ce}$ the development rate is constant. For a given selection, $1/f$ can be described by one of five possibilities: (1) a thermal plane only; (2) a photothermal plane only; (3) a thermal plane and a photothermal plane; (4) a photothermal plane and a plane of minimum rate; (5) all three planes.

In the application of this approach to the results of the experiment, these five possibilities were examined not only for the rate of progress from sowing to flowering, ($1/f$), of each of the three selections, but also for the rate of progress from flowering to podding [$1/(p-f)$]. This is different to Linnemann and Craufurd (1994), who considered the rate from sowing to flowering and the rate from sowing to podding ($1/p$), and did not look at the rate of progress from flowering to podding. However, to study the photothermal

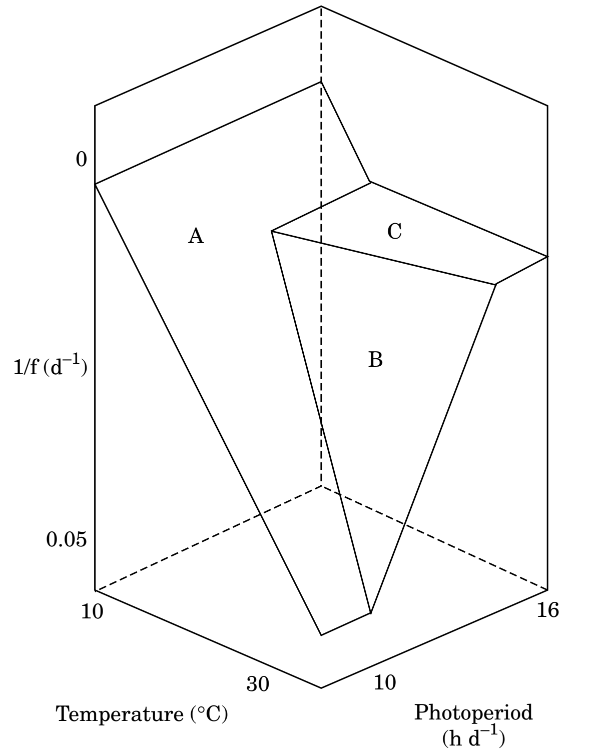


FIG. 1. Rate of progress to flowering ($1/f$; with $f$ being the number of days from sowing to flowering) as a function of temperature and photoperiod (hypothetical example for a short-day plant at temperatures between the base and optimum temperature for flowering; after Linnemann and Craufurd, 1994). A, Thermal plane; B, photothermal plane; C, plane of minimum development rate.

effects on flowering and podding, it seems more appropriate to separate the two phases completely, and not include the time to flowering in the podding analysis.

The best fit was determined by means of the RoDMod computer program (Watkinson *et al*., 1994), which uses an iterative procedure to minimize the combined sums of squares of deviations of observed from estimated rates. The simplest model (only a thermal plane) is fitted first, followed by the more complex models. A more complex model is accepted only if it statistically significantly reduces the residual sums of squares of the deviations of model estimates from observations. The temperature values used in the equations were the measured average temperatures from sowing to flowering or flowering to podding.

### *Model testing*

Predictions of the time from sowing to flowering and the time from flowering to podding in the seven test experiments in Table 1 were made with the PREDICTF routine of the RodMod computer program (Watkinson *et al*., 1994) on the basis of the average daily temperature and photoperiod data from the test experiments and the model parameters derived from the main experiment. The PREDICTF routine calculates the development rate in 1-d time-steps, on the basis of photoperiod and mean temperature of each day separately. The predictions were compared with the times from sowing to flowering and the times from flowering to podding observed in the experiments.

## RESULTS

### *Experiments*

Flowers and pods were formed in all treatments. The time from sowing to 50 % flowering varied from 35 to 53 d for 'Tiga Nicuru', from 40 to 55 d for 'NTSC92' and from 42 to 58 d for 'GabC92'. For all three selections, flowering was influenced by temperature, but photoperiod had no influence (Fig. 2).

