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Flowering intensity in white yam (*Dioscorea rotundata*)

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SUMMARY

White or Guinea yam (*Dioscorea rotundata*), grown for its underground tubers, is an important food in West Africa. Progress in yam breeding is constrained by variable flowering behaviour, making hybridization difficult. Yam clones may be dioecious, monoecious or hermaphrodite with variable sex ratios. The proportion of plants that flower and the flowering intensity also vary with season and location. The objective of the present work was to investigate whether variation in flowering behaviour was related to factors determining rate of development (photoperiod and temperature through sowing date, location and year) or growth (cumulative solar radiation and temperature). Sex ratios, the proportion of plants that had flower buds and open flowers, and the number of flowers or spikes was recorded in one male (TDr 131) and one female (TDr 99-9) clone of white yam grown in the field in Nigeria at three locations and at different sowing dates. Clone TDr 131 was uniformly male flowering, while clone TDr 99-9 exhibited a number of sex types with gynoecious, monoecious and trimonoecious plants observed. The proportion of flowering plants was low in both clones, averaging 0·34 in clone TDr 131 and 0·13 in clone TDr 99-9. Day of vine emergence had a significant and contrasting effect on the proportion of flowering plants and on flowering intensity in the two clones. In clone TDr 131, the proportion of flowering plants and flowering intensity declined with later vine emergence at all locations ($r = 0{\cdot}43$–$0{\cdot}53$; $P < 0{\cdot}05$), whereas in clone TDr 99-9 the proportion of flowering plants increased with later emergence ($r = 0{\cdot}46$, $P < 0{\cdot}01$). In clone TDr 131, this response was strongly associated with warmer temperatures ($r = 0{\cdot}49$–$0{\cdot}50$; $P < 0{\cdot}05$) and greater cumulative radiation ($r = 0{\cdot}85$–$0{\cdot}93$; $P < 0{\cdot}001$) between vine emergence and flowering, rather than photoperiod at vine emergence. This suggests that flowering behaviour in the male clone TDr 131 is strongly influenced by factors that affect growth rather than development. Clone TDr 99-9, on the other hand, exhibited no clear relations between flowering and growth or developmental factors, though the proportion of flowering plants and flowering intensity was greatest at planting dates close to the longest day and at temperatures of 25–26 °C. This might suggest that flowering behaviour in clone TDr 99-9 is controlled by photothermal responses.

INTRODUCTION

Yams (*Dioscorea* spp.) are a very important staple crop of great economic and cultural significance in West Africa (Coursey 1967), as well as being economically important in the Caribbean and in Asia (Scott *et al.* 2000). They are grown for their tubers, which in the case of the most important species in West Africa, white yam (*Dioscorea rotundata*) and water yam (*Dioscorea alata*) are subterranean. Yams are usually propagated from seed tubers or sections of tuber (mini-setts), rather than true seed, because of the higher yield from seed tubers or setts as well as the unpredictable flowering behaviour in yam. Many useful clones, including popular landraces with potential as parents in a hybridization programme (Asiedu *et al.* 1998), have never flowered or have only flowered irregularly and sparsely (i.e. few flowering plants, few flowers per plant). Sex ratios can also vary and yam clones may be dioecious, monoecious, or hermaphrodite (Sadik & Okereke 1975; Abraham & Nair 1979; Abraham 1997; Bai & Ekanayake 1998).

Flowering intensity (the product of the number of flowering spikes per inflorescence and number of flowers per spike), sex ratio and the proportion of

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Table 1. *Ecological characteristics of experimental locations in Nigeria*

Location	Long. N; Lat. E	Altitude (m asl)	Soil type	Annual rainfall (mm)	Duration of rainy season	Min/max temperature (°C)	Min/max RH (%)
Onne	7 °10′; 4 °46′	10	Typic Paleudult	2400	Feb–Nov	23/31	57/94
Ibadan	7 °26′; 3 °54′	210	Ferric Luvisol	1253	Mar–Nov	19/34	47/86
Abuja	9 °16′; 7 °20′	300	Ferric Luvisol	1302	Apr–Oct	21/33	14/37

plants that flower vary greatly with propagule (seed or tuber), genotype (clone), environment (year, location and sowing date) and the interactions between them (Edem 1975; Sadik & Okereke 1975; Abraham 1997; Bai & Ekanayake 1998). Photoperiod, which has a major influence on yam flowering time (Ile *et al.* 2007) and tuberization (Yoshida & Kanahama 1999), as well as growth or vigour (Akoroda *et al.* 1984; Doku 1985) have been suggested as important factors affecting flowering behaviour (Bai & Ekanayake 1998; Zoundjihekpon & Dansi 1998). However, there has been no systematic investigation of the effects of environment on flowering behaviour.

