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Characterization of the Photoperiodic Response of Post-flowering Development in Maturity Isolines of Soyabean [*Glycine max* (L.) Merrill] 'Clark'

R. J. SUMMERFIELD, H. ASUMADU, R. H. ELLIS and A. QI

Plant Environment Laboratory, Department of Agriculture, The University of Reading, Cutbush Lane, Shinfield, Reading RG2 9AD, UK

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Plants of all eight isolines of three maturity genes (all combinations of two alleles at the three loci E_1/e_1, E_2/e_2, E_3/e_3) of soyabean [*Glycine max* (L.) Merrill] were grown in four different photoperiods (12, 13, 14 or 15 h d^{-1}) at 30/24 °C from first flower opening to harvest maturity. Photoperiod, isoline, and their interaction, affected significantly ($P < 0{\cdot}01$) the duration between first and last flowering, and reproductive duration. The interactions between genotype and photoperiod were sufficiently strong that considerable differences in these durations were detected among isolines in the least-inductive environment (15 h d^{-1}) whereas differences were negligible in the most-inductive regime (12 h d^{-1}). There was a negative linear relation between photoperiod and both rate of progress from the appearance of the first to the last flower, and rate of progress from first flowering to harvest maturity; sensitivity to photoperiod varied ($P < 0{\cdot}05$) six- and five-fold, respectively, among the extreme isolines ($e_1e_2e_3$ and $E_1E_2E_3$). The three dominant alleles E_1, E_2 and E_3, singly, had comparatively little effect on post-flowering traits, but considerable epistasis (particularly between E_1 and E_2) was detected for sensitivity to photoperiod in respect of rates of progress from the appearance of the first to the last flower, and from first flower to harvest maturity. Thus the large variations detected for these traits are the consequence of gene × gene (× gene) × environment interactions.

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

INTRODUCTION

The effects of photoperiod on progress to first flowering in soyabean [*Glycine max* (L.) Merrill] are sufficiently well understood to have been modelled for a wide range of contrasting genotypes and production environments (Hadley *et al*., 1984; Summerfield *et al*., 1993); for the effects of three major 'maturity' (E) genes, singly and combined, to have been quantified (Upadhyay *et al*., 1994); and for this knowledge to have been applied in order to understand the adaptation of the global germplasm to the diverse environments in which soyabean is cropped (Roberts *et al*., 1996). Five major loci, each with two alleles, are known to affect flowering and maturity in soyabean. They are designated 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). The dominant allele at the first three of these loci delays flowering, to different extents, by increasing the sensitivity of the duration from sowing to first flowering to photoperiod, but has no effect on the sensitivity of this duration to temperature (Upadhyay *et al*., 1994). The dominant allele E_4 probably has a similar effect to that of E_3 (Cober, Tanner and Voldeng, 1996).

Variation in the duration of the vegetative phase (i.e. from sowing to first flowering) of soyabean development among genotypes and environments typically accounts for around 70% of that for total crop duration (Mayers, Lawn and Byth, 1991). Nevertheless, genotype and environment also affect the development of soyabeans after the plants have come into flower. Responses to photoperiod certainly persist, but their effects on reproductive traits have received less attention than flowering *per se* (Johnson, Borthwick and Leffel, 1960; Raper and Thomas, 1978; Cure *et al*., 1982; McBlain, Hesketh and Bernard, 1987). This paper describes an investigation of the effects of photoperiod after first flowering on various reproductive traits in soyabean, and whether or not the dominant alleles at the loci E_1/e_1, E_2/e_2 and E_3/e_3 affect these responses.

MATERIALS AND METHODS

Plants of eight so-called 'maturity isolines', differing only in certain maturity (E) genes, were grown in a common short-day environment, and then transferred to different photoperiods, in order to determine the effects on subsequent durations to the end of flowering, and to maturity. Consequential effects on other plant characteristics, such as number of flowers, biomass and seed yield, were also determined. The genotypes studied comprised all eight combinations of two alleles at the three loci E_1/e_1, E_2/e_2 and E_3/e_3 (Bernard, 1971; USDA, 1989) in the cultivar 'Clark' background. All eight isolines are homozygous for the alleles E_4 and e_5 at the fourth and fifth loci, respectively (Table 1).