The greatest differences in the time from 50 % flowering

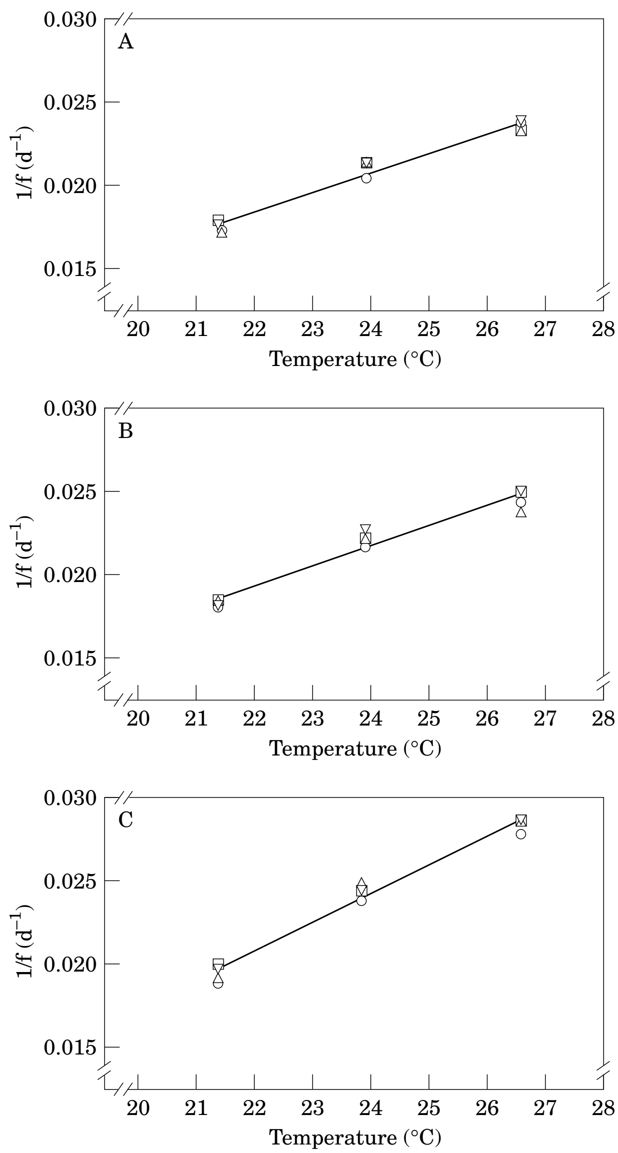


FIG. 2. Rate of progress from sowing to flowering ($1/f$; with $f$ being the number of days from sowing to flowering) in bambara groundnut selections 'GabC92' (A), 'NTSC92' (B) and 'Tiga Nicuru' (C) as a function of temperature under constant photoperiods of 10 h $d^{-1}$ (○), 12·5 h $d^{-1}$ (▽), 13·5 h $d^{-1}$ (△) and 16 h $d^{-1}$ (□). The solid lines refer to the fitted models.

