Development and Seed Number in Indeterminate Soybean as Affected by Timing and Duration of Exposure to Long Photoperiods after Flowering

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INTRODUCTION

The number of pods and seeds in soybean (Glycine max) are determined during a period that begins around flowering, and extends through pod set, including the beginning of the seed-filling period (Pigeaire et al., 1986; Board and Tan, 1995; Jiang and Egli, 1995; Egli, 1997). Due to the high link between pod and seed number and yield (Herbert and Litchfield, 1982; Board et al., 1999, 2003; Ball et al., 2001), these post-flowering phases are often regarded as the critical period for yield determination (Egli, 1998). Manipulations in crop photosynthesis after flowering by shading (Egli and Zhen-Wen, 1991; Jiang and Egli, 1993, 1995), extra light (Mathew et al., 2000), CO₂ enrichment (Hardman and Brun, 1971) or defoliations (Board and Tan, 1995) result in changes in pod and seeds per unit area, highlighting the dependency of soybean yield on crop growth during post-flowering phases. Pod and seed number are also increased when the duration of this phase is lengthened (Egli and Bruening, 2000; Kantolic and Slafer, 2001; Calviño et al., 2003; Cooper, 2003; Kantolic and Slafer, 2005), but the mechanisms underlying this response are not well understood. Therefore, the understanding of the environmental and genetic control of the duration of the critical period and its relationship with seed production may become a potential tool to further rise soybean yield.

Soybean is a short-day plant, and photoperiod and temperature control the duration of both pre- and post-flowering phases. Long photoperiods delay floral initiation and slow down the rate of development of flower primordia (Thomas and Raper, 1977; Caffaro and Nakayama, 1988; Thomas and Kanchanapoom, 1991; Fleming et al., 1997) and, consequently, delay flowering (Borthwick and Parker, 1938; Hadley et al., 1984; Upadhyay et al., 1994; Zhang et al., 2001). Although it is also known that long photoperiods extend the duration of post-flowering phases as well (Thomas and Raper, 1976; Guiamet and Nakayama, 1984; Summerfield et al., 1998; Kantolic and Slafer, 2001; Han et al., 2006), our understanding of photoperiodic control of development in soybean has been mostly restricted to pre-flowering responses, which are in fact the bases for the characterization of soybean cultivars into different maturity groups (Summerfield and Roberts, 1985). In spite of the high importance of post-flowering phases on yield definition, the knowledge of photoperiodic responses after flowering is fragmentary and far less comprehensive. In consequence, the link between post-flowering response to photoperiod and yield has not been established.

Recent studies have found a relationship between soybean responses to photoperiod after flowering and the ability of the plants to produce pods and seeds. When indeterminate soybeans of maturity groups IV and V were exposed to long photoperiods exclusively during

Key words: Glycine max, photoperiod, post-flowering development, seed number, soybean, yield components.
post-flowering stages, the critical period was lengthened and concomitantly more pods and seeds were produced (Kantolic and Slafer, 2001, 2005). In these studies most post-flowering phases (from the beginning-pod stage until maturity) were exposed to treatments of extended photoperiod, precluding the identification of possible changes in the responsiveness throughout them. An understanding of when plants are more sensitive to photoperiod may help to better define likely effects of the duration of these phases on the number of seeds and yield.

A quantitative or continuous response to photoperiod is a pre-requisite for a plant which is permanently sensing a changing photoperiod environment and has a continuous capacity to respond to this perception. Although it has been found that indeterminate soybeans quantitatively responded to the length of photoperiod when the treatments were imposed continuously (Kantolic and Slafer, 2005), it is not clear if post-flowering development is quantitatively responsive to the length of the exposure to long photoperiod or whether the response saturates in just one or few cycles of long photoperiod. Furthermore, the plant reaction during a particular phase may be a consequence of current as well as previous environmental conditions (Slawer and Rawson, 1994). In wheat (Triticum aestivum.), a long-day plant, there is some evidence of the existence of a so-called ‘memorized’ or ‘historic’ effect of photoperiod on development. For instance, the phase from the onset of stem elongation to anthesis is shortened when the previous phases occur under long photoperiods (Slawer and Rawson, 1995).