Seeds, graded by weight in order to ensure uniform seed size within an isoline by excluding the heaviest and lightest 10% of seeds, were surface-sterilized and then inoculated with a slurry of *Bradyrhizobium japonicum* strain CB1809 (supplied by Root Nodule Pty Ltd, Australia) before sowing. Four seeds were sown per pot (18 cm diameter, 2·01 capacity) on 16 Apr. 1993. The growing medium comprised vermiculite, coarse sand, gravel (0·6 cm), and loamless compost

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TABLE 1. *Genetic constitution and parentage of soyabean 'Clark' and its maturity isolines (from McBlain* et al., *1987)*

Isoline	Genetic constitution*	Parentage†	MG‡
L71-920	$e_1e_2e_3E_4e_5$	L63-3117(e_2) × L63-2404(e_3)	I
L80-5914	$E_1e_2e_3E_4e_5$	L70-4478(E_1e_2) × L71-920(e_2e_3)	IV
L63-2404	$e_1E_2e_3E_4e_5$	Clark^6 × PI 84.987	II
L63-3117	$e_1e_2E_3E_4e_5$	Clark^6 × PI 86.024	II
L74-441	$E_1E_2e_3E_4e_5$	L63-2404(e_3) × L65-3366(E_1)	IV
Clark	$e_1E_2E_3E_4e_5$	Lincoln^2 × Richland	IV
L66-432	$E_1e_2E_3E_4e_5$	L62-1932(e_2) × L65-3366(E_1)	IV
L65-3366	$E_1E_2E_3E_4e_5$	Clark^6 × T175	V

* Numbers in subscript refer to the position of that allele on the chromosome.
† Superscripts denote the number of crosses to the recurrent parent.
‡ MG, USA Maturity Group, indicating the approximate latitudes (°N) to which different cultivars are best adapted, i.e. I (43–45°), II (41–43°), IV (36–38°) and V (34–36°) (Whigham and Minor, 1978).

in the ratio 2:1:2:0·5 by volume, respectively (Summerfield, Huxley and Minchin, 1977). The sand and gravel were first steam-sterilized at 96 °C and 3 kg cm^{-3} for 20 min and then mixed thoroughly with the vermiculite and compost. The medium was saturated with water for 24 h, and then allowed to drain freely before sowing. Seedlings were thinned to leave one plant per pot at 14 d after sowing. Pot spacing was 32 × 32 cm. After thinning, plants were irrigated with a complete nutrient solution containing 100 mg l^{-1} inorganic nitrogen (Summerfield *et al.*, 1977). Irrigation occurred as often as five times during each 24 h period and there was no evidence of moisture stress at any stage of plant growth. All plants were staked after first flowering. Infestations of red spider mite (*Tetranychus urticae*) and aphids (*Aphis fabae*) at later stages of plant growth were controlled using the acaricide Childon and the aphicide Dimethoate, respectively. The glasshouse was also fumigated periodically with Primiphos methyl smoke.

The experiment was carried out in a controlled-environment glasshouse facility which provided natural light during the day (12 h), but with four night (12 h) compartments. Day and night temperatures were maintained at 30 and 24 °C, respectively, throughout the experiment, each for 12 h d^{-1}. Relative humidity was not controlled and carbon dioxide was maintained at ambient concentration by ventilation in all compartments. A daylength of 12 h d^{-1} was provided from sowing to first flowering by transferring the trolleys on which the pots stood into and out of the dark compartments at the end and beginning of each day, respectively. Three of the dark compartments were equipped with 60 W tungsten bulbs spaced 1·0 m apart and 1·15 m above the pots. The photon irradiance provided at pot level within these compartments exceeded 0·4 μmol m^{-2} s^{-1}, which is sufficient to saturate the photoperiodic response of soyabean (Summerfield and Roberts, 1987). At first flowering ($\pm$2 d, i.e. when the corolla colour was first visible on the majority of plants), plants were exposed to photoperiods of 12, 13, 14 or 15 h d^{-1} until harvest maturity by extending the natural daylength artificially using tungsten lighting within the night compartments.