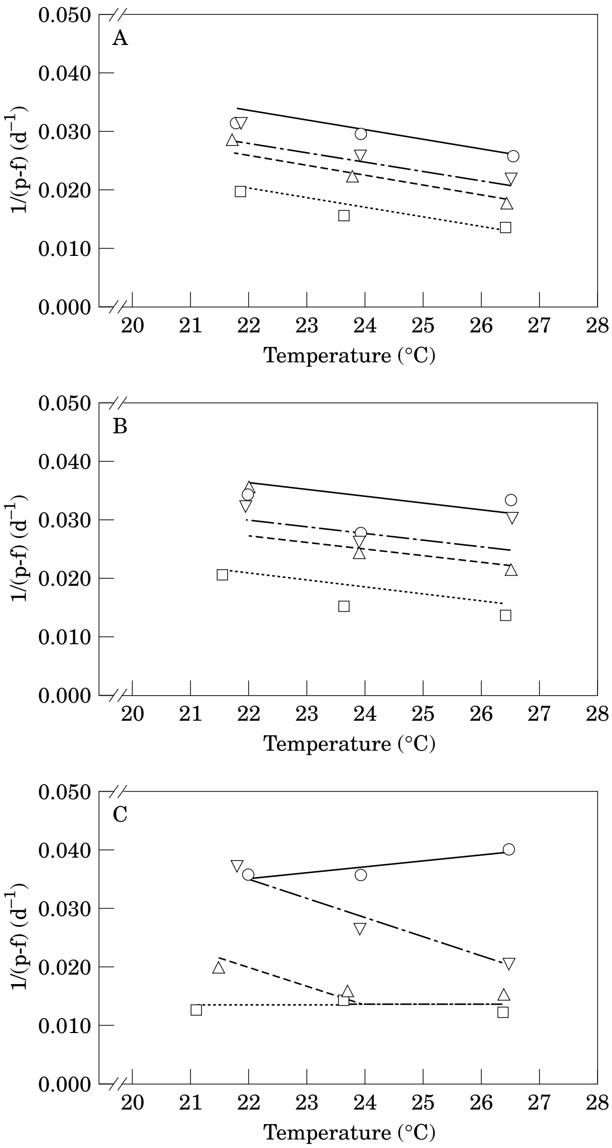


FIG. 3. Rate of progress from flowering to podding [$1/(p-f)$; with $(p-f)$ being the number of days from flowering to podding] in bambara groundnut selections 'GabC92' (A), 'NTSC92' (B) and 'Tiga Nicuru' (C) as a function of temperature under constant photoperiods of 10 h d$^{-1}$ (○), 12·5 h d$^{-1}$ (▽), 13·5 h d$^{-1}$ (△) and 16 h d$^{-1}$ (□). The lines are the fitted model values for 10 h d$^{-1}$ (–––), 12·5 h d$^{-1}$ (– - –), 13·5 h d$^{-1}$ (————) and 16 h d$^{-1}$ (· · · ·).

to 50 % podding were found for 'Tiga Nicuru': 25 to 82 d. For 'NTSC92' the time from 50 % flowering to 50 % podding ranged from 29 to 72 d and for 'GabC92' from 32 to 74 d. Development from flowering to podding in all three selections was influenced by both temperature and photoperiod (Fig. 3).

### *Modelling*

The rate of progress from sowing to flowering of the three selections could be adequately ($r^2 > 95$ %) described by thermal response planes (Table 2, Fig. 2). The fitted equations for the flowering responses of 'GabC92' and 'NTSC92' had very similar parameter values.

The influence of photoperiod and temperature on the rate of progress from flowering to podding of 'GabC92' and 'NTSC92' in the temperature range of the experiment could be described by a photothermal response plane, but the fit was much better for 'GabC92' than for 'NTSC92' (Table 3; Fig. 3). For both selections, the parameters $b_2$ and $c_2$ had negative values, reflecting that in the temperature and photoperiod range of the experiment, the rate of progress from flowering to podding decreased with both temperature and photoperiod.

According to the results of the RoDMod analysis, the rate of progress towards podding of 'Tiga Nicuru' was described by a photothermal plane as well. However, the experimental results indicate a different model, with a thermal plane, a photothermal plane, and a plane of maximum delay (model 5). Therefore, the results for 'Tiga Nicuru' were analysed in an alternative way as well (method 2). The 12 temperature/photoperiod combinations were divided into three groups, with group 1 (the thermal plane) consisting of the 10·0 h d$^{-1}$ treatments; group 2 (the photothermal plane) consisting of the 12·5 h d$^{-1}$ and the 13·5 h d$^{-1}$ treatments, except the 26·2 °C/13·5 h d$^{-1}$ treatment; and group 3 (the plane of minimum development rare) consisting of the 16·0 h d$^{-1}$ treatments and the 26·2 °C/13·5 h d$^{-1}$ treatment. A regression analysis was carried out for each plane separately, using the GENSTAT statistical package (Payne *et al.*, 1993). Results are shown in Table 3. This alternative model fits the experimental results very well (Fig. 3C). In this model, the critical photoperiod for the rate from flowering to podding in 'Tiga Nicuru' decreases from 12·47 h d$^{-1}$ at 22 °C to 11·32 h d$^{-1}$ at 26 °C,

TABLE 2. *Fitted relations between rate of progress towards flowering* ($1/f$) *and mean pre-flowering temperature* (T) *in three bambara groundnut selections grown in combinations of three constant temperatures* (*20·9, 23·4 and 26·2 °C*) *and four constant photoperiods* (*10·0, 12·5, 13·5 and 16·0 h d*$^{-1}$)

| Selection | Fitted equations | $n$ | Parameter values | | $r^2$ (%) |
|---|---|---|---|---|---|
| | | | $a_1$ (s.e.) | $b_1$ (s.e.) | |
| 'GabC92' | $1/f = a_1 + b_1 T$ | 12 | −0·007464 (0·001593)*** | 0·001176 (0·000066)*** | 96·6 |
| 'NTSC92' | $1/f = a_1 + b_1 T$ | 12 | −0·006876 (0·001926)** | 0·001195 (0·000080)*** | 95·3 |
| 'Tiga Nicuru' | $1/f = a_1 + b_1 T$ | 12 | −0·017104 (0·001904)*** | 0·001721 (0·000079)*** | 97·7 |

*** $P \leqslant 0·001$; ** $P \leqslant 0·01$; * $P \leqslant 0·05$; n.s. not significant.
$n$, number of temperature/photoperiod combinations.