Changes in sensitivity to photoperiod during the post-flowering phases and the possibility of memorized effects of photoperiod on later development have to be assessed before it is possible to design breeding or management strategies which apply our understanding of soybean post-flowering response to photoperiod. Moreover, the evaluation of these responses under highly controlled environments as proposed by Adams et al. (2001) is possibly limited if their consequences on seed production and yield are to be drawn. The main aims of this paper were to estimate under field conditions whether sensitivity to photoperiod after flowering (a) is quantitatively related to the length of exposure to long days and (b) persists throughout the whole pod-setting period. It was also evaluated whether changes in the duration of post-flowering phenophases were associated with changes in seed number and yield, irrespective of the timing and length of exposure to long photoperiods.

**MATERIALS AND METHODS**

Two independent field experiments were performed at the experimental field of the Agronomy Faculty, University of Buenos Aires (34°35’S, 58°29’W). Seeds of Glycine max ‘A5409 RG’ (indeterminate growth habit, maturity Group V) were inoculated with Bradyrhizobium liquid inoculant and hand sown at a high planting rate on 9 November 2001. Plots consisted of four rows, 0.35 m apart and 1.5 m long. When the unifoliate leaves were expanded, the plots were hand-thinned to obtain a uniform plant population of 45 plants m$^{-2}$. This population was high enough to attain 95 % of radiation interception at flowering. Fungal diseases were prevented and weeds and insect pests were controlled; irrigation was applied whenever necessary to complement rainfall in order to prevent water limitations to growth. The soil was a silty clay loam classified as Vertic Arguidol.

In both experiments plants were grown under natural daylength from seedling emergence until the beginning-pod stage (R3 stage; Fehr and Caviness, 1977). From then onwards, photoperiod treatments were assigned following a randomized block design with three replicates. In expt 1, treatments consisted of different periods of exposure to a photoperiod 2 h longer than natural daylength (T1 to T9, Fig. 1, top panel), and included a control (T0) with plants always grown under natural photoperiod and a treatment with plants grown under extended photoperiod until maturity (T10). In expt 2, periods of 9 d of 2 h extended photoperiod were consecutively applied from R3 to R6 (i.e. the stage when seeds reach full size), with the rest of the cycle being exposed to natural daylength (Fig. 1, bottom panel).

Photoperiod was extended by means of portable lighting systems combining incandescent and fluorescent lights of low intensity but with a similar quality to that of natural radiation, providing a mean photosynthetic photon flux density of 4.3 μmol m$^{-2}$ s$^{-1}$ and a red : far red quantum ratio of 1.17. Light intensity and quality were measured at the canopy surface at night with a LI-COR line quantum sensor (LI-COR Inc., Lincoln, NE, USA) and a 660/730 Sensor SKR 110 (Skye Instrument Ltd, Powys, UK), respectively. Lights were turned on before sunset and automatically turned off 2 h after the civil twilight ended, mimicking natural change of daylength. The plots were 2 m away from each other in order to prevent the exposure of control plots to artificial light.

Phenology was recorded every 1–3 d, using a conventional scale (Fehr and Caviness, 1977). Only some reproductive stages of this scale were considered: R4 (pods 2 cm long), R5 (seeds 3 mm long) and R6 (seeds filling the pod locule). This scale takes into account the stage of development in the four uppermost nodes of the mainstem of the plants and the stages were recorded when 50 % of the two central rows of each plot, excluding 0.25-cm borders, achieved the stage. Maturity was established when >95 % of the pods lost their green colour and turned yellow.

