*Annals of Botany* **82**: 773–778, 1998
Article No. bo980756

# Variation in the Durations of the Photoperiod-sensitive and Photoperiod-insensitive Phases of Post-first Flowering Development in Maturity Isolines of Soyabean [*Glycine max* (L.) Merrill] 'Clark'

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Received: 12 February 1998 Returned for revision: 12 May 1998 Accepted: 30 July 1998

Plants of eight isolines of soyabean [*Glycine max* (L.) Merrill], comprising all combinations of two alleles at the three loci $E_1/e_1$, $E_2/e_2$ and $E_3/e_3$ in the cultivar 'Clark' background, were transferred after different periods following first flowering from long days (LD, 14 h $d^{-1}$) to short days (SD, 12 h $d^{-1}$) and *vice versa* in a reciprocal-transfer experiment in a plastic house maintained at 30/24 °C (day/night). Photoperiod ($0{\cdot}10 > P > 0{\cdot}05$), transfer time ($P < 0{\cdot}001$), isoline ($P < 0{\cdot}001$), and their interactions ($P < 0{\cdot}001$) all affected flowering duration, i.e. the period from first flowering until the appearance of the last flower. The flowering duration comprised two distinct phases: a photoperiod-sensitive phase beginning at first flowering, and a subsequent photoperiod-insensitive phase. The duration of the photoperiod-sensitive phase varied much more among the isolines in LD than in SD. Only the dominant allele $E_1$ increased the sensitivity of the photoperiod-sensitive phase of flowering duration to photoperiod singly, but positive epistatic effects were detected between $E_1$ and $E_2$, $E_1$ and $E_3$, and especially among all three dominant alleles. The increases in flowering duration resulting from the combined effects of gene and environment (i.e. photoperiod) were associated with considerable increases in biomass and seed yield at harvest maturity.


**Key words:** *Glycine max* (L.) Merrill, soyabean, maturity genes, flowering, photoperiod, reciprocal transfer, yield.

## INTRODUCTION

Five major loci, each with two alleles, $E_1/e_1$, $E_2/e_2$ (Bernard, 1971), $E_3/e_3$ (Buzzell, 1971), $E_4/e_4$ (Buzzell and Voldeng, 1980), and $E_5/e_5$ (McBlain and Bernard, 1987), affect flowering and maturity in soyabean [*Glycine max* (L.) Merrill]. At each of the first three of these loci at least, flowering and maturity are delayed by the dominant allele, but the detection of these effects can be dependent upon the presence of other alleles. Delays arise principally because these dominant alleles increase the sensitivity of plants to photoperiods longer than the critical value for both the vegetative duration, i.e. the period from sowing to first opening flower (Upadhyay *et al.*, 1994*a*), and the flowering duration, i.e. the period from first flower opening to the appearance of the last flower (Summerfield *et al.*, 1998). The dominant allele $E_4$ probably has a similar effect to that of $E_3$ (Cober, Tanner and Voldeng, 1996).

In contrast to temperature, which moderates the rate of plant development throughout the lifecycle, photoperiod-sensitive cultivars of soyabean are not equally sensitive to photoperiod from seedling emergence through to maturity (e.g. Shanmugasundaram and Tsou, 1978; Wilkerson *et al.*, 1989). The respective durations of the photoperiod-insensitive and photoperiod-sensitive phases of pre-flowering development have been estimated for several genotypes of soyabean by Collinson *et al.* (1993), and for several isolines of soyabean (cv. 'Clark' background, differing only in the maturity genes $E_1/e_1$, $E_2/e_2$ and $E_3/e_3$) by Upadhyay *et al.* (1994*b*) using the novel analytical approach developed by Ellis *et al.* (1992). Upadhyay *et al.* (1994*b*) showed that the photoperiod-sensitive phase of pre-flowering development was not affected by either of the alleles $E_2$ and $E_3$ alone, but that $E_1$ singly, $E_2$ and $E_3$ together, and, particularly, all three dominant alleles combined, greatly increased the sensitivity of the photoperiod-sensitive phase to photoperiod (i.e. the increase in duration was considerably greater in long days).