TABLE 3. *Fitted relations between rate of progress from flowering to podding* [$1/(p-f)$] *and mean temperature* (T) *and photoperiod* (P) *between flowering and podding in three bambara groundnut selections grown in combinations of three constant temperatures* (*20·9, 23·4 and 26·2 °C*) *and four constant photoperiods* (*10·0, 12·5, 13·5 and 16·0 h d*$^{-1}$)

| | | | | | Parameter values | | | |
|---|---|---|---|---|---|---|---|---|
| Selection | Method | Plane | Fitted equations | $n$ | $a_1$, $a_2$ or $a_3$ (s.e.) | $b_1$ or $b_2$ (s.e.) | $c_2$ (s.e.) | $r^2$ (%) |
| 'GabC92' | 1 | B | $1/(p-f) = a_2+b_2T+c_2P$ | 12 | 0·091579 (0·007590)*** | −0·001650 (0·000278)*** | −0·002193 (0·000253)*** | 90·4 |
| 'NTSC92' | 1 | B | $1/(p-f) = a_2+b_2T+c_2P$ | 12 | 0·087653 (0·018293)*** | −0·001158 (0·000672)$^{n.s.}$ | −0·002572 (0·000593)** | 63·4 |
| 'Tiga Nicuru' | 1 | B | $1/(p-f) = a_2+b_2T+c_2P$ | 12 | 0·099451 (0·019967)*** | −0·000842 (0·000721)$^{n.s.}$ | −0·004268 (0·000667)*** | 78·2 |
| | 2 | A | $1/(p-f) = a_1+b_1T$ (for $P \leqslant P_{cr}$) | 3 | 0·013100 (0·011400)$^{n.s.}$ | 0·000994 (0·000473)$^{n.s.}$ | — | 63·1 |
| | | B | $1/(p-f) = a_2+b_2T+c_2P$ (for $P_{ce} \geqslant P \geqslant P_{cr}$) | 5 | 0·285300 (0·042600)* | −0·003177 (0·000704)* | −0·014470 (0·002570)* | 89·9 |
| | | C | $1/(p-f) = a_3$ (for $P \geqslant P_{ce}$) | 4 | 0·013591 (0·000755) | — | — | — |

*** $P \leqslant 0·001$; ** $P \leqslant 0·01$; * $P \leqslant 0·05$; n.s. not significant.

Method 1 refers to fitting with the RoDMoD computer programme (Watkinson *et al.*, 1994); method 2 refers to an alternative approach (see text). The letters A, B, and C refer to the planes in Fig. 1. $P_{cr}$, Critical photoperiod; $P_{ce}$, ceiling photoperiod; $n$, number of temperature/photoperiod combinations.

the ceiling photoperiod 13·95 h d$^{-1}$ at 22 °C to 13·07 h d$^{-1}$ at 26 °C (Table 4).

In summary, within the temperature (20·9–26·2 °C) and photoperiod (10–16 h d$^{-1}$) ranges considered, the rates from flowering to podding of 'GabC92' and 'NTSC92' decrease with both temperature and photoperiod. The rate from flowering to podding of 'Tiga Nicuru' increases with temperature at short photoperiods, is constant at long photoperiods and decreases with photoperiod and temperature at intermediate photoperiods.

### *Model testing*

Application of the fitted models shown in Tables 2 and 3 to data sets from the test experiments showed that the time from sowing to flowering was well predicted: all deviations were within 10% of the predicted values (Fig. 4A). Predictions for the time from sowing to podding were less accurate (Fig. 4B), especially for expt 5 (Table 5). For 'Tiga Nicuru', the podding model derived by method 2 gave better predictions than the method 1 model (Table 5). The values for 'Tiga Nicuru' in Fig. 4B are those derived with method 2. Predictions of the time from sowing to podding, calculated by adding the predictions of the time to flowering and the time from flowering to podding were in good agreement with observed data: deviations between predicted and observed times from sowing to podding were less than 10% (Fig. 4C), except for expt 5 (Table 5).