A split-plot design with four replicates was used. Main plot treatments were the four photoperiods, each of which was split into eight sub-plots (the eight isolines). Flowering and reproductive durations were calculated from records of dates of first flowering, termination of flowering (i.e. the last flower to open) and harvest maturity. Plants were harvested at 'harvest maturity', developmental stage R8, when 95% of the pods had reached the mature pod colour (brown) (Fehr and Caviness, 1977). Reproductive and vegetative structures were separated at harvest, the latter including nodulated roots which were carefully washed to separate them from the rooting media. 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. Harvest index (HI) was calculated as the ratio of seed to total dry weight per plant at harvest maturity (including roots and nodules). Fruit set was estimated by dividing the number of mature pods by the number of flowers. The statistical programme GENSTAT V (GENSTAT V Committee, 1987) was used for all analyses. Initial analyses employed analysis of variance. Where significant differences were detected ($P \leqslant 0{\cdot}05$), the standard errors of differences of means (s.e.d.) were used to compare treatments.

Analyses of the effect of photoperiod on flowering and reproductive durations were based on modifications of the three-plane photothermal flowering response model (Hadley *et al.*, 1984; Summerfield *et al.*, 1991, 1993). In the model, the rate of progress from sowing to first flowering at a given temperature is related linearly to photoperiod, P (h d^{-1}), between certain limits, such that

$$1/f = a' + c'P \quad (1)$$

where f is the duration (d) from sowing to first flowering and a' and c' are genotypic constants (Summerfield *et al.*, 1991). Here, variation in the rate of progress from the appearance of the first to the appearance of the last flower to open (i.e. the reciprocal of flowering duration), and in the rate of progress from first flowering to harvest maturity (i.e. the reciprocal of reproductive duration), with respect to photoperiod, were analysed using regression analysis as follows:

$$1/fd = a_2 + c_2 P \quad (2)$$

$$1/rd = a_3 + c_3 P \quad (3)$$

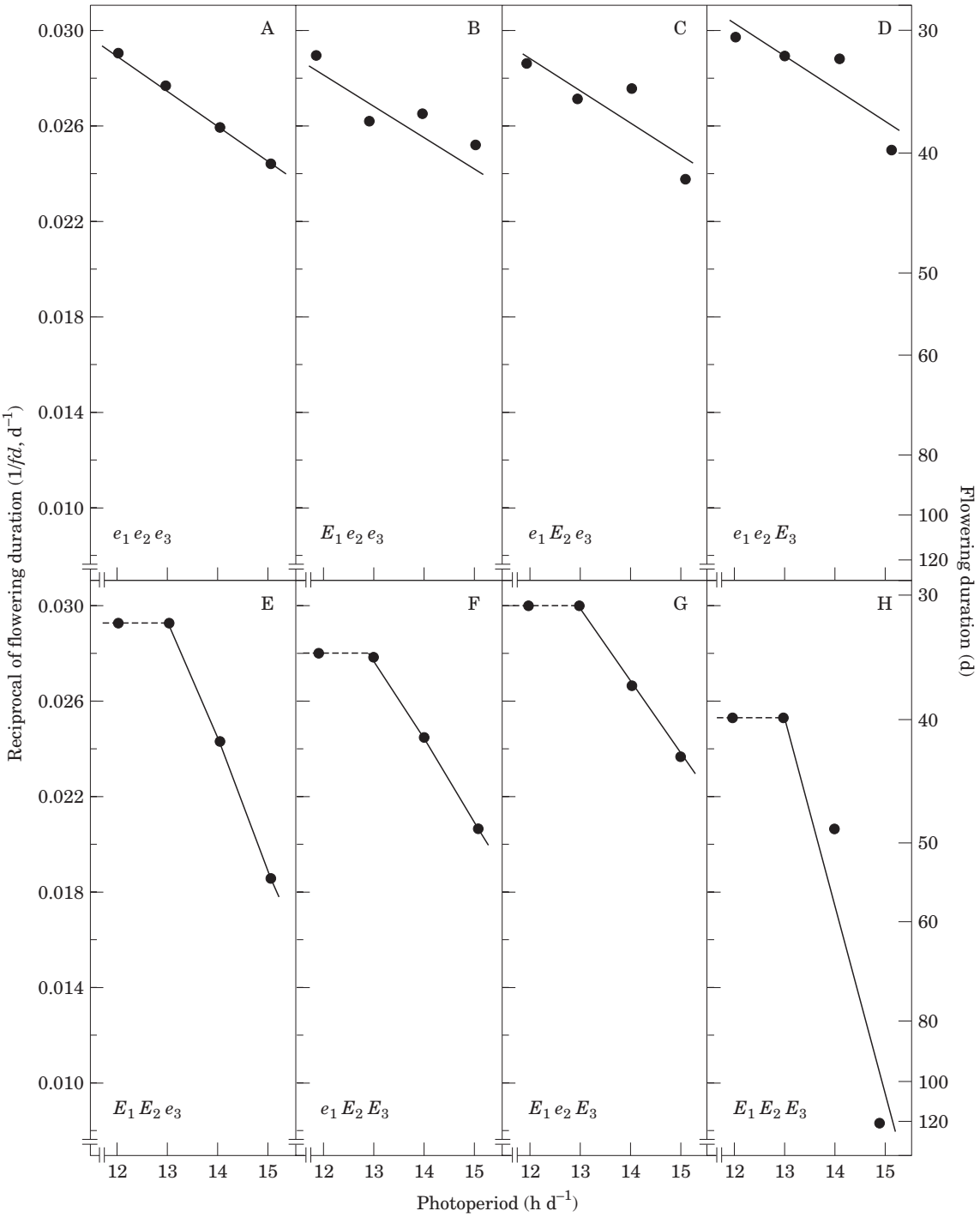

FIG. 1. Effect of photoperiod on rate of progress from first to last flower opening for eight maturity isolines of soyabean 'Clark'. The vertical scale (1/*fd*) on the left-hand ordinate is converted to *fd* (flowering duration in days) as a non-linear scale on the right-hand ordinate. Solid circles denote the observed flowering durations; solid lines show the fitted responses (Table 2), and broken lines show the rate of progress at photoperiods shorter than the critical value.

where *fd* and *rd* are the flowering and reproductive durations (d), respectively, and a_2, c_2, a_3, and c_3 are constants. Regressions were compared to determine whether or not isolines differed significantly in the sensitivity of rate of development to photoperiod.

RESULTS

Durations from sowing to first flowering varied only between 24 and 28 d among isolines, and the different photoperiod treatments were begun at these times. Significant ($P < 0{\cdot}01$)

