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Duration from vine emergence to flowering suggests a long-day or rate of change of photoperiod response in white yam (*Dioscorea rotundata* Poir.)

E.I. Ile[a], P.Q. Craufurd[a,*], R. Asiedu[b], N.H. Battey[c]

[a] *Plant Environment Laboratory, The University of Reading, Cutbush Lane, Shinfield, Reading RG2 9AF, UK*
[b] *International Institute of Tropical Agriculture, Oyo Road, Ibadan, Nigeria*
[c] *School of Biological Sciences, The University of Reading, Whiteknights, Reading RG6 6AS, UK*

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Abstract

The objective of this study was to quantify the effect of photoperiod on the duration from vine (shoot) emergence to flowering in white or Guinea yam (*Dioscorea rotundata*). The duration from vine emergence to flowering in two clonal varieties of yam (TDr 131 and TDr 99-9) was recorded at 10 different sowing dates/locations in Nigeria. Durations to flowering varied from 40 to >88 days. Mean daily temperature and photoperiod between vine emergence and flowering varied from 25 to 27 °C and 13.1 to 13.4 h day^{-1}, respectively. Both clones had similar responses to temperature, with base and optimum temperatures of 12 and 25–27 °C, respectively. Thermal durations to flowering were strongly related ($r^2 > 0.75$–0.83) to absolute photoperiod (h) at vine emergence as well as to rate of change of photoperiod (s day^{-1}) at vine emergence. The response to absolute photoperiod suggests that white yams are quantitative LDPs, flowering sooner in long than short days. Yams also flowered earlier when the rate of change of photoperiod was positive but small, or was negative. It is suggested that yams may use a combination of photoperiod and rate of change in order to fine tune flowering time.

Keywords: *Dioscorea rotundata*; Flowering; Photoperiod; Rate of change of photoperiod; Yam

1. Introduction

Yams (white yam, *Dioscorea rotundata* and water yam, *Dioscorea alata*) are annuals that produce underground tubers. The tubers are an important source of carbohydrate for millions of people in the humid and dry tropics of West Africa (Coursey, 1967; Scott et al., 2000). Planting is carried out at the start of the rainy season, between February and June in West Africa, and flowering usually occurs between June and September (Asiedu et al., 1998). Tubers are mostly harvested when the shoot senesces, between October and December (Orkwor and Asadu, 1998). Flowering and non-flowering types of the white and water yam are found. Among flowering types, flowers are mostly dioecious, though monoecious and hermaphrodite types have been reported (Sadik and Okereke, 1975). The presence of non-flowering clones, as well as erratic and unpredictable flowering in flowering clones, is a major constraint to yam improvement (Abraham, 1997; Asiedu et al., 1998).

Yams (white and water yam) have been described as short-day plants (SDP) for flowering (Degras, 1993; Bai and Ekanayake, 1998), though these statements appear to be largely based on anecdote and not experimentation. The initiation and growth of tubers in white and water yam, however, does exhibit a short-day response (Shiwachi et al., 2000, 2002). Among other yam species, both long-day (Chinese yam, *Dioscorea opposita*: Yoshida and Kanahama, 1999) and short-day (*Dioscorea spiculiflora*: Preston and Haun, 1963) flowering responses are found. Most tropical grain crop species grown in West Africa, such as sorghum (*Sorghum bicolor*) and cowpea (*Vigna unguiculata*), are quantitative SDPs that exhibit substantial variation in photoperiod-sensitivity (Roberts and Summerfield, 1987). In contrast, duration to flowering or the appearance of the first reproductive branch in cassava (*Manihot esculenta*), a major tropical root crop, exhibits a long-day response (Keating et al., 1982; Matthews and Hunt, 1994).

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[*] Corresponding author. Tel.: +44 118 988 3000; fax: +44 118 988 5491.
E-mail address: p.q.craufurd@rdg.ac.uk (P.Q. Craufurd).

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Responses to photoperiod and temperature have been quantified in many crop species using models that calculate daily or seasonal rates of development, usually expressed through thermal time (DTT), and predominately linear responses to daily or mean photoperiod (Roberts and Summerfield, 1987; Hoogenboom et al., 1994; McCown et al., 1996). Rate of change of photoperiod (e.g. in s day^{-1}) has also been used to quantify responses to photoperiod, notably in cassava (Matthews and Hunt, 1994). Recently, Clerget et al. (2004) have shown that rate of change of photoperiod can help predict flowering dates in photoperiod-sensitive sorghum cultivars in Mali, particularly when sowings occur before the longest day and plants experience lengthening and then shortening days. Rate of change of photoperiod has also been implicated in the induction of flowering in tropical rainforest trees (Borchert et al., 2005).

The objective of this study was to quantify the effects of temperature and photoperiod (absolute and rate of change) on the duration from vine emergence to the appearance of the first flower bud in two flowering clones of white yam from field experiments in Nigeria. We tested: (i) whether white yam was a conventional quantitative SDP wherein flowering occurs sooner in absolute short than long days; (ii) whether white yam responded to rate of change in photoperiod, and whether this response was a better predictor of flowering time than absolute photoperiod.