## DISCUSSION

### *Temperature and photoperiod responses*

The results of the main experiment clearly show that flowering in the three bambara groundnut selections, in the temperature and photoperiod ranges considered, is influenced by temperature but not by photoperiod (Fig. 2). The onset of podding, on the other hand, is clearly influenced by both temperature and photoperiod (Fig. 3). This is a pattern which has been found in most of the bambara groundnut selections included in experiments to date, though some selections have been found for which not only podding, but also flowering is influenced by both temperature and photoperiod (Linnemann, 1991, 1993). Photoperiod research in other legumes has usually been confined to the flowering response, though the existence of photoperiod effects on development phases beyond flowering has also been reported for soya bean (*Glycine max*) (Grimm *et al.*, 1994) and groundnut (*Arachis hypogaea*) (Flohr, Williams and Lenz, 1990).

### *Modelling*

For all three selections, the rates of progress from sowing to flowering of the 12 treatments in the experiment could be adequately quantified as a function of temperature only (Table 2; Fig. 2). The rate of progress from flowering to podding of 'GabC92' was well described by a photothermal response plane, and that of 'Tiga Nicuru' by a combination of a thermal response plane, a photothermal response plane, and a plane of minimum development rate (Table 3; Fig. 3). The rate from flowering to podding of 'NTSC92' could not be quantified well, which might be due to the greater heterogeneity of this selection.

The critical photoperiod for the rate from flowering to podding in 'Tiga Nicuru' decreased from 12·47 h d$^{-1}$ at 22 °C to 11·32 h d$^{-1}$ at 26 °C (Table 4). These critical photoperiods are comparable with those found in other studies. Linnemann and Craufurd (1994) found similar critical photoperiods for podding for the bambara ground-

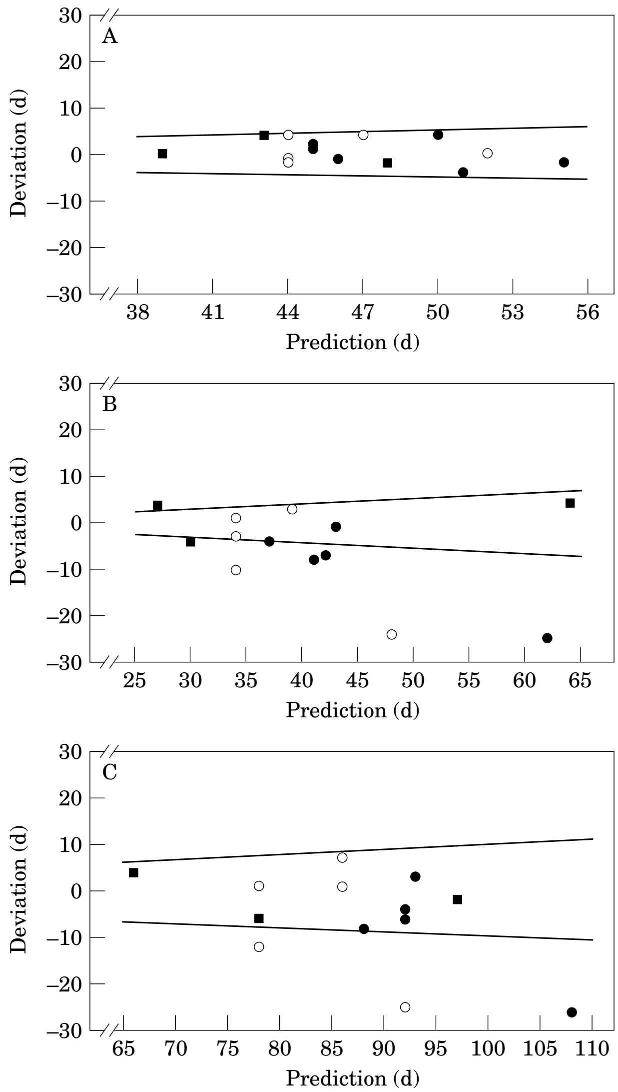


FIG. 4. Deviations (predicted number of days minus observed number of days in independent test experiments) of the time from sowing to flowering (A), the time from flowering to podding (B), and the time from sowing to podding (C) for bambara groundnut selections 'GabC92' (●), 'NTSC92' (○) and 'Tiga Nicuru' (■). Solid lines show the limits of $\pm 10$% deviation. Predictions of the time from sowing to flowering and the time from flowering to podding are based on the models in Tables 2 and 3; the predicted time from sowing to podding was calculated by adding the predicted time from sowing to flowering and the predicted time from flowering to podding.