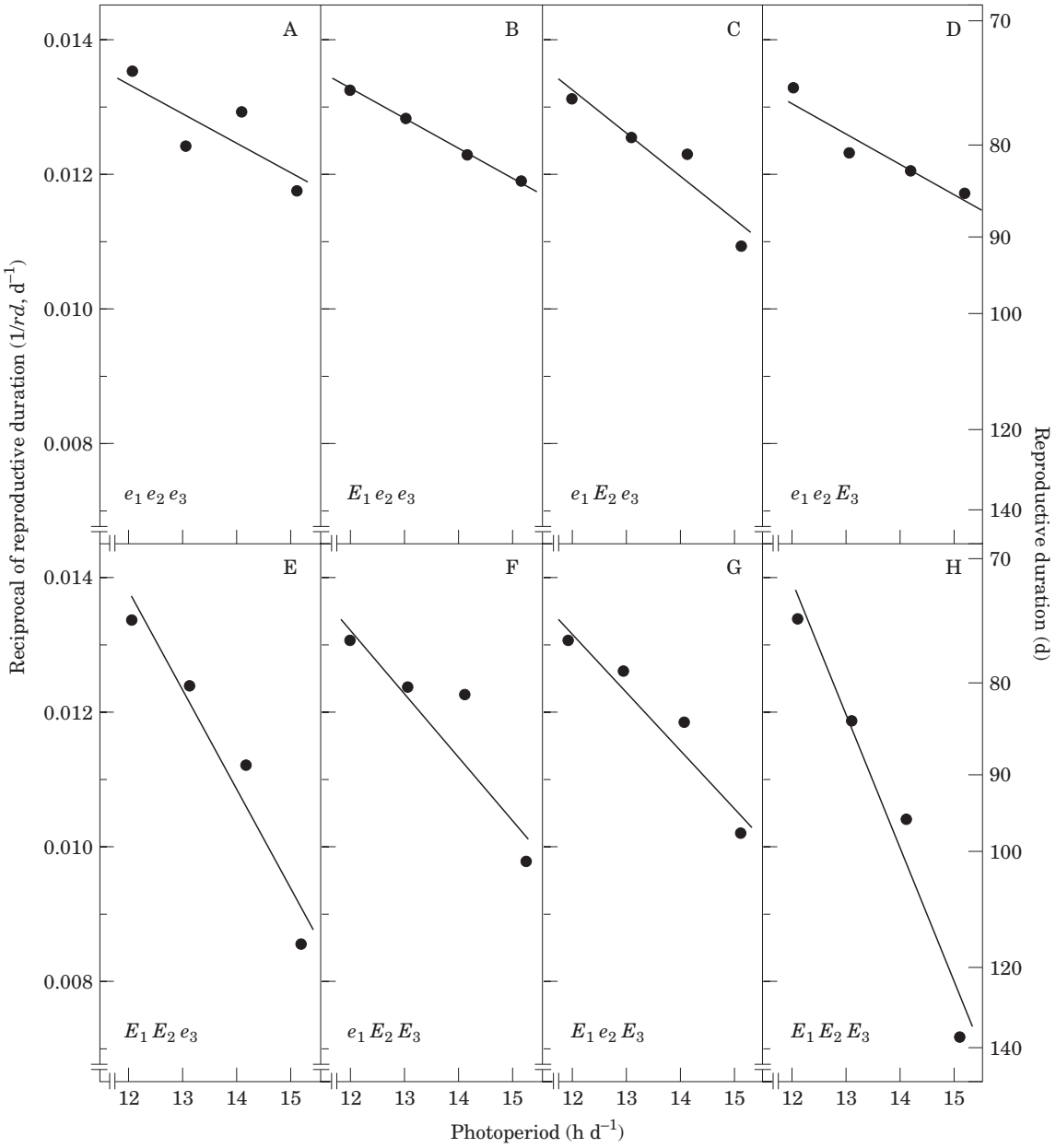

FIG. 2. Effect of photoperiod on rate of progress through the reproductive phase of development (i.e. from the first flower opening to seed maturity) for eight maturity isolines of soyabean 'Clark'. The vertical scale (1/*rd*) on the left-hand ordinate is converted to *rd* (reproductive duration in days) as a non-linear scale on the right-hand ordinate. Solid circles denote the observed reproductive durations and solid lines show the fitted responses (Table 3).

effects of photoperiod and isoline, and their interaction, were detected for flowering duration, reproductive duration (R1 to R8), number of flowers, total dry matter and seed yield per plant.

The flowering and reproductive durations (Figs 1 and 2) were most affected by photoperiod in the isoline with dominant alleles present at all three loci ($E_1E_2E_3$); these durations were fairly sensitive to photoperiod for the three isolines with two dominant alleles present (i.e. $E_1E_2e_3$, $e_1E_2E_3$, $E_1e_2E_3$), and least affected in the four isolines with no, or only one, dominant allele (i.e. $e_1e_2e_3$, $E_1e_2e_3$, $e_1E_2e_3$ and $e_1e_2E_3$).