2. Materials and methods

2.1. The study site

The study was conducted in Nigeria at three research stations within the yam-growing belt of West Africa belonging to the International Institute of Tropical Agriculture (IITA). The stations were at Onne (4°46′N; 7°10′E) in the humid rainforest agroecological zone (mean annual rainfall 2501 mm), Ibadan (7°26′N; 3°54′E) in the moist savannah transition zone (mean annual rainfall 1253 mm) and Abuja (9°16′N; 7°20′E) in the Guinea savannah zone (mean annual rainfall 1302 mm). Total rainfall, mean minimum and maximum temperature and RH during the experimental periods in 1999 and 2000 are given in Table 1.

2.2. Planting material, field operations and observations

The two varieties of *D. rotundata* used in this study were TDr 131, a profuse male flowering clone, and TDr 99-9, a monoecious flowering clone. The varieties were planted on 10 occasions in a randomised complete block design with three replications. Tuber sets (from the yam head region only) weighing 200 g were planted in ridges at a spacing of 1 m × 1 m inter- and intra-row spacing, giving a total of 30 plants per replication and 90 plants per variety. Planting was done once in 1999 and 2000 at Onne, Ibadan and Abuja, as well as at monthly intervals from March through August at Ibadan in 2000. Plants in each of the environments therefore experienced different temperature and photoperiod regimes. Plants were staked 1 month after planting, hand weeding was done as needed and no chemical inputs were applied. The date of vine (shoot) emergence and the appearance of the first flower bud (hereafter referred to as flowering) were recorded for each of the 90 plants.

Yam tubers exhibit dormancy and dates of vine emergence within individual sowing dates may vary by as much as 40 days. Furthermore, yam tubers that break dormancy and sprout before planting do not produce any true leaves until after planting. This might be thought of as a juvenile period, though there is no information on this in yam. Assuming that the organ that senses photoperiod is the true leaf, then the most appropriate measure of rate of development in yam is the duration from vine emergence to flowering.

2.3. Data analysis

Developmental durations are usually analysed as rates of development, either in days^{-1} or thermal time (°C day^{-1}), modified by a function describing the response to photoperiod. In this study we followed approaches adopted by DSSAT and many other models, whereby progress from vine emergence (DR = 0) to flowering (DR = 1) is computed from daily rates of development as:

$$\mathrm{DR} = \sum_{i=1}^{j} \frac{\mathrm{DTT}_i}{f(P)} \tag{1}$$

where j is the number of days after vine emergence, DTT_i is the 'effective' thermal time on day i and $f(P)$ is a function describing the response to photoperiod.

The effect of temperature on flowering has not been studied in white yam and the cardinal temperatures have not been determined. As mean daily temperature between vine emergence and flowering only varied from 24.8 to 27.0 °C between sites and sowing dates, cardinal temperatures could not be determined from relations between the reciprocal of duration to flowering

Table 1
Total rainfall, mean minimum and maximum temperature, and mean RH at Onne, Ibadan and Abuja during the experiments in 1999 and 2000

Location	Experimental period	Year	Rainfall (mm)	Minimum/maximum temperature (°C)	Mean RH (%)
Onne	April–August	1999	1251	22.8/29.7	71
		2000	1473	22.9/30.3	81
Ibadan	March–August	1999	961	22.1/31.2	81
		2000	1038	22.5/31.0	82
Abuja	May–September	1999	1030	21.9/29.8	85
		2000	1069	22.4/30.2	82

and mean temperature (Roberts and Summerfield, 1987). Therefore optimisation procedures (Microsoft Evolutionary Solver) that minimised the root mean square deviation (RMSD) for observed and predicted flowering times were used to estimate values of a constant a, and base (T_b) and optimum (T_o) temperature from mean daily temperature (T) using the following equations:

$$\begin{aligned} &\text{when } T_b < T \le T_o, \quad \mathrm{DR} = a(T - T_b);\\ &\text{when } T_o < T \le T_m, \quad \mathrm{DR} = a(T_o - T_b)\left[1 - \frac{T - T_o}{T_m - T_o}\right] \end{aligned} \qquad (2)$$

The maximum temperature (T_m) was fixed at 42 °C, the value found for cassava (Matthews and Hunt, 1994). Optimisation gave similar values for a and T_b in both clones and these were fixed at 0.0012 and 12 °C, respectively. The value of T_o was different in the two clones, 25.8 °C in TDr 99-9 and 27.5 °C in TDr 131. Models without an optimum temperature response had RMSDs between 10% and 26% greater than models with an optimum temperature response. These equations were then applied to daily temperature data to calculate the effective daily temperature, DTT_i.