In order to more accurately assess the responsiveness to photoperiod under field conditions with variable temperature and compare present with previous experiments, thermal effects on the duration of developmental phases were taken into account by correcting the durations by daily mean temperature using the three segmented function proposed by Piper et al. (1996). Briefly, one thermal day equals one calendar day when temperature is within an optimum range (e.g. 25–30 °C from seedling emergence to R5 stage), while it varies linearly by a coefficient between zero and one outside this range. No development (i.e. one calendar day equals zero thermal day) is expected when mean temperature is below a base temperature (e.g. 2.5 °C) or above a maximum temperature (55 °C).
The accumulated thermal days between two stages, e.g. R3 and R4, represented the corrected duration of the phase. Further details of the correcting procedure are given in Kantolic and Slafer (2005).

After maturity, an area of 0.7 m² was harvested by hand from the two central rows from each plot, excluding borders. The whole harvested area was used to estimate the number of pods and seeds per unit land area and seed yield. The number of nodes in the mainstem and branches was counted in five plants per plot and average seed weight was estimated from sub-samples of 100 seeds per experimental unit. Data were analysed by linear regressions and correlation analysis and analysis of variance with mean separation according to LSD (InfosStat, 2002).

RESULTS

Development

The duration of the R3–R6 phase increased quantitatively in response to the length of exposure to the extended photoperiod (Fig. 2). A maximum duration of 75.7 ± 0.4 days was attained when the exposure to long photoperiod was maintained until maturity. From T0 to T9, the duration of R3–R6 linearly increased about 1.5 days per 2 days of exposure to extended photoperiod (r² = 0.94, P < 0.05), reflecting the quantitative nature of the response of the reproductive development rate to the cumulative number of long photoperiod cycles perceived by the plants. Assuming this linearity holds until the saturation of the response, an exposure to 45 cycles of a long photoperiod seemed to be necessary to saturate the response of reproductive development in this cultivar.

The increments in the duration of the whole R3–R6 phase resulted from the delay of the successive stages of development. In expt 1, most of the responses were associated with the changes in the duration of R3–R4 sub-phase (Table 1). The R4 stage was delayed in all the treatments of extended photoperiod and the phase R3–R4 quantitatively increased in approx. 1 day per 2 days of exposure to extended photoperiod (Fig. 3A). When the photoperiod extension was maintained until maturity, the continued exposure to long days delayed R4, but it finally occurred at 40.7 ± 4.7 days after R3 (Fig. 3A).

The period between R4 and R5 was longer in all the treatments of extended photoperiod than in the control
remaining always under the natural photoperiod. However, a quantitative response to the number of cycles was not so clear in this case (Fig. 3B). It should be noted that in all treatments except T10, the R4 stage occurred after the photoperiod extension was imposed, so that developmental stages following R4 occurred under the natural photoperiod. Due to the naturally shortening photoperiod at that time of the year, the R4–R5 phase occurred under slightly shorter photoperiods in the plants that had been previously exposed to long photoperiods than in the control plants (Table 2).

The phase R5–R6 was longer than in the control only in the plants grown under long photoperiods until maturity (T10, Fig. 3C). In the rest of the extended-photoperiod treatments (T1 to T9), R5–R6 was as long as in T0, in spite of the fact that this phase occurred under naturally shorter photoperiods (Table 2), again by virtue of the lengthened duration of previous phases. After R6, the time to achieve maturity tended to be shorter as the time of previous exposure to long days increased (Fig. 3D). As mean temperature during these sub-phases tended to be lower when the time of exposure to the long photoperiod increased (Table 2), the durations were corrected by daily mean temperature as proposed by Piper et al. (1996). This correction did not modify the significance of the differences observed without corrections (data not shown).

In the study of the effect of different timings of exposure to long photoperiods (expt 2), three out of the four extended-photoperiod regimes increased the whole critical period, R3–R6 (Table 3). In the two earliest treatments (TA and TB), photoperiod extension occurred during the R3–R4 phase (Fig. 1). This sub-phase as well as the following one, R4–R5, was extended in both treatments (Table 3). In TC, the extension of photoperiod was applied after R4 (Fig. 1), and the durations of both R4–R5 and R5–R6 periods were lengthened. In TD the extension of photoperiod was imposed when the plants had already achieved the R5 stage and the length of none of the phases was modified in relation with T0 plants. Across treatments, most of the variation in the whole critical period R3–R6 was related to changes in R4–R5 duration (Table 1).