The duration of flowering (Fig. 1) was similar at 12 h d^{-1} (33–36 d) for seven of the eight isolines, but 4 d longer, on average, in $E_1E_2E_3$. Increase in daylength from 12 to 15 h d^{-1} extended these durations by as few as 6 d for $e_1e_2e_3$ or as many as 79 d for $E_1E_2E_3$. These responses were quantified in accordance with eqn (2). There was a negative linear response of rate of progress from the appearance of the first to last flower to photoperiod in $e_1e_2e_3$, $E_1e_2e_3$, $e_1E_2e_3$ and $e_1e_2E_3$ throughout the range investigated (12 to 15 h d^{-1}), whereas in $E_1E_2e_3$, $e_1E_2E_3$, $E_1e_2E_3$, and $E_1E_2E_3$ no effect of photoperiod was detected between 12 and 13 h d^{-1}, but there was a negative linear relation between 13 and

TABLE 2. *Fitted relationships between rate of progress from first to last flower opening* (1/fd) *and post-flowering photoperiod in eight maturity isolines of soyabean* '*Clark*'

Gene combination	a_2 (d^{-1})	c_2 ($d^{-1}[hd^{-1}]^{-1}$)	r^2	d.f.
$e_1e_2e_3$	0·0474	−0·00154	0·58	14
	(0·0045)	(0·00033)		
$E_1e_2e_3$	0·0450	−0·00139	0·29	14
	(0·0071)	(0·00052)		
$e_1E_2e_3$	0·0458	−0·00142	0·45	14
	(0·0052)	(0·00039)		
$e_1e_2E_3$	0·0475	−0·00143	0·52	14
	(0·0047)	(0·00035)		
$E_1E_2e_3$	0·0986	−0·00533	0·84	10
	(0·0098)	(0·00070)		
$e_1E_2E_3$	0·0761	−0·00370	0·97	10
	(0·0025)	(0·00018)		
$E_1e_2E_3$	0·0710	−0·00316	0·72	10
	(0·0082)	(0·00058)		
$E_1E_2E_3$	0·1359	−0·00841	0·87	10
	(0·0136)	(0·00097)		

Values in parentheses are s.e. of parameter estimates.

TABLE 3. *Fitted relationships between rate of progress from first flower opening to harvest maturity* (1/rd) *and post-flowering photoperiod in eight maturity isolines of soyabean* '*Clark*'

Gene combination	a_3 (d^{-1})	c_3 ($d^{-1}[hd^{-1}]^{-1}$)	r^2	d.f.
$e_1e_2e_3$	0·0186	−0·00044	0·43	14
	(0·0017)	(0·00013)		
$E_1e_2e_3$	0·0184	−0·00044	0·54	14
	(0·0014)	(0·00010)		
$e_1E_2e_3$	0·0211	−0·00066	0·73	14
	(0·0014)	(0·00010)		
$e_1e_2E_3$	0·0185	−0·00046	0·50	14
	(0·0015)	(0·00011)		
$E_1E_2e_3$	0·0314	−0·00148	0·87	14
	(0·0019)	(0·00014)		
$e_1E_2E_3$	0·0247	−0·00097	0·70	14
	(0·0022)	(0·00016)		
$E_1e_2E_3$	0·0239	−0·00089	0·79	14
	(0·0016)	(0·00012)		
$E_1E_2E_3$	0·0380	−0·00202	0·94	14
	(0·0018)	(0·00014)		

Values in parentheses are s.e. of parameter estimates.

15 h d^{-1} (Fig. 1). Thus critical photoperiods for the latter group of isolines (i.e. those with two or three dominant alleles) close to 13 h d^{-1} were demonstrated by these analyses. Photoperiod sensitivity (c_2) varied ($P < 0·01$) six-fold between extreme isolines (Table 2).

All eight isolines showed a negative linear response of the rate of progress from first flowering to harvest maturity (i.e. reproductive duration) to photoperiod throughout the entire range of photoperiods imposed (Fig. 2); i.e. critical photoperiod was $\leqslant$ 12 h d^{-1}. Substantial (almost five-fold) differences ($P < 0·01$) in sensitivity to photoperiod (c_3) were detected among the isolines (Table 3).