Assuming yam plants are SDP, the photoperiod function, $f(P)$, is a linear function describing the delay in flowering (in thermal time) when mean photoperiod (P) is greater than a critical value:

$$\begin{aligned} &\text{when } P > P_c, \quad f(P) = \mathrm{DTT}_m + P_s(P - P_c);\\ &\text{when } P \le P_c, \quad f(P) = \mathrm{DDT}_m \end{aligned} \qquad (3)$$

where DDT_m is the minimum thermal duration (°C day) to FL, P_s is the slope or photoperiod-sensitivity (expressed as °C day h^{-1}) and P_c the critical photoperiod, i.e. that photoperiod at and below which photoperiod does not delay flowering. Photoperiod, including civil twilight, was calculated from the US Navy Observatory website (http://www.aa.usno.navy.mil/data/docs/RS_OneYear.html). Values of DDT_m, P_s and P_c were determined from linear regressions of thermal duration to flowering ($\Sigma\mathrm{DDT}_i$) on mean photoperiod between vine emergence and flowering or on photoperiod at vine emergence.

The response of thermal duration to flowering to rate of change of photoperiod (s day^{-1}) at vine emergence was also determined using Eq. (3), substituting rate of change for photoperiod. Rate of change in photoperiod at vine emergence was interpolated from the daily photoperiods given above. Annual variation in photoperiod and rate of change at Onne and Abuja are given in Fig. 1.

Initially, all equations were fitted using mean temperature and mean photoperiod between vine emergence and flowering. Thereafter models derived from these relations were fitted to daily temperature and photoperiod data to predict flowering. The RMSD was used to measure the goodness of fit of the models, where:

$$\mathrm{RMSD} = \sqrt{\frac{1}{n}\sum (f_{\mathrm{obs}} - f_{\mathrm{pre}})^2} \qquad (4)$$

where n is the number of observations and f_{obs} and f_{pre} are observed and predicted durations from vine emergence to flowering.

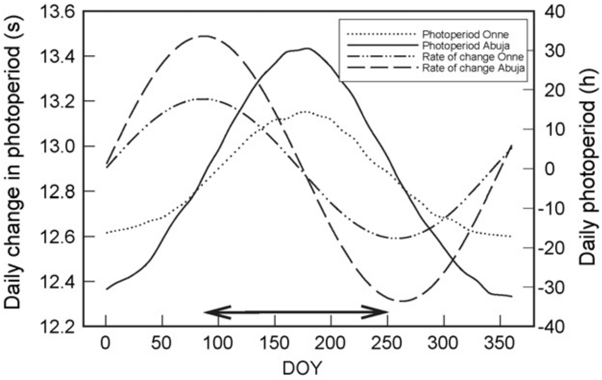

Fig. 1. Daily photoperiod (including civil twilight), and the rate of change of photoperiod, at Onne (4°46′N) and Abuja (9°16′N) in Nigeria. Arrows show the period over which vines emerged. DOY, day of year.

3. Results

3.1. Weather conditions during plant growth

Growing conditions at all three locations were good during 1999 and 2000 with adequate rainfall and no periods of stress. Mean minimum and maximum temperatures were very similar at all three sites at about 22 and 32 °C (Table 1). Mean temperature was slightly warmer at Ibadan and Onne than Abuja, and warmer at Ibadan in March–May than June–September. Photoperiod, and the rate of change of photoperiod, varied between sites and sowing dates (Fig. 1). The maximum photoperiod experienced by plants ranged from 13.16 h day^{-1} at Onne to 13.42 h day^{-1} at Abuja. Rates of change of photoperiod ranged from 30 to −30 s day^{-1}.

3.2. Response of flowering time to planting date

Across years and locations planting dates ranged from start of March, i.e. from day of the year (DOY) 63, through to the start of August (DOY 215) (Table 2). Tubers planted in August 2000 at Ibadan did not flower. In TDr 131, vines emerged on average 20–40 days after planting (DAP) and flowers 50–76 DAP. Across planting dates vine emergence and flowering therefore occurred between 13 April and 3 September, and 28 June and 14 August, respectively. Within planting dates, vine emergence and flowering also varied from 20 to >40 days (Fig. 2) due to variable tuber dormancy (see Craufurd et al., 2001).

There was a strong negative relation between duration from vine emergence to flowering and date of planting in both clones (Fig. 3), indicating a strong response to photoperiod and/or temperature. The later tubers were planted and the closer to the longest day (DOY 180) vines emerged, the shorter the duration from vine emergence to flowering in both clones. TDr 131 flowered about 10 days earlier on average than TDr 99-9, except at Abuja in 1999 where flowering in TDr 99-9 occurred after 46

Table 2
Effect of location and planting date on mean dates of vine emergence, appearance of first flower and the thermal duration from vine emergence to flowering in TDr 131 and TDr 99-9