**Seed number and weight**

In expt 1, the exposure to extended photoperiods increased the number of seeds per unit land area, and plants exposed to more cycles of extended photoperiod tended to establish more seeds than those exposed to fewer cycles (Table 4). A positive linear relationship was found between seed number and days of exposure to extended photoperiod ($r^2 = 0.78$, $P < 0.05$). On average, 50 seeds m$^{-2}$ were added per day of exposure to extended photoperiod. The number of nodes per plant, both in the mainstem and in the branches, increased in response to increased exposure to long photoperiod. The number of nodes per plant, both in the mainstem and in the branches, increased in response to increased exposure to long days (Table 4). The number of seeds per node increased in several treatments with extended photoperiod, but not in others (Table 4). The higher number of seeds per unit land area resulted from increments in the number of pods, as seeds per pod remained unchanged. Seed weight was only affected in T10 – plants exposed to long photoperiods until maturity had a slightly smaller average seed weight than the control and all other treatments (Table 4).
Seed number also increased in the four treatments of extended photoperiod from expt 2 with respect to the control, but they did not differ among themselves (Table 5). In accordance with the results of expt 1, no changes in seeds per pod or in average seed weight were found while a slight increment in seed per node was detected. The number of nodes in the mainstem was increased in the three earliest exposures to extended photoperiod, and remained unchanged in TD, compared with the control (T0). In contrast, significantly more nodes were produced in the branches of the TD plants (Table 5).

A high correlation was found between seed number per unit land area and the duration of the R3–R6 period (Table 6). In expt 1, changes in seed number were highly associated with the increase in the duration of the R3–R4 period and there was also a significant relationship between seed number and the duration of R4–R5. In expt 2, the correlations between seed number and the durations of post-flowering phases were not significant (Table 6); this absence of correlation coincides with the findings that the response in seed number was similar in the four extended photoperiod regimes, including treatment TD, in which the duration of the phases was unaffected by photoperiod. Due to the absence of differences in seed number among the longest durations of R3–R6, the data of both experiments were fitted by a bi-linear adjustment. Excluding data from treatment TD of expt 2, the adjustment was highly significant and suggested that a maximum number of seeds was attained when the R3–R6 was about 65 d long (Fig. 4). As no effects were found on seed dry weight beyond the rather small decrease in T10 compared with the control, all differences in seed number per unit land area due to exposures to long photoperiods during pod formation, resulted in concomitant changes in yield (Fig. 4, inset).

**DISCUSSION**

During the critical period for setting pods, soybean ‘A5409-RG’ showed a quantitative response to the length of exposure to long days. This quantitative response complements what was previously found with ‘A5409’, a parent of the line used in the present experiments. When this cultivar was exposed to daylength extended from 1.5 to 6 h in relation to natural photoperiod, from R3 until maturity, the duration of R3–R6 was quantitatively extended (Kantolic and Slafer, 2005). When the duration of the R3–R6 phase in expt 1 was plotted against the mean photoperiod of the phase, a close match between present and former results was found (Fig. 5). This coincidence suggests that the mean photoperiod of R3–R6 is a good predictor of the...
duration of the phase, disregarding whether this mean photoperiod is a result of the exposure to an increasing number of long photoperiod cycles or to different day-lengths during the whole phase.