The photoperiod after first flower opening influences developmental durations in a predictable manner (Summerfield *et al.*, 1998). However, the persistence of photoperiod sensitivity after first flowering and its genetic control in soyabean are unknown. The aim of this investigation was to determine the relative durations of the photoperiod-sensitive and photoperiod-insensitive phases during the reproductive period (i.e. subsequent to first flowering) among eight maturity isolines of cultivar 'Clark' with different photoperiod-sensitivity genes, and to determine whether or not each dominant allele at the three loci $E_1/e_1$, $E_2/e_2$, $E_3/e_3$ affects these durations.

## MATERIALS AND METHODS

Eight isolines of cultivar 'Clark' comprising all possible combinations of two alleles at the three loci $E_1/e_1$, $E_2/e_2$ and $E_3/e_3$ were selected for study. The accession numbers and the pedigree of these isolines have been summarized by Summerfield *et al.* (1998). Seeds were sown in 18 cm

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diameter pots on 16 Apr. 1993, and plant culture and husbandry were as described by Summerfield *et al.* (1998), except that in this investigation plants were grown in a plastic house. The environment from sowing to first flowering was common to all treatment combinations and comprised a photoperiod of 12 h $d^{-1}$ and an alternating-temperature regime of 30/24 °C [day (12 h)/night (12 h)].

Within the plastic house, two 'blackout' compartments were constructed by supporting a 125 $\mu$m thick black polythene sheet on a 2 m high galvanized steel pipe frame. One of the blackout compartments contained 60 W tungsten bulbs spaced 1·0 m apart and 1·15 m above the pots. The photon irradiance provided at pot level by this lighting exceeded 0·4 $\mu$mol $s^{-1}$ $m^{-2}$, which is sufficient to saturate the photoperiodic response of soyabean (Summerfield and Roberts, 1987). The other compartment did not have artificial lighting. Natural light was provided for 12 h $d^{-1}$ by opening and closing the blackout manually each morning and evening, respectively. Forced ventilation was provided under each blackout compartment, and temperature control was based on sensors located within each compartment.

From first flower opening (corolla colour first visible) until maturity, two different photoperiods were imposed: short days (SD), which comprised 12 h $d^{-1}$ natural light followed by 12 h $d^{-1}$ darkness; and long days (LD), 12 h $d^{-1}$ natural light, then 2 h $d^{-1}$ tungsten light, then 10 h $d^{-1}$ darkness. Day/night temperatures were maintained at 30/24 °C ($\pm$1 °C) throughout. At, or within 2 d of, first flowering, 21 plants of each of the eight isolines were transferred into each of the two blackout compartments. Individual plants (one per pot) were arranged in three blocks with a spacing of $40 \times 40$ $cm^2$ in a split-split plot design. The main plot treatments were the two photoperiods, and reciprocal-transfers of plants were then made between the two regimes. The subplots were the (seven) times of transfer from SD to LD and *vice versa*, namely 0, 5, 10, 15, 20, 30 and 50 d after first flowering. The transfers at 0 d provided the continuous SD and continuous LD controls from first flowering (but note that all plants had received SD between sowing and first flowering). The sub-subplots were the eight isolines.

Various phenological events and reproductive parameters were recorded or calculated, based on the developmental stages R1–R8 (Fehr and Caviness, 1977). These were: flowering duration [days from first open flower (R1) to end of flowering]; reproductive duration [R1 to harvest maturity (R8)]; duration from the end of flowering to the beginning of maturity (R7); duration from R7 to harvest maturity (R8); total plant dry weight (including roots and nodules); seed dry weight per plant; and harvest index (HI, ratio of seed dry weight to total plant dry weight) at R8. At R8, all plant components, including senesced and abscised leaves (collected several times each week), were oven-dried at 80 °C for 72 h and weighed. The pods were then carefully threshed by hand and the seeds counted, dried and re-weighed.