The present paper investigates whether variation in flowering intensity and the proportion of plants with flower buds (FBs) and open flowers (FLs) in one male and one female clone of white yam (*D. rotundata* Poir) grown in the field in Nigeria was related quantitatively to factors affecting development (photoperiod, temperature through sowing date, location and year) or growth (incident radiation and temperature).

MATERIALS AND METHODS

Clones

Two clones were used in these experiments, TDr 131 and TDr 99-9. TDr 131 is a male flowering clone that usually has a high proportion of profusely flowering plants. TDr 99-9 is a dioecious but largely female flowering clone.

Experimental locations and ecological characteristics

The current study was conducted in Nigeria at three locations: Abuja in the Guinea savanna, Ibadan in the forest/savanna transition and Onne in the humid rainforest. The experimental plots at each location had been planted to fallow rotations of *Histrics* and *Mucuna* for 2–3 years prior to the experiment and therefore had similar soil fertility management practices. Selected characteristics of the locations are presented in Table 1. Daily values of air temperature (°C), rainfall (mm) and solar radiation ($MJ/m^2/d$) were obtained from meteorological stations at each research site.

Sowing dates and experimental design

Experiments were conducted at Abuja, Ibadan and Onne in 1999 and 2000 (see Table 2). At Abuja and Onne, experiments were planted on two occasions in each year, while at Ibadan experiments were planted once in 1999 and on five occasions in 2000.

The two clones were planted in a randomized complete block design with three replicates. Each replicate comprised 30 plants except for Abuja in 1999, where there were 20 plants per replicate. Tuber setts (from the yam head region only, i.e. tuber region nearest to point of attachment of the corm) weighing 200 g were planted on ridges at a spacing of 1×1 m. Plants were staked 1 month after planting. All plots were hand weeded and no fertilizer was applied. There were no significant pest or disease problems.

Observations

Observations were made on every individual plant ($n = 90$, except Abuja in 1999, where $n = 60$). The dates of vine (shoot) emergence, appearance of FBs and FLs were recorded. Proportions of plants with FB and FL were calculated relative to the number of plants that emerged.

Sex ratios were scored as: 1, non-flowering; 2, male (staminate) flowers only [M]; 3, female (pistilate) flowers only [F]; 4, more male than female flowers [M > F]; and 5, more female and than male flowers [F > M].

Flowering intensity was measured once, at the opening of the first flower within a planting date and clone. By this stage no more FBs were expected to appear. At each planting date, a random sample of 15 (i.e. five plants per replicate) plants was tagged for the estimation of flowering intensity. In any instance where the number of flowering plants per planting date was less than 15, then flowering intensity was measured on all available flowering plants.

TDr 131, which is a male flowering clone, has numerous short spikes (inflorescences) and the flowers are small. Therefore, manual counting of individual spikes and flowers was impractical under field conditions, especially as yams are trained on stakes >3 m high. The number of flowering spikes was therefore estimated using the following scoring system,

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Table 2. *Effect of planting date on the duration from vine emergence to FB, FB to FL and sex expression (male = M; female = F) in clone TDr 131 and clone TDr 99-9*

		Clone TDr 131			Clone TDr 99-9		
Location	Planting date	Days to FB	Days from FB to FL	Sex expression	Days to FB	Days from FB to FL	Sex expression
Onne	11 Apr 2000	68	34	M	70	24	F
Onne	07 May 1999	65	31	M	60	25	F > M
Abuja	14 May 1999	50	36	M	46	38	F > M
Abuja	24 May 2000	45	38	M	58	23	F > M
Ibadan	03 Mar 2000	74	53	M	88	27	F
Ibadan	03 Apr 2000	67	40	M	77	25	F
Ibadan	23 Apr 1999	59	37	M	61	27	M > F
Ibadan	02 May 2000	54	37	M	64	27	F
Ibadan	01 Jun 2000	54	31	M	58	25	F
Ibadan	01 Aug 2000	–	–	–	–	–	–

–, did not flower.

modified from Abraham (1997): 1, ⩽10 spikes; 2, 11–20 spikes; 3, 21–30 spikes; 4, 31–40 spikes; and 5, ⩾41 spikes. The number of flowers per spike was estimated by counting the number of FBs on five randomly selected spikes per plant. Flowering intensity in clone TDr 131 was estimated from the number of spikes × number of flowers per spike. In contrast, female flowers are much larger and easily distinguished, and so in clone TDr 99-9 the total number of female flowers per plant was recorded to give flowering intensity.