Location	Year	Planting date (DOY)	TDr 131			TDr 99-9		
			Vine emergence (DOY) ± S.E. ($n = 80$–90)	Flowering (DOY) ± S.E. ($n = 21$–73)	Vine emergence to flowering (°C day)	Vine emergence (DOY) ± S.E. ($n = 80$–90)	Flowering (DOY) ± S.E. ($n = 21$–73)	Vine emergence to flowering (°C day)
Abuja	1999	135	161 ± 1.3	215 ± 1.9	740	172 ± 2.1	218 ± 2.2	612
Abuja	2000	145	174 ± 1.1	223 ± 3.9	656	182 ± 2.8	240 ± 3.7	770
Ibadan	1999	113	146 ± 1.0	207 ± 1.5	859	157 ± 1.9	218 ± 2.1	805
Ibadan	2000	63	103 ± 1.0	179 ± 1.2	1081	111 ± 1.7	199 ± 2.1	1133
Ibadan	2000	94	130 ± 1.3	201 ± 2.8	981	134 ± 2.3	211 ± 3.0	1073
Ibadan	2000	123	148 ± 1.0	202 ± 2.8	739	160 ± 1.8	224 ± 2.3	836
Ibadan	2000	153	173 ± 1.0	226 ± 2.6	681	189 ± 2.5	247 ± 7.7	749
Ibadan	2000	215	241 ± 1.1	[a]	[a]	246 ± 15.6	[a]	[a]
Onne	1999	127	149 ± 1.1	212 ± 3.1	891	165 ± 1.9	225 ± 3.0	810
Onne	2000	102	130 ± 1.1	199 ± 2.5	965	134 ± 1.7	204 ± 3.2	918

[a] Did not flower.

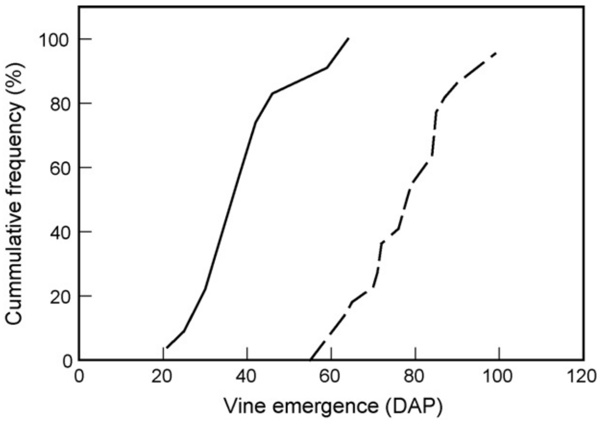

Fig. 2. Cumulative frequency of vine emergence (—) and flowering (– – –) in TDr 99-9 sown in April 2000 at Ibadan. DAP, days after planting.

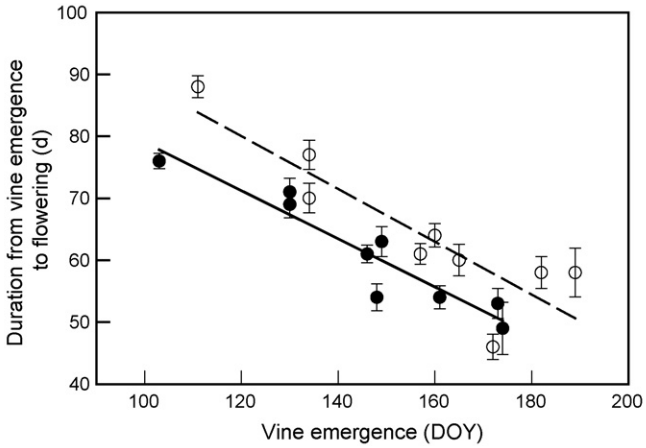

Fig. 3. Relation between duration from vine emergence to flowering and day of vine emergence in TDr 131 (solid circle) and TDr 99-9 (open circle). Solid line is the linear regressions for TDr 131 ($y = -0.386x + 117$, $r^2 = 0.88$) and hashed line that for TDr 99-9 ($y = -0.426x + 131$, $r^2 = 0.78$). Bars are SE mean.

days. This value appears to be too early for TDr 99-9, and minimum durations to flowering are approximately 50 and 60 days in TDr 131 and TDr 99-9, respectively.

Thermal durations to flowering ranged from 656 to 1081 °C day in TDr 131 and 612 °C day (770 °C day excluding Abuja 1999) to 1133 °C day in TDr 99-9 (Table 2). Thermal durations were generally shorter in TDr 99-9 than TDr 131 for the same calendar duration to flowering because of the lower T_o in TDr 99-9.

3.3. Effect of mean photoperiod on thermal duration to flowering

Mean photoperiod (h day^{-1}) between vine emergence and flowering did not differ much across planting dates or locations, ranging from 13.1 to 13.4 h day^{-1} in both clones. The highest values of mean photoperiod were for the two sowings at Abuja, the location at the highest latitude. In neither variety was there a significant relation between the thermal duration to flowering and mean photoperiod (Fig. 4), though in TDr 131 flowering occurred earlier at longer photoperiods. As vine emergence occurred before the longest day, plants were exposed to both lengthening and shortening photoperiods (Fig. 1). Thus plants emerging in April (103 DOY) and June (173 DOY) had the same mean photoperiod (13.3 h day^{-1}) but clearly very different thermal durations (1081 and 681 °C day, respectively in TDr 131). Therefore, variation in mean photoperiod could not explain variation in thermal duration to flowering at these planting dates.