The FITNONLINEAR directive of GENSTAT V (GENSTAT V Committee, 1987) and the analytical routine developed by Ellis *et al.* (1992) were applied in order to estimate the durations of the photoperiod-sensitive and photoperiod-insensitive phases of post-first flowering development in each isoline. Since the original application of this analytical approach was for durations from sowing to first flowering, various minor modifications were necessary. The dependent variable became duration of flowering (*fd*, i.e. the number of days from first to last flower appearance) in place of duration to first flowering; the transfer time ($t$) was set at first flowering, rather than sowing; $a_1$ was the initial photoperiod-insensitive phase beginning at first flowering; $a_3$ was the final photoperiod-insensitive phase ending at the appearance of the last flower; $I_s$ was the duration of the photoperiod-sensitive phase in SD; and $I_l$ was the duration of the photoperiod-sensitive phase in LD. Initial analyses using this approach provided estimates of $a_1$ that were not significantly different from zero since the plants were already sensitive to photoperiod at first flowering. The analytical approach was, therefore, modified by deleting $a_1$ and quantifying all results using three parameters $I_s$, $I_l$ and $a_3$. Thus, in short days (e.g. in the SD control) the flowering duration is given by:

$$fd = I_s + a_3 \quad (1)$$

and in long days (e.g. in the LD control) by:

$$fd = I_l + a_3. \quad (2)$$

Equation 1 also applies to plants transferred from SD to LD where $t \geqslant I_s$ and eqn 2 also applies for the LD to SD transfer treatments where $t \geqslant I_l$. In a treatment where a plant was grown initially in LD and then transferred to SD after the beginning but before the completion of the photoperiod-sensitive phase:

$$fd = t + I_s - (tI_s)/I_l + a_3. \quad (3)$$

In the opposite situation, where a plant was grown initially in SD and then transferred to LD during the photoperiod-sensitive phase:

$$fd = t + I_l - (tI_l)/I_s + a_3. \quad (4)$$

## RESULTS AND DISCUSSION

All genotypes first flowered within 24–28 d from sowing in the initial SD regime. Durations from first flowering to the appearance of the last flower were affected considerably by photoperiod ($0{\cdot}10 > P > 0{\cdot}05$), transfer time ($P < 0{\cdot}001$), isoline ($P < 0{\cdot}001$), and their interactions ($P < 0{\cdot}001$). Flowering durations were greater in the LD than in the SD controls within each isoline (transfers at 0 d after first flowering, Fig. 1). Isolines had similar flowering durations in continuous SD (varying only between 32·5 and 35·5 d). The response of flowering duration to the different photoperiod transfer treatments imposed was virtually identical in $e_1e_2e_3$, $e_1E_2e_3$ and $e_1e_2E_3$ (Figs 1A, C, D); the pattern was similar in $e_1E_2E_3$ (Fig. 1F) but with generally shorter durations. However, differences in flowering durations among the different transfer treatments were larger in the remaining, and more photoperiod-sensitive, isolines. For example, in the most photoperiod-sensitive isoline ($E_1E_2E_3$), flowering duration was extended in the LD compared with the SD control by 14·3 d (Fig. 1H) but by just 2·2 d in the