Data analysis

Numbers of plants with FB were converted to proportions of emerged plants (δFB), and FL plants as a proportion of FB (δFL) plants. All proportions and flower counts were transformed prior to analysis to make the distribution normal and to improve homogeneity of variance. In biological data analysis, square root transformations are common for count data while log transformations are usually best for size data (McDonald 2008). Count and intensity data were transformed using the square root function, while proportion values (X) were transformed using the following logit function:

$$\ln\left[\frac{(X+0{\cdot}05)}{(100{\cdot}05-X)}\right]\times 0{\cdot}5$$

Mean or total values of minimum and maximum temperature, rainfall and solar radiation were calculated from daily values for each clone at each site between vine emergence, appearance of FBs and anthesis. Average photoperiod (civil twilight) between vine emergence and FB and the photoperiod at vine emergence were also estimated from daily photoperiod. Simple linear regressions were used to examine relations between flowering behaviour and climatic factors.

RESULTS

Sex ratios

FBs and FLs were recorded at all planting dates/locations except that at Ibadan in August 2000, where no flowering occurred (Table 2). All flowering plants of clone TDr 131 were male (M) only. In contrast, clone TDr 99-9 exhibited sex types that were variants of dioecism and monoecism. At the majority of sites, plants were dioecious and female flowering (i.e. F). However, at some sites in 1999 monoecious and dioecious plants were found, generally with more female than male plants, as well as more female than male flowers. In the monoecious types, variants of monoecism were observed. In some plants, a spike carried both male and female flowers, while in other plants, a spike could be completely female, another completely male and the rest have both male and female flowers. The April 1999 planting at Ibadan was the only site where male plants predominated over female plants.

Clone TDr 131

The proportion of emerged plants was high in the male flowering clone TDr 131, >0·80 and there was no significant effect of planting date on the proportion that emerged ($P > 0{\cdot}50$). In contrast, the proportion of emerged plants that produced FBs (δFB) varied with planting date. Values ranged from 0·87 for the earliest planting date (March at Ibadan) to zero for

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Table 3. *Effect of planting date on the proportions of emerged plants that had FBs and FLs and the ratio of FL to FB in clone TDr 131 and clone TDr 99-9*

		Proportion of emerged plants that reached					
		FB		FL		Ratio FL to FB	
Location	Planting date	TDr 131	TDr 99-9	TDr 131	TDr 99-9	TDr 131	TDr 99-9
Onne	11 Apr 2000	0·32	0·26	0·19	0·02	0·59	0·09
Onne	07 May 1999	0·24	0·25	0·17	0·08	0·71	0·32
Abuja	14 May 1999	0·58	0·32	0·47	0·16	0·80	0·50
Abuja	24 May 2000	0·08	0·38	0·07	0·18	0·85	0·47
Ibadan	03 Mar 2000	0·87	0·48	0·80	0·06	0·92	0·12
Ibadan	03 Apr 2000	0·34	0·38	0·31	0·20	0·92	0·52
Ibadan	23 Apr 1999	0·68	0·58	0·62	0·25	0·91	0·42
Ibadan	02 May 2000	0·29	0·42	0·28	0·18	0·96	0·43
Ibadan	01 Jun 2000	0·24	0·16	0·20	0·08	0·82	0·50
Ibadan	01 Aug 2000	–	–	–	–	–	–

–, did not flower.