3.4. Effect of photoperiod at vine emergence on thermal duration to flowering

Some models assume that the duration of the photoperiod-sensitive phase is proportional to the photoperiod at vine emergence rather than mean photoperiod between vine emergence and flowering (e.g. Huda, 1987). Values of photoperiod at vine

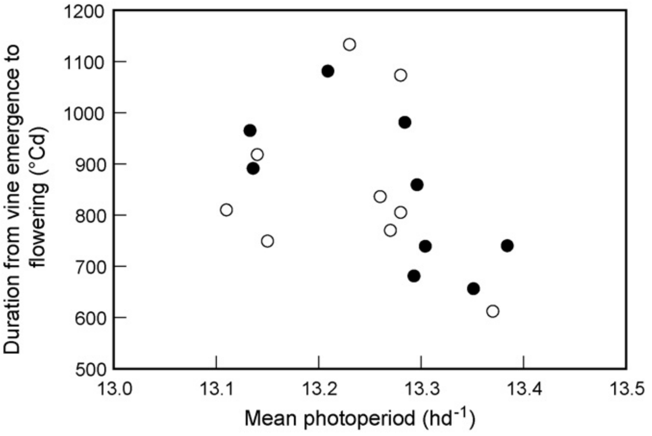

Fig. 4. Relation between thermal duration from vine emergence to flowering (°C day) and mean photoperiod between vine emergence and flowering in TDr 131 (solid circle) and TDr 99-9 (open circle).

emergence ranged from 12.98 to 13.43 h day^{-1} and there were significant ($P < 0.001$) negative relations between thermal duration to flowering and photoperiod at vine emergence in both clones (Fig. 5). Both clones had similar slopes based on a comparison of regressions, i.e. photoperiod-sensitivity, wherein thermal duration increased by 870 °C day h^{-1} as photoperiod became shorter. The values of P_c, estimated from the intercept at the minimum thermal duration to flowering (656 °C day in TDr 131 and set at 700 °C day in TDr 99-9), were 13.44 and 13.53 h in TDr 131 and TDr 99-9, respectively. Thus the thermal duration to flowering was shortened as photoperiod increased. Therefore white yams are quantitative long-day plants (LDP), or at least behave as LDP over the range of sowing dates analysed here.

3.5. *Effect of rate of change of photoperiod on thermal duration to flowering*

The rate of change of photoperiod at vine emergence ranged from −7.3 to 25.4 s day^{-1} in TDr 131 and TDr 99-9. Rate of change at vine emergence and photoperiod at vine emergence were inversely though not strongly related ($R^2 = 0.52$–0.57, $P < 0.05$). Plants emerging before the longest day (21 June) had positive rates of change, particularly at the earliest sowings, and those close to or after the longest day small or negative rates of change. In both clones there was a strong and significant linear and positive relation between rate of change at vine emergence and thermal duration (Fig. 6). There was no relation with absolute rate of change (not presented), indicating that the direction as well as rate of change is important. Both clones exhibited a similar sensitivity to rate of change at vine emergence of 14–16 °C day s^{-1}, though values of P_c were different at −0.26 s in TDr 131 and −7.3 s in TDr 99-9 (Table 3).

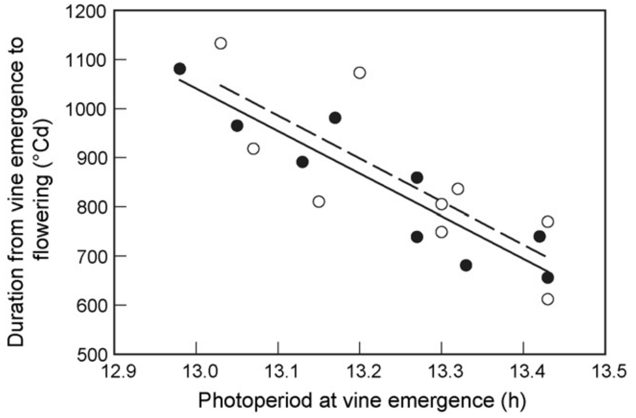

Fig. 5. Relation between thermal duration from vine emergence to flowering (°C day) and photoperiod at vine emergence in TDr 131 (solid circle) and TDr 99-9 (open circle). Solid line is linear regression for TDr 131 ($y = 1041x + 14742$, $r^2 = 0.83$) and hashed line that for TDr 99-9 ($y = 1237x + 17409$, $r^2 = 0.75$).

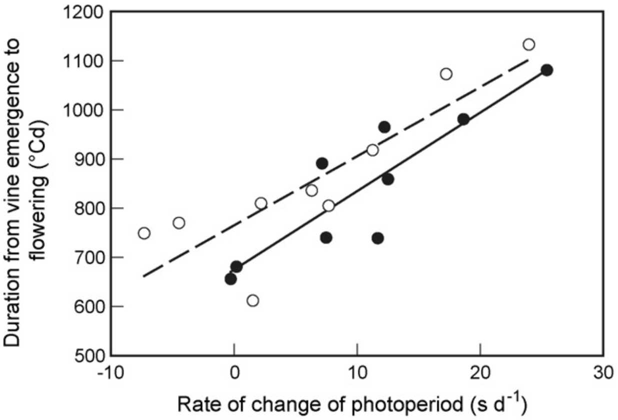

Fig. 6. Relation between thermal duration from vine emergence to flowering (°C day) and rate of change of photoperiod at vine emergence in TDr 131 (solid circle) and TDr 99-9 (open circle). Solid line is linear regression for TDr 131 ($y = 15.9x + 675$, $r^2 = 0.78$) and hashed line that for TDr 99-9 ($y = 14.1x + 764$, $r^2 = 0.74$).