Variations among treatments in the number of flowers, total dry matter and seed yield per plant were broadly similar to those detected for flowering and reproductive durations with values ranging approx. five-(5·3), four-(3·7), and three-(3·3) fold respectively between extreme treatments (data not presented for dry matter and seed yield). The number of flowers per plant (Table 4) was affected by isoline ($P < 0·01$), photoperiod ($P < 0·01$) and their interaction ($P < 0·01$). Not surprisingly, variation in the number of flowers per plant was strongly correlated with that for flowering duration ($r = 0·95$, 126 d.f., $P < 0·01$).

TABLE 4. *Effect of post-flowering photoperiod on the number of flowers per plant in eight maturity isolines of soyabean* '*Clark*'

Gene combination	Photoperiod (hd^{-1}) 12	13	14	15 (21·7)*	Mean	s.e.d.
$e_1e_2e_3$	125	128	117	148	129	
$E_1e_2e_3$	157	167	164	164	163	
$e_1E_2e_3$	127	120	121	139	126	
$e_1e_2E_3$	118	119	131	122	122	
$E_1E_2e_3$	141	138	177	262	179	
$e_1E_2E_3$	124	119	136	189	142	
$E_1e_2E_3$	150	136	147	190	156	
$E_1E_2E_3$	179	180	255	662	319	
Mean	140	138	156	234	167	(8·0)
s.e.d.					(10·8)	

* s.e.d. for isoline × photoperiod treatment combinations.

Differences in fruit set among isolines were significant ($P < 0·05$) but minor (from 0·654 to 0·704). Harvest index varied between extremes of 0·32 and 0·41. It was affected by both isoline ($P < 0·01$), being greatest in $e_1e_2e_3$ and smallest in $E_1E_2E_3$, and photoperiod ($P < 0·01$), being greatest in 12 h d^{-1} and smallest in 15 h d^{-1}. Harvest index was negatively correlated with crop duration ($r = -0·50$, 126 d.f., $P < 0·01$), biomass yield per plant ($r = -0·42$, 126 d.f., $P < 0·01$), and seed yield per plant ($r = -0·23$, 126 d.f., $P < 0·05$). Not surprisingly, both biomass and seed yield were positively correlated with crop duration ($r = 0·84$, 126 d.f., $P < 0·01$, and $r = 0·78$, 126 d.f., $P < 0·01$, respectively).

DISCUSSION

Photoperiod influenced developmental progress from first flowering to maturity, with the effects varying greatly among isolines (Figs 1 and 2). In turn, these differences affected total dry matter production, and thus seed yield (data not presented). Such yield differences among the isolines in long days, understandable from the perspective of resource capture (Monteith, 1977), are considered in detail in a forthcoming publication.

Individually, the three dominant alleles had little or no effect on sensitivity to photoperiod post-first flowering, such that comparison of regressions showed no significant increase in deviance ($P > 0·05$) if the estimates of each of c_2 and c_3 were constrained to the same value for $e_1e_2e_3$, $E_1e_2e_3$, $e_1E_2e_3$, and $e_1e_2E_3$. However, the combined effects of the three dominant alleles E_1, E_2, and E_3 increased ($P < 0·05$)