The present studies illustrate the ability of soybeans to continuously perceive the photoperiod under which they are grown during their reproductive development, as found in other crop species (e.g. wheat and barley; Miralles et al., 2003). During most of post-flowering phases plants were sensitive to changes in photoperiod. In soybean, it has been found previously that photoperiod effects persist throughout flowering, podding, seed filling and maturation phases of soybean of maturity group IX, when evaluating highly contrasting and constant photoperiod regimes (12 h against 18 h; Han et al., 2006). The present studies clearly show in detail that soybean of an intermediate maturity group also responds continuously to changes in a photoperiodic environment that is commensurate with field conditions. Moreover, current as well as the previous photoperiod modified the duration of the whole critical period for setting pods. The arrangement of the treatments in expt 1 highlighted that the response during the sub-phase R3–R4 is quantitative rather than qualitative, as the continuous exposure to photoperiods 2 h longer than natural daylength delayed but did not prevent the occurrence of the R4 stage. Plants were still sensitive after the R4 stage and the duration of R4–R5 seemed to be also dependent on the photoperiod explored by the plants during previous phases. Although changes in R5–R6 were found in some treatments, the present results did not clearly show that sensitivity to photoperiod still persisted after the R5 stage. In treatment TC of expt 2, the photoperiod extension ended before the R5 stage, suggesting that the greater duration of R5–R6 was a memorized effect of previous exposure to photoperiod. In expt 1, R5–R6 was only longer when photoperiod was extended until maturity. Although the photoperiod explored during this phase was effectively longer than those of the other treatments, it had also been longer during the previous sub-phase, R4–R5, thus making it impossible to discriminate between previous or current effects of photoperiod in the case of this particular phase. The duration of the final phase of development, R6 to maturity, seemed to be highly dependent on the photoperiod explored during the phase itself, which is consistent with the short day response previously reported for this phase (Grimm et al., 1994).

Memorized effects of photoperiod can be interpreted as the plant being committed to a developmental pattern well before a particular developmental stage could be identified (Slafer and Rawson, 1995). In the case of the present studies with indeterminate soybeans, memorized effects on the duration of the sub-phases R4–R5 (i.e. when responses

### Table 4. Yield components in soybean crops grown under natural photoperiods (T0) or subjected to long days after R3 stage for increasing durations (treatments T1 to T9) or exposed to long days from R3 until maturity (T10)

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Seed number (10^3 m^-2)</th>
<th>Number of nodes</th>
<th>Seed weight (mg seed^-1)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>(pod^-1) (node^-1)</td>
<td>in mainstem (plant^-1)</td>
<td>in branches (plant^-1)</td>
</tr>
<tr>
<td>T0</td>
<td>3.0 1.9 2.4</td>
<td>17.4</td>
<td>19.1</td>
</tr>
<tr>
<td>T1</td>
<td>3.1 1.9 2.5</td>
<td>16.1</td>
<td>22.0</td>
</tr>
<tr>
<td>T2</td>
<td>3.9 2.0 2.9</td>
<td>18.9</td>
<td>18.4</td>
</tr>
<tr>
<td>T3</td>
<td>3.6 2.0 2.7</td>
<td>18.4</td>
<td>24.0</td>
</tr>
<tr>
<td>T4</td>
<td>4.1 2.0 2.8</td>
<td>19.5</td>
<td>25.8</td>
</tr>
<tr>
<td>T5</td>
<td>3.7 2.0 2.7</td>
<td>20.3</td>
<td>31.9</td>
</tr>
<tr>
<td>T6</td>
<td>3.9 1.9 2.2</td>
<td>22.3</td>
<td>31.5</td>
</tr>
<tr>
<td>T7</td>
<td>4.8 1.9 2.7</td>
<td>22.1</td>
<td>32.2</td>
</tr>
<tr>
<td>T8</td>
<td>4.6 1.9 2.8</td>
<td>21.6</td>
<td>34.2</td>
</tr>
<tr>
<td>T9</td>
<td>5.3 1.9 2.8</td>
<td>23.4</td>
<td>29.5</td>
</tr>
<tr>
<td>T10</td>
<td>4.5 2.1 2.8</td>
<td>24.8</td>
<td>24.5</td>
</tr>
<tr>
<td>LSD</td>
<td>0.6 0.1 0.3</td>
<td>2.6</td>
<td>4.0</td>
</tr>
</tbody>
</table>

Least significance difference (LSD, P < 0.05) is included for comparisons between means of different treatments.