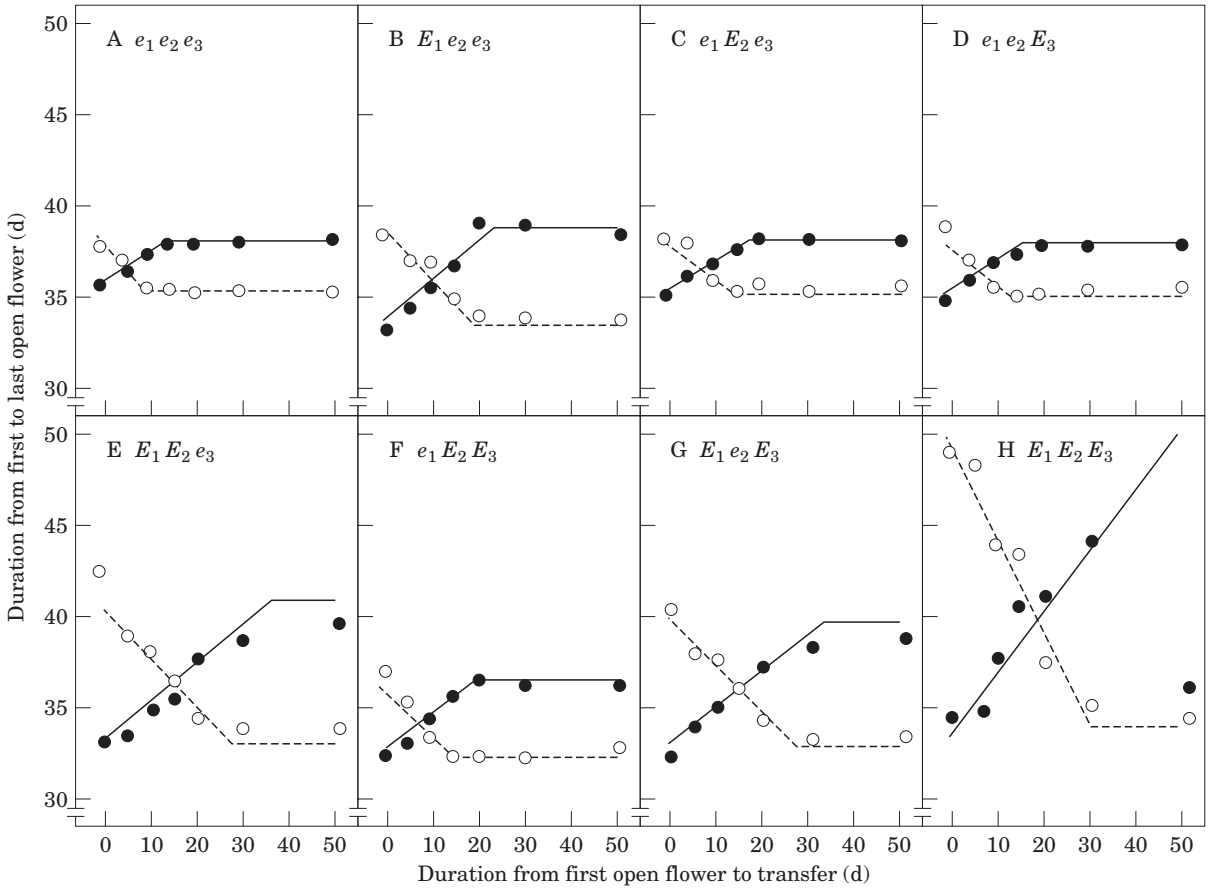


FIG. 1. Durations (d) from the appearance of the first open flower to the appearance of the last open flower (i.e. flowering duration) for eight maturity isolines of soyabean 'Clark' transferred from SD to LD (○) or from LD to SD (●) at different times (d) after first flowering. Solid and broken lines represent the fitted relationships (Table 1) for transfers from LD to SD and SD to LD, respectively. The end of the photoperiod-sensitive phase is marked by the point of intersection between the linear regression lines and the horizontal lines.

least photoperiod-sensitive isoline ($e_1e_2e_3$, Fig. 1A). The increase (or decrease) in flowering duration in continuous LD relative to $e_1e_2e_3$ was minimal in each of $E_1e_2e_3$, $e_1E_2e_3$, $e_1e_2E_3$ and $e_1E_2E_3$ (0·8, 0·6, 1·3 and −0·7 d, respectively), but was greater in isolines in which $E_1$ was present with either $E_2$ or $E_3$ or both, i.e. $E_1E_2e_3$, $E_1e_2E_3$, and $E_1E_2E_3$ (5·9, 3·0 and 11·3 d, respectively). This trend reflects the differences among these maturity genes, as has previously been shown in terms of sensitivity to photoperiod of the duration of the vegetative phase (Upadhyay *et al.*, 1994*a*) and the subsequent flowering duration (Summerfield *et al.*, 1998).