TABLE 4. *Critical* ($P_{cr}$) *and ceiling* ($P_{ce}$) *photoperiods of bambara groundnut selection 'Tiga Nicuru' at temperatures from 22 to 26 °C*

| $T$ (°C) | $P_{cr}$ (h d$^{-1}$) | $P_{ce}$ (h d$^{-1}$) |
|---|---|---|
| 22 | 12·47 | 13·95 |
| 23 | 12·18 | 13·73 |
| 24 | 11·89 | 13·51 |
| 25 | 11·61 | 13·29 |
| 26 | 11·32 | 13·07 |

The model in Table 3 was used to calculate $P_{cr}$ and $P_{ce}$.

nut selections 'Yola' and 'Ankpa4' from Nigeria (12·6 and 13·2 h d$^{-1}$ at 20 °C to 11·4 and 11·8 h d$^{-1}$ at 26 °C, respectively). The critical photoperiod for flowering in a cowpea genotype from Uganda ('TVu 1188') has been found to range from 16·0 h d$^{-1}$ at 15 °C to 11·5 h d$^{-1}$ at 25 °C (Ellis *et al.*, 1994*a*). Reports on soya bean are contradictory: in a controlled environment study, critical photoperiods for flowering in eight cultivars have been found to increase with temperature (Hadley *et al.*, 1984), while in field experiments, the critical photoperiods for flowering in nine different soya bean genotypes decreased with temperature (Summerfield *et al.*, 1993). In the latter study, critical photoperiods of 12·6 to 13·6 h d$^{-1}$ at 20 °C and 11·7 to 13·3 h d$^{-1}$ at 25 °C have been found.

The ceiling photoperiod for the rate from flowering to podding in 'Tiga Nicuru' decreased from 13·95 h d$^{-1}$ at 22 °C to 13·07 h d$^{-1}$ at 26 °C (Table 4). Summerfield *et al.* (1993) found that ceiling photoperiods for the rate to flowering in soya bean increased with temperature. The difference is due to the fact that the parameter $b_2$ in the photothermal response plane of 'Tiga Nicuru' has a negative value ($1/(p-f)$ decreases with temperature), while this parameter has a positive value (development rate increasing with temperature) for the soya bean genotypes used by Summerfield *et al.* (1993). This means that the photothermal plane of 'Tiga Nicuru' is tilted differently than the photothermal plane in Fig. 1.

### *Model testing*

Model testing showed that the predictions of the time from sowing to flowering, based on the linear models derived from the main experiment, were in good agreement with the observed times to flowering in the test experiments: deviations between predicted and observed values were always less than 10 % (Fig. 4A).

Predictions of the time from flowering to podding were less accurate. Deviations were often higher than 10 % (Fig. 4B), but in all test experiments except expt 5 the difference between predicted and observed times from flowering to podding was less than 10 d (Table 5). The extreme long times to podding of 'GabC92' and 'NTSC92' in expt 5 might be a result of the maximum temperatures for podding being exceeded, because expt 5 was carried out in a glasshouse without forced cooling, and maximum temperatures of 35–40 °C were common in the months after flowering. Deviations between predicted and observed times from sowing to podding were less than 10 %, except for expt 5 (Fig. 4C; Table 5).

In the main experiment, the photoperiod was prolonged beyond 8 h d$^{-1}$ by means of low intensity artificial light. In the expts 3, 4, 6 and 7, there was no photoperiod extension by means of low intensity light, but high intensity natural and/or artificial light throughout the light period. The good prediction of the times to flowering and podding in expts 3, 4, 6 and 7 with models based on the main experiment indicates that light integral has no effect on development.

TABLE 5. *Predicted and observed times from sowing to flowering* (f), *flowering to podding* (p−f) *and sowing to podding* (p) *for three bambara groundnut selections in various test experiments* (*experiment numbers refer to Table 1*)