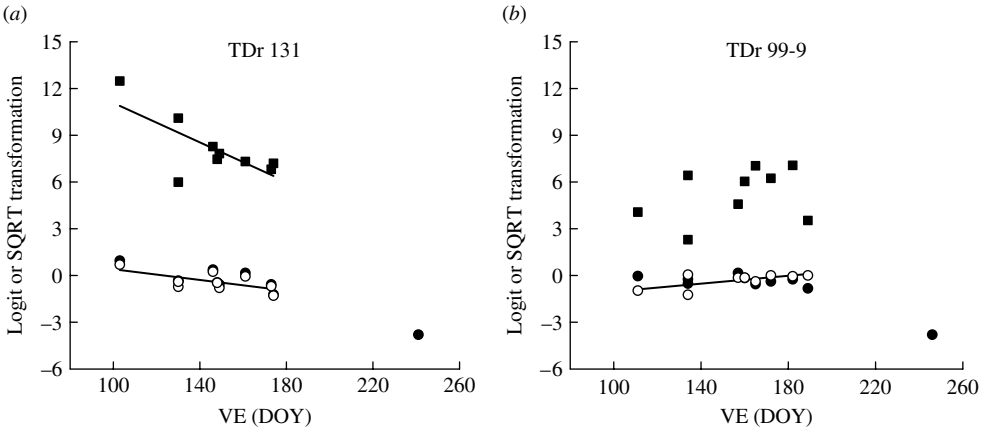


Fig. 1. Relations between δFB (●), δFL (○), flowering intensity (■) and day of vine emergence (VE) in TDr 131 and TDr 99-9 grown at different sowing dates at three locations in Nigeria. Proportions (δ) are logit transformed; intensity is square root (SQRT) transformed. Fitted lines: TDr 131: ○, $y = 17{\cdot}41 - 0{\cdot}063x$, $R^2 = 0{\cdot}53$; ■, $y = 2{\cdot}13 - 0{\cdot}017x$, $R^2 = 0{\cdot}43$; TDr 99-9: ○, $y = -2{\cdot}28 + 0{\cdot}016x$, $R^2 = 0{\cdot}46$.

the last planting date in August at Ibadan, and at Abuja and Onne values were also higher at the earlier sowing date. There was a significant negative linear relationship between δFB and date of vine emergence ($r = 0{\cdot}80$, $P < 0{\cdot}001$, $n = 10$; excluding August planting date $r = 0{\cdot}43$, $P < 0{\cdot}05$, $n = 9$), and earlier vine emergence at Onne, Ibadan or Abuja resulted in more plants with FB (Fig. 1*a*).

The number of plants with FB that subsequently produced FLs (δFL) was fairly consistent in clone TDr 131 and was $> 0{\cdot}80$ at all sowings except those at Onne, with no effect of sowing date (Table 3). This proportion also declined with later vine emergence, though not significantly ($R^2 = 0{\cdot}34$, $P = 0{\cdot}057$, $n = 9$), thereby reflecting the effect of vine emergence on δFB (Fig. 1*a*). Overall, the proportion of plants that had FLs in clone TDr 131 was 0·34 on average, but only the sowings at Ibadan in April 1999 and March 2000 had a ratio $> 0{\cdot}50$ of flowering plants.

In the male flowering clone TDr 131, flowering intensity was estimated as the product of the number of flowering spikes or inflorescences per plant and the number of flowers per spike (Table 4). The number of spikes per plant ranged from 1·7 to 4·3, and flowers per spike from 21 to 36. The greatest number of spikes per plant and flowers per spike were produced at the

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Table 4. *Effect of planting date on number of spikes per plant, FBs per spike per plant and flowering intensity per plant in clone TDr 131 and flowering intensity in clone TDr99-9*

		TDr 131			TDr 99-9
Location	Planting date	No. spikes per plant (a)	FBs per spike (b)	Flowering intensity (a) × (b)	Flowering intensity
Onne	11 Apr 2000	1·7	21·0 ± 0·11	35·9	5·3
Onne	07 May 1999	2·3	26·3 ± 0·12	61·3	49·6
Abuja	14 May 1999	2·3	23·7 ± 0·10	53·6	39·0
Abuja	24 May 2000	2·2	23·9 ± 0·17	51·9	50·0
Ibadan	03 Mar 2000	4·3	36·0 ± 0·10	155·9	16·6
Ibadan	03 Apr 2000	3·4	30·0 ± 0·10	102·0	41·3
Ibadan	23 Apr 1999	2·3	29·4 ± 0·10	68·5	21·0
Ibadan	02 May 2000	2·2	25·2 ± 0·11	55·7	36·5
Ibadan	01 Jun 2000	1·7	27·2 ± 1·11	46·5	12·5
Ibadan	01 Aug 2000	–	–	–	–

–, did not flower.