Comparisons between the observations and fitted lines in Fig. 1 confirm that the approach developed by Ellis *et al.* (1992), summarized for this application by eqns (1)–(4), described the responses well (Table 1). Thus, flowering durations comprised two distinct phases: a photoperiod-sensitive phase beginning at first flowering, and a subsequent photoperiod-insensitive phase.

Within an isoline, the duration of the photoperiod-sensitive phase was greater in LD than in SD (Table 1), the difference being least in $e_1e_2e_3$ and greatest in $E_1E_2E_3$ (i.e. the least- and most-photoperiod-sensitive isolines, respectively), such that values ranged between extremes of 12·9 to 46·3 d in LD and from 10·2 to 31·2 d in SD.

TABLE 1. *Estimates of the durations in days* (*s.e. in parentheses*) *of the photoperiod-sensitive phases in SD and LD* ($I_s$ *and* $I_l$) *and the photoperiod-insensitive phase* ($a_3$) *of post-flowering development in eight maturity isolines of soyabean* '*Clark*'

| Gene combination | $I_s$ | $I_l$ | $a_3$ | $R^2$ | d.f. |
|---|---|---|---|---|---|
| $e_1e_2e_3$ | 10·2 (1·60) | 12·9 (1·71) | 25·2 (1·67) | 0·63 | 39 |
| $E_1e_2e_3$ | 18·9 (1·98) | 24·0 (2·09) | 15·0 (2·03) | 0·74 | 39 |
| $e_1E_2e_3$ | 14·1 (2·15) | 16·8 (2·22) | 21·1 (2·17) | 0·63 | 39 |
| $e_1e_2E_3$ | 13·8 (2·06) | 16·7 (2·12) | 21·5 (2·08) | 0·67 | 39 |
| $E_1E_2e_3$ | 27·2 (2·31) | 34·6 (2·42) | 6·3 (2·35) | 0·76 | 39 |
| $e_1E_2E_3$ | 14·7 (1·83) | 18·8 (1·88) | 17·6 (1·85) | 0·76 | 39 |
| $E_1e_2E_3$ | 26·7 (1·85) | 33·2 (1·92) | 6·7 (1·87) | 0·84 | 39 |
| $E_1E_2E_3$ | 31·2 (1·36) | 46·3 (1·59) | 3·2 (1·48) | 0·91 | 39 |