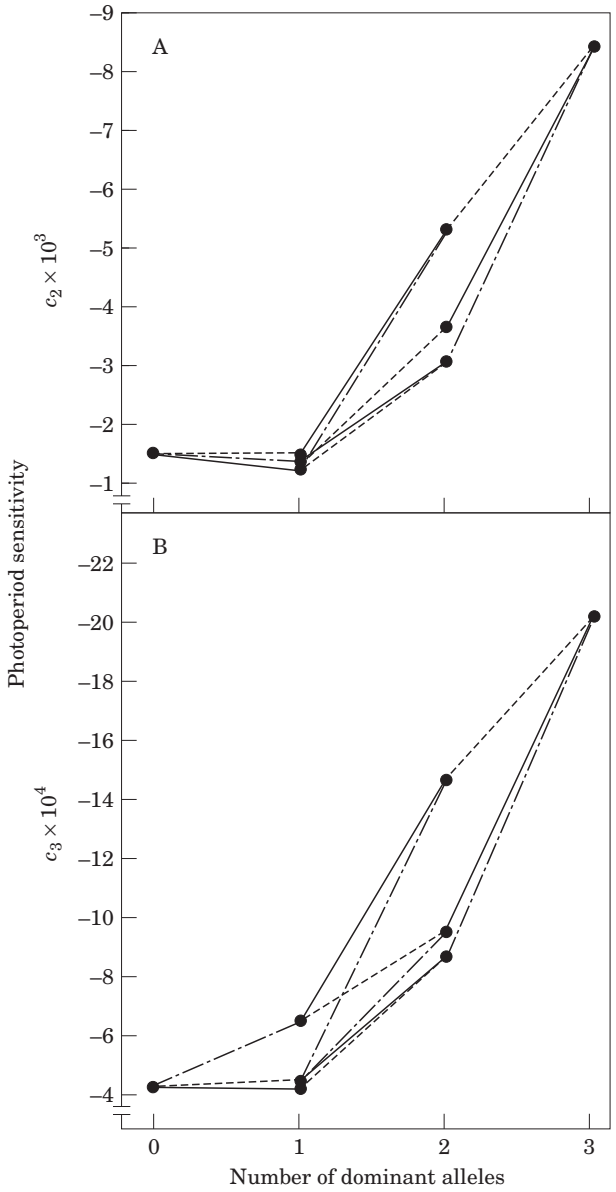

FIG. 3. Richards diagrams showing: differences in photoperiod sensitivity of rate of progress from first to last open flower (A) (c_2, d^{-1} $[hd^{-1}]^{-1}$); and of rate of progress from first flowering to harvest maturity (B) (c_3, d^{-1} $[hd^{-1}]^{-1}$) as affected by the dominant alleles E_1 (—)E_2 (–.–.–) and E_3 (– – –) in eight maturity isolines of soyabean 'Clark'.

the sensitivity of post-first flowering durations to photoperiod, thereby delaying development towards maturity (Figs 1 and 2). Since all factorial combinations of the two alleles at all three loci were investigated, the effects of each dominant allele singly, and in combination, on photoperiod sensitivity can be illustrated using Richards diagrams (Richards, 1941). Figure 3 presents Richards diagrams for sensitivity to photoperiod for both flowering duration (c_2) and reproductive duration (c_3). In a Richards diagram the eight possible combinations of alleles provide six quadrilaterals which resolve into parallelograms if there is no interaction between the genes. For the sensitivity of flowering duration to photoperiod (i.e. c_2), none of the dominant alleles alone had any effect (Fig. 3A). However, epistasis (interallelic interaction) was detected between all three dominant alleles, with that between E_1 and E_2 being the greatest. The Richards diagram for sensitivity of the reproductive duration to photoperiod (c_3) (Fig. 3B) was broadly similar to that for c_2 (the apparent effect of E_2 alone not being significant). These responses are similar to those reported for the effects of these three dominant alleles on the sensitivity of rate of development to first flowering to photoperiod (Upadhyay *et al.*, 1994), except that effects of E_1 alone were detected for durations from sowing to first flowering.

This investigation has shown clearly that post-first flowering development is influenced by photoperiod, that such effects can be quantified, and that this sensitivity to photoperiod is under genetic control. However, it is not possible from the current results to say at what stage during their development post-first flowering soyabean plants no longer respond to photoperiod, or to what extent this may vary among isolines. In fact, significant effects of photoperiod, isoline and their interaction were detected ($P < 0{\cdot}001$) as late as the developmental phase from R7 to R8 (i.e. during plant senescence and pod desiccation). However, this effect may well be indirect and simply reflect the variation in plant mass in the different treatments, with heavier plants taking longer to senesce. Accordingly, a companion paper (Asumadu *et al.*, 1998) investigates the stage during post-first flowering development when soyabean plants no longer respond to photoperiod, and the effects of the maturity genes thereon.

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