| Selection | | Experiment | $P$ (h d$^{-1}$) | $f$ (d) | | $p-f$ (d) | | $p$ (d) | |
|---|---|---|---|---|---|---|---|---|---|
| | | | | Pred. | Obs. | Pred. | Obs. | Pred. | Obs. |
| 'GabC92' | | 1 | 10 | 45 | 43 | 35 | n.a. | 80 | n.a. |
| | | | 12 | 45 | 44 | 41 | n.a. | 86 | n.a. |
| | | 2 | 12 | 46 | 47 | 41 | n.a. | 87 | n.a. |
| | | | 14 | 46 | 47 | 49 | n.a. | 95 | n.a. |
| | | 4 | 12 | 51 | 55 | 41 | 33 | 92 | 88 |
| | | 5 | 11 | 46 | 47 | 42 | 49 | 88 | 96 |
| | | | 14 | 46 | 47 | 62 | 87 | 108 | 134 |
| | | 6 | 12·5 | 55 | 57 | 37 | 41 | 92 | 98 |
| | | 7 | 13·5 | 50 | 46 | 43 | 44 | 93 | 90 |
| 'NTSC92' | | 3 | 11·5 | 44 | 40 | 34 | 37 | 78 | 77 |
| | | 5 | 11 | 44 | 46 | 34 | 44 | 78 | 90 |
| | | | 14 | 44 | 45 | 48 | 72 | 92 | 117 |
| | | 6 | 12·5 | 52 | 52 | 34 | 33 | 86 | 85 |
| | | 7 | 13·5 | 47 | 43 | 39 | 36 | 86 | 79 |
| 'Tiga Nicuru' | Method 1 | 3 | 11·5 | 39 | 39 | 34 | 23 | 73 | 62 |
| | | 6 | 12·5 | 48 | 50 | 37 | 34 | 85 | 84 |
| | | 7 | 13·5 | 43 | 39 | 46 | 60 | 87 | 99 |
| | Method 2 | 3 | 11·5 | | | 27 | 23 | 66 | 62 |
| | | 6 | 12·5 | | | 30 | 34 | 78 | 84 |
| | | 7 | 13·5 | | | 64 | 60 | 97 | 99 |

The predicted values of $f$ and $p-f$ were calculated with the models in Table 2 and Table 3, respectively; the predicted value of $p$ was calculated by adding the values of $f$ and $p-f$.

## CONCLUSION

This study has shown that the times from sowing to flowering and from flowering to podding in bambara groundnut may be predicted with simple linear models (relating the rates of progress from sowing to flowering and from flowering to podding to photoperiod and temperature), based on a semi-controlled environment experiment. Observed times from sowing to flowering and podding are between 90 and 110 % of the predicted values.

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## LITERATURE CITED

**Ellis RH, Lawn, RJ, Summerfield RJ, Qi A, Roberts EH, Chay PM, Brouwer JB, Rose JL, Yeates SJ. 1994*a*.** Towards the reliable prediction of time to flowering in six annual crops. III. Cowpea (*Vigna unguiculata*). *Experimental Agriculture* **30**: 17–29.

**Ellis RH, Lawn RJ, Summerfield RJ, Qi A, Roberts EH, Chay PM, Brouwer JB, Rose JL, Yeates SJ, Sandover S. 1994*b*.** Towards the reliable prediction of time to flowering in six annual crops. IV. Cultivated and wild mung bean. *Experimental Agriculture* **30**: 31–43.

**Ellis RH, Lawn RJ, Summerfield RJ, Qi A, Roberts EH, Chay PM, Brouwer JB, Rose JL, Yeates SJ, Sandover S. 1994*c*.** Towards the reliable prediction of time to flowering in six annual crops. V. Chickpea (*Cicer arietinum*). *Experimental Agriculture* **30**: 271–282.

**Ellis RH, Summerfield RJ, Roberts EH. 1990.** Flowering in faba bean: genotypic differences in photoperiod sensitivity, similarities in temperature sensitivity, and implications for screening germplasm. *Annals of Botany* **65**: 129–138.

**Erskine W, Hussain A, Tahir M, Baksh A, Ellis RH, Summerfield RJ, Roberts EH. 1994.** Field evaluation of a model of photothermal flowering responses in a world lentil collection. *Theoretical and Applied Genetics* **88**: 423–428.

**Flohr ML, Williams JH, Lenz F. 1990.** The effect of photoperiod on the reproductive development of a photoperiod sensitive groundnut (*Arachis hypogaea* L.) cv. NC Ac 17090. *Experimental Agriculture* **26**: 397–406.

**Grimm SS, Jones JW, Boote KJ, Herzog DC. 1994.** Modeling the occurrence of reproductive stages after flowering for four soybean cultivars. *Agronomy Journal* **86**: 31–38.