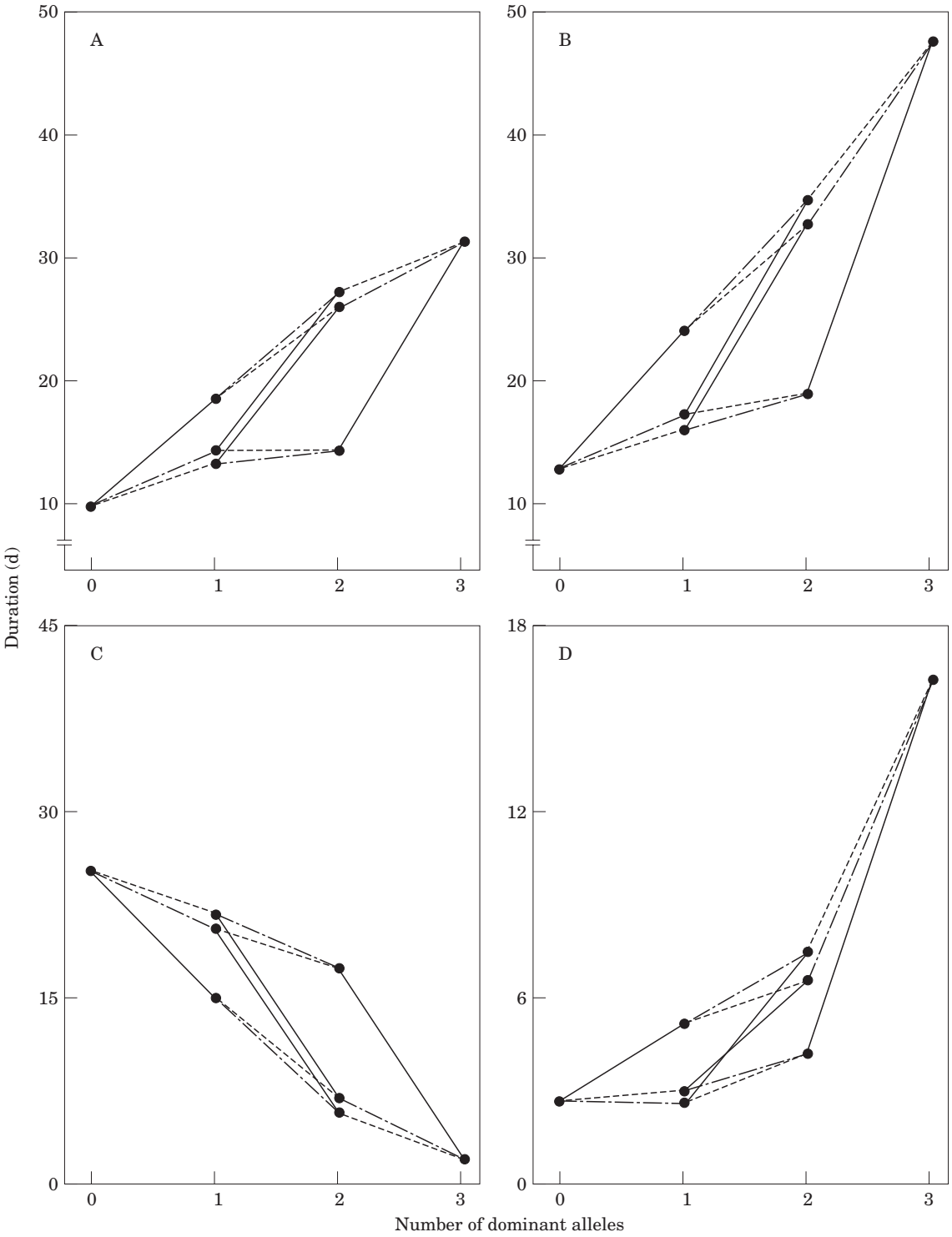


FIG. 2. Richards diagrams (Richards, 1941) showing the durations of: A, the photoperiod-sensitive phase of post-flowering development in SD ($I_s$); B, the photoperiod-sensitive phase of post-flowering development in LD ($I_l$); C, the photoperiod-insensitive phase of post-flowering development ($a_3$); and D, the effect of a 2 h $d^{-1}$ difference in photoperiod on the duration of the photoperiod-sensitive phase ($I_l$-$I_s$) of post-flowering development as influenced by the three dominant alleles $E_1$ (——), $E_2$ (—·—·) and $E_3$ (– – –) in eight maturity isolines of soyabean 'Clark'. Note the variation in ordinate scale.

Variation among the isolines in $I_s$ provided an almost perfect mirror image of that for $a_3$ (Fig. 2A and C), such that $a_3$ was greatest in the least- and shortest in the most-photoperiod-sensitive isoline. This variation in $a_3$ was so great that photoperiod sensitivity in $E_1E_2E_3$ continued until only 3·2 d before the appearance of the last flower.