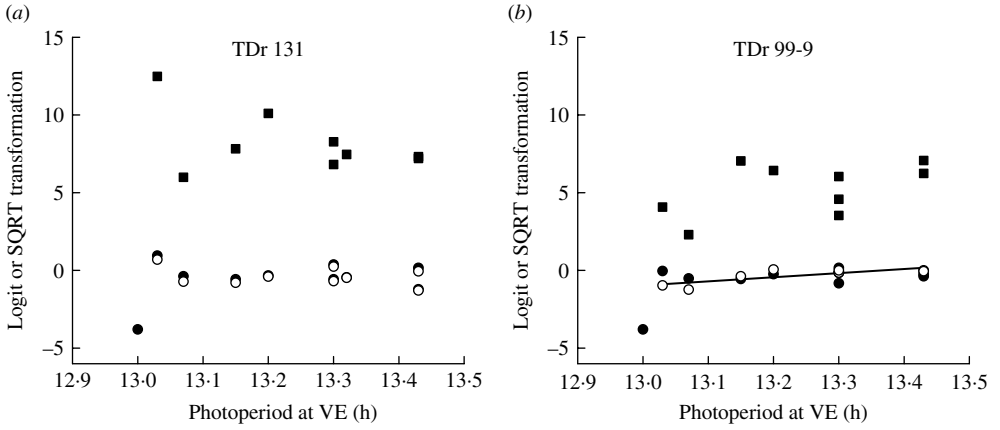


Fig. 2. Relations between δFB (●), δFL (○), flowering intensity (■) and photoperiod at vine emergence (VE) in TDr 131 and TDr 99-9 grown at different sowing dates at three locations in Nigeria. Proportions (δ) are logit transformed; intensity is SQRT transformed. Fitted line: TDr 99-9: ○, $y = -35{\cdot}19 + 2{\cdot}63x$, $R^2 = 0{\cdot}65$.

earliest planting date, March 2000 at Ibadan and there was a strong response to planting date at Ibadan. However, at Onne and Abuja planting date did not have the same effect. Nonetheless, there was a strong response of flowering intensity (expressed on a square root scale) to time of vine emergence ($r = 0{\cdot}53$, $P < 0{\cdot}05$, $n = 9$; Fig. 1). The flowering intensity in the planting at Onne in April 2000 (VE DOY = 134) was lower than expected based on the other data.

A strong relationship with the date of vine emergence is indicative of a developmental response to photoperiod and/or temperature. The duration from vine emergence to FB in clone TDr 131 (Table 2) was affected by photoperiod at vine emergence (Ile *et al.* 2007), durations being shorter when photoperiod at vine emergence was longer (i.e. a long-day response). However, in clone TDr 131, photoperiod at vine emergence apparently had no effect on δFB or δFL, though flowering intensity was generally lower when photoperiod at vine emergence was higher (Fig. 2*a*). This suggests that in clone TDr 131 photoperiod *per se* had little influence on flowering behaviour. There was also no effect of rate of development (the inverse of duration from vine emergence to FL), i.e. of an indirect effect of photoperiod (not presented).

Warmer temperature, in addition to influencing the rate of development, also affects growth rate, which has been implicated in flowering behaviour in yam (Degras 1993). Warmer temperatures, which occurred in the earlier sowing dates at Ibadan and at Onne, did increase both δFB and δFL ($r = 0{\cdot}50$, $P < 0{\cdot}05$, $n = 9$) and flowering intensity ($r = 0{\cdot}49$, $P < 0{\cdot}05$, $n = 9$) in clone TDr 131 (Fig. 3*a*). Another factor that strongly influences growth is radiation intensity (Degras 1993),