Thus although sowings in Abuja experienced the longest photoperiod at vine emergence, photoperiods were either almost constant or becoming shorter after vine emergence. In contrast, early sowings at Ibadan emerged into short-days (13 h) that were becoming longer. White yams therefore exhibit a quantitative response to rate of change, as well as absolute photoperiod.

Table 3
Minimum thermal duration to flowering (DTT_m), critical photoperiod (P_c), photoperiod-sensitivity (P_s) and r^2 derived from photothermal models with absolute photoperiod at vine emergence and rate of change of photoperiod at vine emergence in TDr 131 and TDr 99-9

Model	DTT_m (°C day)	P_c (h)	P_s (°C day h^{-1})	r^2
TDr 131				
Photoperiod at vine emergence	656	13.44	−867	0.83
Rate of change at vine emergence	656	−0.26	15.99	0.75
TDr 99-9				
Photoperiod at vine emergence	700	13.53	−875	0.78
Rate of change at vine emergence	700	−7.3	14.07	0.74

All significant at $P < 0.001$.

Table 4
Root mean square deviations (days) for daily models of rate of development against temperature, photoperiod at vine emergence, and rate of change of photoperiod in TDr 131 and TDr 99-9

Variety	Temperature	Photoperiod at vine emergence	Rate of change of photoperiod
TDr 131	17.9	8.1	11.4
TDr 99-9	14.4	12.5	8.1

RMSD values for each of the models given above fitted to daily temperature and photoperiod data to predict flowering times are given in Table 4. These values show that RMSD were reduced by including photoperiod in the models in both clones, from 17.9 to 8.1 days in TDr 131 and 14.4–8.1 days in TDr 99-9. The best photothermal model in TDr 131 used photoperiod at vine emergence, whereas in TDr 99-9 it was rate of change at vine emergence. Both models predicted flowering dates well ($R^2 > 0.90$, not presented), though rate of change predictions had intercepts and slopes closer to 0 and 1, respectively, than photoperiod at vine emergence. A multiple regression with both photoperiod and rate of change at vine emergence did not significantly ($P > 0.05$) improve predictions.

3.6. Relations between photoperiod and rate of change at vine emergence and duration to flowering within a sowing date

Within any given planting date, the date of vine emergence and flowering varied by 20 to >40 days (Fig. 2) and so individual plants were exposed to a range of photoperiods at vine emergence. Nonetheless, flowering dates in these individual plants should still be predictable based on photoperiod at vine emergence (or rate of change at vine emergence). Within the April sowing at Ibadan in TDr 99-9, vine emergence occurred between 20 and 65 DAP and flowering between 55 and 99 DAP. Photoperiod at vine emergence ranged from 13.07 to 13.30 h. There was a significant negative relation between thermal duration to flowering and photoperiod at vine emergence within this sowing date (Fig. 7), though the slope (photoperiod-sensitivity) was double that based on mean flowering dates across sowing dates and sites (see Fig. 5). Within a sowing date photoperiod and rate of change at vine emergence were highly correlated ($r = 0.97$) and so relations with rate of change at vine emergence were also significant.

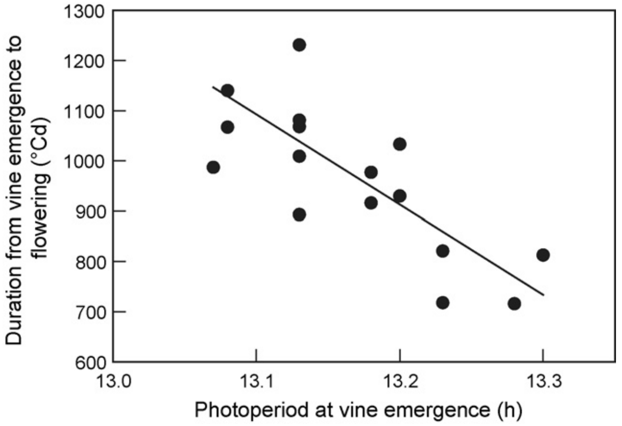

Fig. 7. Relation between thermal duration from vine emergence to flowering (°C day) and photoperiod at vine emergence in individual plants of TDr 99-9 sown at Ibadan in April 2000. Fitted line: $y = 24635 - 1797x$, $r^2 = 0.63$.

4. Discussion

The effect of photoperiod and temperature on the duration from vine emergence to flowering in white yam has not been studied before. Furthermore there have been no quantitative studies of the effects of photoperiod, and particularly temperature, on the duration to flowering in other yam species either, such as water yam (*D. alata*) or Chinese yam (*D. opposita*). The work reported here shows that white yam has a strong quantitative response of rate of development towards flowering to photoperiod, both absolute photoperiod and the rate of change of photoperiod.