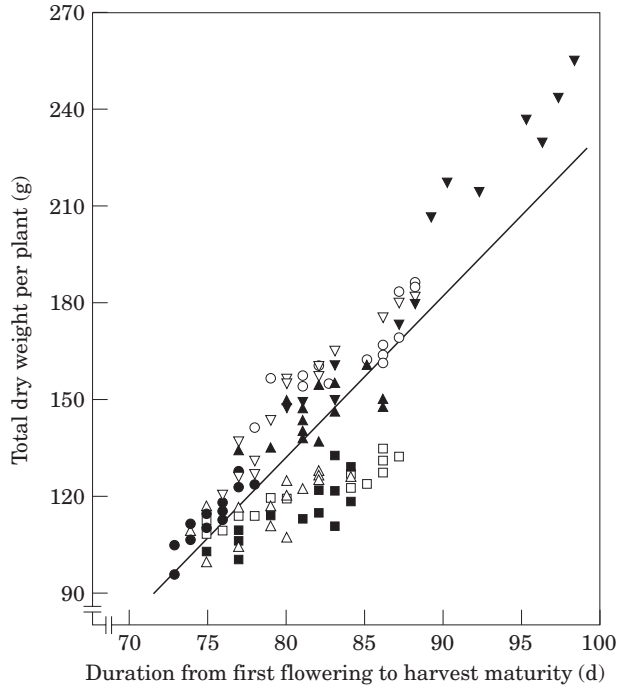


FIG. 3. Relationship between total dry weight (g) per plant at harvest maturity and duration from first flowering to harvest maturity (d) for eight maturity isolines of soyabean 'Clark' with maturity gene complements $e_1e_2e_3$ (●), $E_1e_2e_3$ (▲), $e_1E_2e_3$ (□), $e_1e_2E_3$ (△), $E_1E_2e_3$ (▽), $e_1E_2E_3$ (■), $E_1e_2E_3$ (○) and $E_1E_2E_3$ (▼) transferred from SD to LD and *vice versa* at different times after first flowering [$r^2 = 0{\cdot}70$ (333 d.f.)].

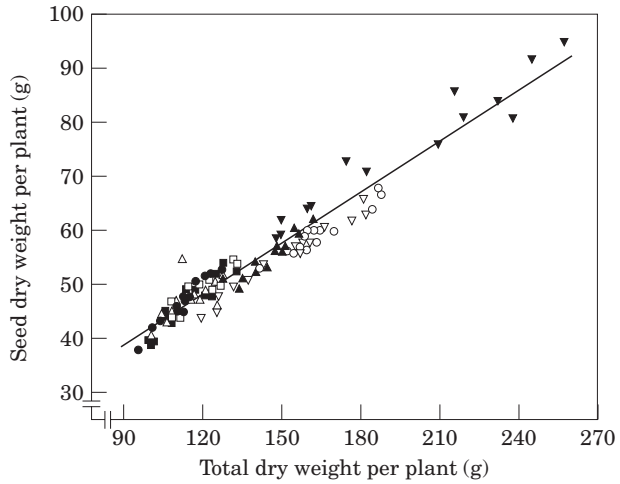


FIG. 4. Relationship between seed dry weight (g) per plant and total dry weight (g) per plant at harvest maturity for eight maturity isolines of soyabean 'Clark' with maturity gene complements $e_1e_2e_3$ (●), $E_1e_2e_3$ (▲), $e_1E_2e_3$ (□), $e_1e_2E_3$ (△), $E_1E_2e_3$ (▽), $e_1E_2E_3$ (■), $E_1e_2E_3$ (○) and $E_1E_2E_3$ (▼) transferred from SD to LD and *vice versa* at different times after first flowering [$r^2 = 0{\cdot}88$ (333 d.f.)].

All the dominant alleles increased the duration of the photoperiod-sensitive phase in both SD (Fig. 2A) and LD (Fig. 2B), but $E_1$ was the only single dominant allele to show an appreciable effect. The dominant allele $E_1$ was also the only allele to show an appreciable effect of photoperiod on the duration of the photoperiod-sensitive phase (Fig. 2D). It is acknowledged, however, that the other two dominant alleles might have shown an effect if the LD treatment had been greater than 14 h $d^{-1}$. Nevertheless, Fig. 2D also shows positive epistatic combination between $E_1$ and $E_2$, between $E_1$ and $E_3$, and among all three dominant alleles, for the effect of photoperiod on the duration of the photoperiod-sensitive phase.

The mean duration from the end of flowering to the beginning of maturity (R7) was generally longer for the less-than for the more-photoperiod-sensitive isolines, but these differences were small, varying only between extremes of 18·3 d ($E_1e_2E_3$) and 23·9 d ($e_1E_2E_3$) (s.e.d. = 0·39). Indeed, the value for the least-photoperiod-sensitive isoline ($e_1e_2e_3$, 19·4 d) was almost identical to that for the most-photoperiod-sensitive one ($E_1E_2E_3$, 18·8 d). Similarly, the effects of the photoperiod-transfer treatments on these durations were negligible, and, indeed, these durations were marginally shorter in LD (18·1 d) than in SD (22·9 d) (s.e.d. = 0·62). Accordingly, it can be concluded that (as quantified in Table 1) the sensitivity of development to photoperiod in these soyabean isolines ended before the end of the flowering period.