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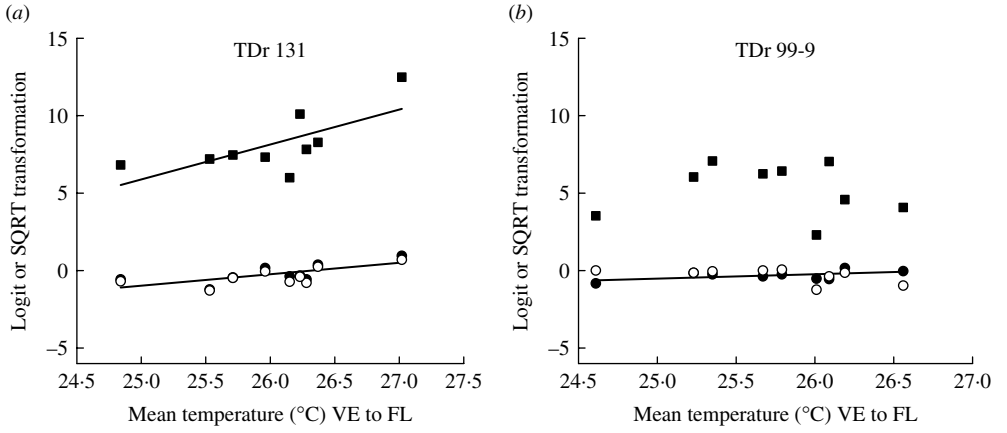


Fig. 3. Relations between δFB (●), δFL (○), flowering intensity (■) and mean temperature between vine emergence (VE) and flowering (FL) in TDr 131 and TDr 99-9 grown at different sowing dates at three locations in Nigeria. Proportions (δ) are logit transformed; intensity is SQRT transformed. Fitted lines: TDr 131 ○, $y=-50{\cdot}47+2{\cdot}254x$, $R^2=0{\cdot}49$; ■, $y=-19{\cdot}39+0{\cdot}737x$, $R^2=0{\cdot}50$; TDr 99-9: ●, $y=-7{\cdot}61+0{\cdot}284x$, $R^2=0{\cdot}32$.

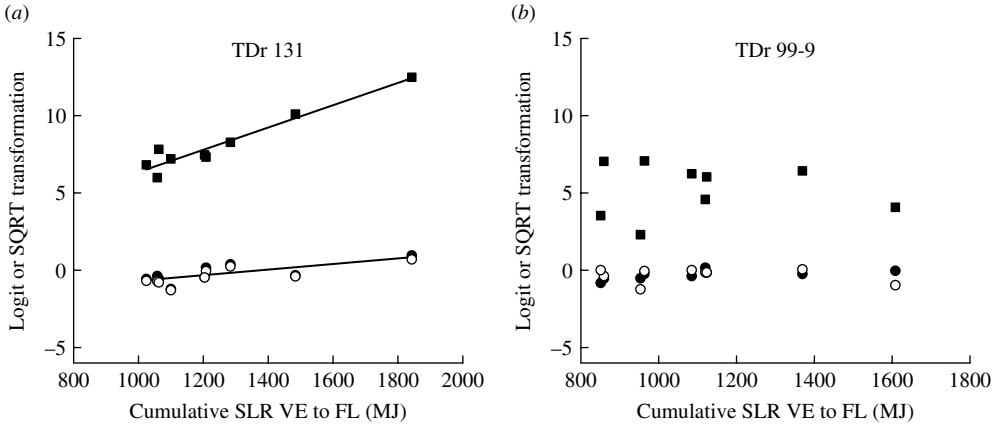


Fig. 4. Relations between δFB (●), δFL (○), flowering intensity (■) and total cumulative solar radiation between vine emergence (VE) and flowering (FL) in TDr 131 and TDr 99-9 grown at different sowing dates at three locations in Nigeria. Proportions (δ) are logit transformed; intensity is SQRT transformed. Fitted lines: TDr 131: ○, $y=-0{\cdot}86+7{\cdot}210x$, $R^2=0{\cdot}93$; ■, $y=-2{\cdot}49=1{\cdot}81x$, $R^2=0{\cdot}85$.

which varied greatly between locations (highest in the savanna at Abuja, lowest in the forest at Onne). In clone TDr 131, δFB, δFL and the intensity of flowering were greater ($R^2=0{\cdot}85$ to 0·9, $P<0{\cdot}001$, $n=9$) at higher levels of incident radiation (Fig. 4*a*). The low value of flowering intensity associated with Onne (Fig. 1*a*) could be explained by low incident radiation level at this location in 2000.