The range of locations and sowing dates used in this field study resulted in only a narrow range of mean daily temperatures, between 24.9 and 27.0 °C in TDr 131 and 24.8–26.5 °C in TDr 99-9, and the response of rate of development to temperature could not be quantified directly. Therefore iterative techniques were used to estimate cardinal temperature values for T_b and T_o, which were estimated to be 12 °C and between 25 and 27 °C in both clones, respectively. These values of T_b and T_o are typical of other tropical crops such as cassava (Matthews and Hunt, 1994) or sorghum (Craufurd et al., 1999) growing in similar environments.

Our initial hypothesis was that variation in the duration from vine emergence to flowering could be predicted from responsiveness to mean (absolute) photoperiod, in common with many other crop species (Roberts and Summerfield, 1987). Clearly, though, mean photoperiod between vine emergence and flowering could not explain variation in duration to flowering in white yam. However, absolute photoperiod at vine emergence, and rate of change of photoperiod at vine emergence, both accounted for much of the observed variation in flowering times. It is not surprising that mean photoperiod between vine emergence and flowering could not predict flowering times in this study as vine emergence occurred before the longest day and flowering at or after the longest day, and so increasing and decreasing photoperiods were confounded (Constable and Rose, 1988). In many field situations though, where plants only experience photoperiods that are either shortening or lengthening, then approaches using mean photoperiod (Roberts and Summerfield, 1987), photoperiod at emergence or the end of the juvenile phase (Huda, 1987), or a threshold or critical photoperiod (Wien and Summerfield, 1980) will all quantify photoperiod-sensitivity equally effectively.

Our second hypothesis was that white yam is a quantitative SDP, wherein flowering occurs sooner under short than long days. Clearly this was also not true, with both clones exhibiting a quantitative long day response to absolute photoperiod at vine emergence over the range of sowing dates and locations used. There was also a significant relation with rate of change of photoperiod, which is discussed later. Hence as photoperiod at vine emergence increased from 13 to 13.5 h day^{-1}, flowering occurred sooner. Both clones exhibited a similar response to photoperiod, with a photoperiod-sensitivity of −870 °C day h^{-1} and values for P_c of ≥13.4 h day^{-1}. Individual plants within a sowing date that emerged over a 40-day period also exhibited a quantitative long day response. These clones were therefore highly sensitive to photoperiod, the magnitude of sensitivity being similar to that found in the SDP sorghum (Vaksmann et al., 1998; Clerget et al., 2004). These data suggest very strongly that white yams are quantitative LDPs, and not SDPs as hypothesized. Although responses to photoperiod and temperature have not been quantified in white yam or other species, data published in Degras (1993) from Guadeloupe, does show that white yam flowers when days are longest.

There was not a wide enough range of photoperiod to detect the true value of P_c, the longest absolute photoperiod experienced being 13.44 h day^{-1}. The value of P_c in the LDP cassava is about 15.5 h day^{-1} (Matthews and Hunt, 1994). Likewise, the ceiling (P_{ce}) or maximum photoperiod, i.e. that photoperiod at and below (in LDP) which rate of progress towards flowering is zero and plants will not flower, could also not be determined. However, it is of note that plants from the August sowing at Ibadan that emerged at the end of September (DOY 240) never flowered. The photoperiod at vine emergence at this sowing was 13.0 h day^{-1}, and photoperiod decreased to 12.45 h day^{-1} in December. Based on photoperiod at vine emergence, simulations suggest these plants should have flowered about 90 days after vine emergence, at the start of December if the ceiling photoperiod was <12.45 h day^{-1} (Fig. 8). However, if the ceiling photoperiod was about 13 h day^{-1}, plants would not have flowered until May, when day length exceeded this threshold again. At all other sites and planting dates flowering always occurred while photoperiod was >13 h day^{-1}. Additional data from a wider range of photoperiods and temperatures are needed to determine values for P_c and the ceiling photoperiod, as well as temperature responses and interactions between temperature and photoperiod.

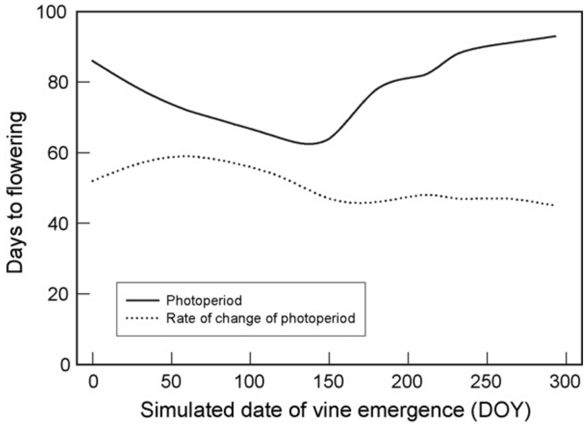

Fig. 8. Simulated durations from vine emergence to flowering in TDr 131 at different sowing dates at Onne with absolute (solid line) or rate of change (hashed line) models.