**Hadley P, Roberts EH, Summerfield RJ, Minchin, FR. 1983*a*.** 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.

**Hadley P, Roberts EH, Summerfield RJ, Minchin FR. 1984.** Effects of temperature and photoperiod on flowering in soya bean [*Glycine max* (L.) Merrill]: a quantitative model. *Annals of Botany* **53**: 669–681.

**Hadley P, Summerfield RJ, Roberts EH. 1983*b*.** Effects of temperature and photoperiod on reproductive development of selected grain legume crops. In: Jones DG, Davies DR, eds. *Temperate legumes: physiology, genetics and nodulation*. London: Pitman, 19–41.

**Harris D, Azam-Ali SN. 1993.** Implications of daylength sensitivity in bambara groundnut (*Vigna subterranea*) for production in Botswana. *Journal of Agricultural Science, Cambridge* **120**: 75–78.

**Hodges T. 1991.** Modeling and programming philosophies. In: Hodges T, ed. *Predicting crop phenology*. Boca Raton: CRC Press, 101–114.

**Lawn RJ, Summerfield RJ, Ellis RH, Qi A, Roberts EH, Chay PM, Brouwer JB, Rose JL, Yeates SJ. 1995.** Towards the reliable prediction of time to flowering in six annual crops. VI. Applications in crop improvement. *Experimental Agriculture* **31**: 89–108.

**Linnemann AR. 1991.** Preliminary observations on photoperiod regulation of phenological development in bambara groundnut (*Vigna subterranea*). *Field Crops Research* **26**: 295–304.

**Linnemann AR. 1993.** Phenological development in bambara groundnut (*Vigna subterranea*) at constant exposure to photoperiods of 10 to 16 h. *Annals of Botany* **71**: 445–452.

**Linnemann AR, Azam-Ali S. 1993.** Bambara groundnut (*Vigna subterranea*). In: Williams JT, ed. *Pulses and vegetables*. London: Chapman and Hall, 13–58.

**Linnemann AR, Craufurd PQ. 1994.** Effects of temperature and photoperiod on phenological development in three genotypes of bambara groundnut (*Vigna subterranea*). *Annals of Botany* **74**: 675–681.

**Linnemann AR, Westphal E, Wessel M. 1995.** Photoperiod regulation of development and growth in bambara groundnut (*Vigna subterranea*). *Field Crops Research* **40**: 39–47.

**Payne RW, Lane PW, Digby PGN, Harding SA, Leech PK, Morgan GW, Todd AD, Thompson R, Tunnicliffe Wilson G, Welham SJ, White RP. 1993.** *Genstat 5 release 3 reference manual*. Oxford: Clarendon Press.

**Roberts EH, Hadley P, Summerfield RJ. 1985.** Effects of temperature and photoperiod on flowering in chickpeas (*Cicer arietinum* L.). *Annals of Botany* **55**: 881–892.

**Roberts EH, Summerfield RJ. 1987.** Measurement and prediction of flowering in annual crops. In: Atherton JG, ed. *Manipulation of flowering*. London: Butterworths, 17–50.

**Sinclair TR, Kitani S, Hinson K, Bruniard J, Horie T. 1991.** Soybean flowering date: linear and logistic models based on temperature and photoperiod. *Crop Science* **31**: 786–790.

**Squire GR. 1990.** *The physiology of tropical crop production*. Wallingford: C.A.B. International.

**Summerfield RJ, Lawn RJ, Qi A, Ellis RH, Roberts EH, Chay PM, Brouwer JB, Rose JL, Shanmugasundaram S, Yeates SJ, Sandover S. 1993.** Towards the reliable prediction of time to flowering in six annual crops. II. Soyabean (*Glycine max*). *Experimental Agriculture* **29**: 253–289.

**Summerfield RJ, Roberts EH, Ellis RH, Lawn RJ. 1991.** Towards the reliable prediction of time to flowering in six annual crops. I. The development of simple models for fluctuating field environments. *Experimental Agriculture* **27**: 11–31.

**Summerfield RJ, Roberts EH, Erskine W, Ellis RH. 1985.** Effects of temperature and photoperiod on flowering in lentils (*Lens culinaris* Medic.). *Annals of Botany* **56**: 659–671.

**Watkinson AR, Lawn RJ, Ellis RH, Qi A, Summerfield RJ. 1994.** *RoDMoD. A computer program for characterising genotypic variation in flowering responses to photoperiod and temperature*. CSIRO, IPGRI, University of Reading.