Clone TDr 99-9

The value of δFB was lower in the predominantly female clone TDr 99-9 than in TDr 131, ranging from 0 in August 1999 at Ibadan to 0·58 in April 1999 at Ibadan. However, there was no relationship between δFB and vine emergence (Fig. 1*b*) when the August planting date was excluded ($r=0{\cdot}08$, $n=9$; including August $r=0{\cdot}62$, $P<0{\cdot}01$, $n=10$). The value of δFL was both lower (average 0·34) and slightly more variable than in clone TDr 131 (Table 3) and in contrast to clone TDr 131 there was a positive relationship between δFL and the date of vine emergence ($r=0{\cdot}46$, $P<0{\cdot}01$, $n=9$; Fig. 1*b*). Hence later vine emergence in clone TDr 99-9 had little or no effect on the number of plants with FB but did increase the proportion of these plants that flowered slightly. The overall proportion of plants that flowered in clone TDr 99-9 was therefore very low, 0·13 on average,

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and only in April sowings at Ibadan in 1999 and 2000 did the proportion reach 0·20–0·25.

In clone TDr 99-9, the total number of flowers per plant was counted to give flowering intensity (Table 4). The number of flowers ranged from 5·3 to 50 per plant with the greatest number of flowers at Abuja. There were no effects of planting date at Ibadan on the number of flowers. In contrast to clone TDr 131, then, there was no relationship between intensity and vine emergence (Fig. 1*b*) and flowering intensity was greatest when vine emergence occurred between day of year 160 and 180.

Photoperiod also affected the rate of development in clone TDr 99-9 (Ile *et al*. 2007), though in contrast to TDr 131 there was no clear effect of planting date on the duration from FB to FL (Table 2), which was between 23 and 27 days at all plantings except Abuja in 1999. Photoperiod at vine emergence had no significant effect on δFB in clone TDr 99-9 (Fig. 2*b*), but longer photoperiods did increase δFL slightly ($r = 0{\cdot}65$, $P < 0{\cdot}01$, $n = 9$). Flowering intensity was not affected by photoperiod at vine emergence (Fig. 2*b*). Mean temperature from vine emergence to FL affected δFB very slightly ($r = 0{\cdot}40$, $P < 0{\cdot}05$, $n = 9$) but not δFL or flowering intensity (Fig. 3*b*). In contrast to clone TDr 131, there were no relationships between δFB, δFL, flowering intensity and cumulative radiation (Fig. 4*b*).

DISCUSSION

The present study has shown that plants of clone TDr 131 are consistently unisexual, bearing male flowers only (i.e. androecious). In contrast, clone TDr 99-9 exhibited a number of sex types; some plants were female flowering (i.e. gynoecious), some were found to be monoecious, while others were trimonoecious (i.e. on the same plant some spikes carried both male and female flowers, while others were either completely male or female). Androecious, gynoecious and monoecious plants have been reported in *D. rotundata* as well as a few occurrences of hermaphrodite flowers (Burkill 1960; Coursey 1967; Sadik & Okereke 1975; Abraham & Nair 1979; Degras 1993), but not trimonoecious flowering types. Sex expression has been reported to vary with generation (seed-derived plants *v*. clonal plants) and year (Sadik & Okereke 1975; Abraham & Nair 1979; Doku 1985; Segnou *et al*. 1992), and environment has been postulated as an important factor. In the present study, monoecious and trimonoecious plants were observed at all three locations in 1999 and also at Abuja in 2000. Rainfall between the appearance of FBs and FLs was lower than normal in 1999 at Abuja and Ibadan, but not at Onne, and mean temperatures slightly higher in all four locations. However, there were insufficient observations to say whether this variation in weather was significant. Sex expression is not, however, related to flowering intensity.

Both clones exhibited a low proportion of flowering plants, 0·34 on average in the male clone TDr 131 and 0·13 in the female clone TDr 99-9. Most of this variation was due to variation in the number of plants with FBs rather than variation in the proportion of FB that produced FLs (δFL); this proportion was about 0·85 ($n = 8$) in clone TDr 131 and 0·45 ($n = 7$) in clone TDr 99-9. It is perhaps to be expected that flower bud abortion or arrested development is greater in the female clone, as female flowers are much larger (100 times) and require a larger investment of resources (Abraham 1997). Many other studies have reported similar variation in yam flowering characteristics under contrasting environments created by planting at different dates, locations or years (Edem 1975; Okereke 1978; Akoroda 1984; Abraham 1997). For example, Sadik & Okereke (1975) reported floral abortion of between 0·38 and 0·86 in three female cultivars of *D. rotundata*. The above studies, however, did not investigate this phenomenon in any systematic way to see if planting date or other factors control it.