In general, most annual grain crops originating in the tropics are SDPs (Roberts and Summerfield, 1987), a mechanism that ensures flowering and grain-filling occur before the season ends and under favourable (lower RH) conditions (Craufurd and Qi, 2001). On the other hand, cassava, a major tropical root crop, is, like white yam, an LDP with respect to duration to flowering, but an SDP with respect to root bulking (Matthews and Hunt, 1994). A short day response for tuber or root bulking ensures that plants sown with the first rains before the longest day have a long vegetative period and attain a large leaf area before bulking, as well as ensuring bulking during the growing season. A long day response for flowering would generally result in flowering occurring early in the season, ensuring a temporal separation between vegetative and reproductive growth.

One facet of photoperiod that has received little attention is the direction and rate of change of photoperiod (Thomas and Vince-Prue, 1997), although this has been implicated in flowering studies on soyabean (Constable and Rose, 1988), sorghum (Clerget et al., 2004) and most relevantly cassava (Matthews and Hunt, 1994). Rate of change of photoperiod, or more precisely the timing of sunset, has also been implicated in the induction of flowering in tropical rainforest trees at equatorial latitudes, where it is suggested that the average daylength signal is too small to modulate flowering (Borchert et al., 2005). In contrast, Slafer et al. (1994) and Kernich et al. (1995) reported that rate of change of photoperiod had no effect on the rate of development in wheat or barley independent of the mean photoperiod. However, these two studies only exposed LDPs to two lengthening and hence inductive, rates of change; they did not investigate variable, lengthening and shortening rates of change, as occurred with yam.

In the two clones studied, there was a strong positive linear relation between rate of change of photoperiod and duration to flowering. This response could be quantified in a similar manner to absolute photoperiod, with a slope and critical photoperiod. Thus plants emerging in March/April experienced days that were getting longer rapidly (large, positive rates of change) and the duration to flowering was long; conversely, plants emerging closer to or after June 21 (the longest day), irrespective of latitude and hence absolute photoperiod, experienced either almost constant photoperiods or small, negative rates of change (i.e. shortening day lengths) and the duration to flowering was short. On the basis of this response, white yam may also be described as a low rate of change of photoperiod plant.

Overall, there was no major difference in predicted flowering times between the two models over the range of sowing dates and locations used. We also simulated flowering times from sowing dates throughout the year using daily photoperiod and temperature data (1999 data) at the three locations for TDr 131. Seasonal differences in flowering times between the two models were similar at all sites and are illustrated by Onne, the site with the lowest latitude (Fig. 8). Both models show that flowering occurs sooner as days lengthen and rates of change decrease from March through to mid-June, the longest day. However, after the longest day the absolute photoperiod model predicts increasingly later flowering times as days shorten. In contrast, the rate of change model predicts early flowering times until December because rates of change are mostly below the critical rate (i.e. P_c). Based on these simulations we would have expected flowering to occur in the August sowing at Ibadan, which it did not, supporting the view that there may be a ceiling photoperiod or a qualitative response to photoperiod. Additional sowing dates after the longest day at any of the three locations used here should show which model is correct.

While accepting that flowering times in white yam can be predicted with confidence using conventional models with absolute photoperiod at vine emergence, it is interesting to speculate about the possible role for rate of change in the control of flowering times in the light of previously cited work. Most photothermal studies in controlled environments use constant photoperiods and not variable photoperiods, and so the phenomenon of rate of change has not been thoroughly investigated. Clearly rate of change is a sensitive environmental signal whose signal strength varies temporally during the year from that of absolute photoperiod (Fig. 1). Furthermore, flowering in tropical rainforest trees can be induced by changes of only 6 min or so in the timing of sunset, which varies around the equinox even at the equator (Borchert et al., 2005). Responses to rate of change are known in the animal kingdom (Thomas and Vince-Prue, 1997) and plants can measure daily changes in photoperiod by relating these to phases of the endogenous circadian clock (Imaizumi et al., 2003). Rates of change and absolute photoperiod at vine emergence may at least then be complementary signals. Perhaps plants integrate both absolute and iterative changes in daylength to 'fine tune' flowering times, particularly in the tropics and subtropics where mean temperatures during the growing season are similar (cf. Table 1) and do not provide a useful signal to fine tune flowering at different latitudes. In contrast, in temperate latitudes temperature and vernalization responses can be used to place reproductive development in the most favourable time of the year. Given current knowledge of flowering pathway genes and their expression under long and short photoperiods in *Arabidopsis* and *Oryza* (Hayama et al., 2003; Izawa et al., 2003), it would be interesting to examine the effects of rate of change in these model species.

In conclusion, this study has shown that duration from vine emergence to flowering in two clonal varieties of white yam grown in the field can be quantified by linear responses to temperature and photoperiod. Flowering times can be predicted using absolute photoperiod at vine emergence and the rate of change at vine emergence. In terms of responsiveness to absolute photoperiod, white yams would be classified as quantitative long-day plants; in terms of rate of change, low rate of change plants.

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