Durations from the end of flowering to harvest maturity (R8) were longer in the more photoperiod-sensitive isolines. The mean differences in this duration among six of the isolines and the most photoperiod-sensitive isolines ($E_1E_2E_3$) were small (within 5 d), but in $e_1e_2e_3$ this duration was 9 d shorter. However, this is probably an indirect effect of isoline since the smaller mass of the $e_1e_2e_3$ plants (see below) probably resulted in more rapid pod desiccation.

There were significant effects of transfer time, isoline, and their interaction, on total dry matter and seed yield per plant ($P < 0{\cdot}001$), both variables being greatest for $E_1E_2E_3$ in LD and least for $e_1e_2e_3$ in either photoperiod. No effects ($P > 0{\cdot}05$) of photoperiod or transfer time, nor the interactions between transfer time and isoline or between photoperiod and isoline, on harvest index (HI) were detected. Only the main effect of isoline influenced HI significantly: values ranged from 0·36 in $E_1E_2e_3$ and $E_1e_2E_3$ to 0·41 in $e_1e_2e_3$, $e_1E_2e_3$, and $e_1e_2E_3$. Nevertheless, HI tended to be greater in treatment combinations in which flowering durations were short and *vice versa*, as found in the previous study (Summerfield *et al.*, 1998).

As expected from resource capture considerations (Monteith, 1977), variation in duration from first flowering (R1) to harvest maturity (R8) explained much of the variation in total plant dry weight at R8 (Fig. 3), whereas variation in seed dry weight per plant was strongly dependent upon variation in total dry matter per plant (Fig. 4). Thus, plants of isolines with allelic combinations involving $E_1$, $E_1$ plus $E_2$, $E_1$ plus $E_3$, or (especially) $E_1$ plus both $E_2$ and $E_3$ gave higher yields than the other allelic combinations (Figs 3 and 4), particularly when grown in LD after first flowering, as a result of their longer reproductive durations (Fig. 1). Moreover, comparison between Figs 2 and 3 shows that it was those isolines with a prolonged photoperiod-sensitive phase, and, therefore, longer flowering durations, which produced correspondingly large seed yields.

The clear conclusions from this investigation are that: photoperiod sensitivity in soyabean continues after first flowering but ends before the appearance of the last flower; that sensitivity to photoperiod during flowering, and, therefore, the duration of the photoperiod-sensitive phase of post-first flowering development, is influenced by the maturity genes $E_1/e_1$, $E_2/e_2$ and $E_3/e_3$; that epistatic effects among these alleles are considerable; and that these gene effects can influence seed yield considerably in LD. Consequently, it is not correct to presume that photoperiod-sensitivity in soyabean ends at first flowering. Instead, there is a need for similar investigations on a larger sample of the soyabean germplasm, particularly given the striking effect of increased flowering duration on total dry matter and seed yields. This is especially so for germplasm that is potentially better adapted to the tropics, where rates of development under strongly-inductive photothermal conditions are often so rapid that crop durations may be too short to exploit fully the water-defined growing season (Summerfield and Lawn, 1987; Lawn, 1989). It remains unclear, however, from this study, as well as that of Summerfield *et al*. (1998), as to whether or not the considerable effects on biomass and seed yield, detected when plants of isolines with the dominant alleles $E_1$, $E_2$ and $E_3$ are grown in long days after first flowering, are due solely to their greater reproductive duration, and hence their greater opportunity for resource capture. This topic is investigated in the forthcoming third and final paper in this series.

## ACKNOWLEDGEMENTS

We thank Messrs K. Chivers and S. Gill for engineering support, Mrs C. Hadley and Mr A. Pilgrim for technical support, and the Ghana Grains Development Project for providing a research studentship to HA.

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