The time of vine emergence clearly has some influence on the proportion of flowering plants and on flowering intensity, and the two clones responded differently (Fig. 1). The male clone TDr 131 had more flowering plants and flowering spikes at earlier sowing dates. Although photoperiod directly influences the rate of progress towards flowering in yam and the rate of flower appearance in legumes (e.g. Flohr *et al*. 1990), photoperiod or the rate of development did not appear to be important in influencing proportion of flowering plants. These responses in clone TDr 131 suggest that growth-related factors have the largest influence on flowering. Earlier sowings experience warmer temperatures, and due to longer life-cycle durations (Table 2) associated with shorter photoperiod at vine emergence (Ile *et al*. 2007), potentially greater radiation interception. The period of floral bud differentiation and growth (between FB and FL), for example, varied from 31 to 53 days. Other studies in yam have also shown that growth and vigour influence flowering behaviour (Akoroda *et al*. 1984; Akoroda 1985; Degras 1993). For example, flowering intensity was positively linked to vigour or leafiness (Akoroda *et al*. 1984; Doku 1985) and was reduced by shading (Degras 1993).

The female clone TDr 99-9 responded differently to clone TDr 131. The proportion of plants with FBs or δFL, and flowering intensity, generally increased with later sowing and δFL was positively associated with longer photoperiod at vine emergence. There was a small effect of temperature on δFB, but no effect of radiation, suggesting that growth was not a major factor in determining the number of flowering plants or flowering intensity in clone TDr 99-9. Given that

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the duration from FB to FL did not vary much in clone TDr 99-9 either, a strong response to cumulative radiation is less likely. The response to photoperiod and temperature was, however, not strong, though the temperature response of flowering intensity could be interpreted as an optimum temperature response (Fig. 3*b*). The control of flowering behaviour is therefore still unclear in clone TDr 99-9, though plantings close to the middle of the year or the longest day seem to produce more flowering plants and flowers per plant.

No flowering plants were observed in either clone in the August sowing. This sowing experienced the shortest photoperiod at vine emergence among sites and sowing dates, and rapidly shortening days thereafter. The response of flowering to photoperiod in yam appears to be a long-day response (Ile *et al.* 2007), and it is possible that 13 h, the photoperiod at vine emergence in the August sowing, is close to a critical value below which flowering does not occur (Roberts & Summerfield 1987). Controlled environment experiments would be required to ascertain this.

There are two other factors that could affect flowering: partitioning and seedling vigour. Yams exhibit a short-day response with regard to the timing of tuber initiation and growth (Yoshida & Kanahama 1999) and so later sowings would have less time to accumulate biomass before tuber initiation, which occurs 4–70 days after sowing (Swannell *et al.* 2003). Later sowings also flower sooner, which may reduce the number leaves and leaf axils, the cells of which have the capacity to differentiate into floral buds or branches, i.e. reduce the number of potential flowering sites (Degras 1993). Hence partitioning of resources to tubers rather than shoots may reduce the proportion of plants with FBs in later sowings. Another factor that may influence plant vigour and hence flowering in yams is prolonged sprouting during storage. Clone TDr 131, for example, typically begins to sprout in March. Yams planted at this time that are supplied with adequate moisture will germinate and rapidly produce true leaves. Yams that are not planted will produce a xerophytic vine, but will not produce true leaves (Craufurd *et al.* 2001). Nevertheless, the physiology of the storage organ does change when dormancy breaks, starch starts to be broken down and respiration increases (Hariprakash & Nambisan 1996). So it is possible that yams planted later, even if stored in cold rooms to delay sprouting, may have inherently lower storage organ reserves and hence vigour. This was probably the case in the August planting date. Although the present study was not intended to determine the effects of edaphic factors on flowering behaviour, a study that determines and quantifies the contribution of variable soil fertility levels (especially available nitrogen and phosphorus and potassium) on flowering characteristics may provide additional information. Currently, it is contentious whether a difference in nitrogen level contributes to variability in yam flowering behaviour (Bai & Ekanayake 1998).

It is concluded that in the male flowering clone TDr 131 the proportion of flowering plants and flowering intensity is strongly influenced by growth potential, which in the present study is the product of duration (early *v.* late planting) and radiation environment (savanna *v.* forest). The female clone TDr 99-9, on the other hand, exhibited no clear relations between flowering and growth or developmental factors, with the proportion of flowering plants and flowering intensity flowering being greatest at planting dates close to the longest day and at temperatures of 25–26 °C.

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