### Table 5. Yield components in soybean crops grown under natural photoperiods (T0) or subjected to 9 d of long photoperiods in different moments during the R3–R6 phase (treatments TA to TD)

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Seed number (10^3 m^-2)</th>
<th>Number of nodes</th>
<th>Seed weight (mg seed^-1)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>(pod^-1) (node^-1)</td>
<td>in mainstem (plant^-1)</td>
<td>in branches (plant^-1)</td>
</tr>
<tr>
<td>T0</td>
<td>2.6 1.9 2.3</td>
<td>16.2</td>
<td>22.8</td>
</tr>
<tr>
<td>TA</td>
<td>3.6 2.1 2.7</td>
<td>18.7</td>
<td>23.5</td>
</tr>
<tr>
<td>TB</td>
<td>3.6 1.9 2.6</td>
<td>18.9</td>
<td>25.8</td>
</tr>
<tr>
<td>TC</td>
<td>3.4 1.9 2.5</td>
<td>19.2</td>
<td>24.3</td>
</tr>
<tr>
<td>TD</td>
<td>3.6 2.0 2.5</td>
<td>16.7</td>
<td>27.4</td>
</tr>
<tr>
<td>LSD</td>
<td>0.6 0.2 0.2</td>
<td>1.0</td>
<td>3.2</td>
</tr>
</tbody>
</table>

Least significance difference (LSD, P < 0.05) is included for comparisons between means of different treatments.
were evident to treatments that ended before R4) and R5–R6 (i.e. for treatments that ended before R5) could be interpreted as long photoperiods controlling pod and seed growth from early stages of pod development and affecting seed enlargement before the beginning of the effective seed filling period (Egli, 1998). However, part of this memorized effect of photoperiod in delaying phenological stages in the present studies may also be linked to responses in node production. As mainstem nodes continued to appear for a longer period under increased exposure to long days (data not shown), it is feasible that the occurrence of R5 – described as the moment when seeds were 3 mm long in one of the four uppermost nodes (Fehr and Caviness, 1977) – had been recorded in different nodes than those where R4 was recorded, and not necessarily included a delay in the onset of growth of seeds at an individual node position. Studies describing progress of development at individual nodes in response to changes of photoperiod may bring to light the mechanisms underlying the delay in reproductive stages of development in response to both the current and the previous photoperiod.

Photoperiodic effects during post-flowering on node number have been reported in previous research (Kantolic and Slafer, 2001, 2005; Han et al., 2006). In the present studies, node number increased when the exposure to the long photoperiod began as late as 30 d after flowering, illustrating the large degree of responsiveness that can be expected in an indeterminate soybean of maturity group V. As the morphology of the apex was not observed, it is not possible to tell whether the long photoperiod delayed the moment when the terminal apex ceased to differentiate leaves and begun to develop floret primordia (Thomas and Raper, 1983; Caffaro et al., 1988) of whether flowering reversion occurred in response to the alteration of photoperiod (Wu et al., 2006).

Recent studies suggest that pod and seed set are related to the dynamics of flower production (Egli and Bruening, 2006). The continued production of nodes during flowering and pod set, especially in indeterminate cultivars, probably also plays a role in determining the total duration of flowering of soybean plants (Egli et al., 1985; Egli, 2005). In this context, the present results suggest that the response in node number to photoperiod may be an important component of the mechanisms involved in the increment of seed number by long photoperiods. One interesting response in expt 2 was found in TD, in which seed number increased despite a lack of response in the duration of R3–R6. This absence of a response in developmental rate is coincident with the lack of response in the number of nodes in the mainstem in this treatment. However, the plants were still responsive in secondary structures, as shown by the increments in nodes in branches. Branch development is usually delayed in relation with the mainstem development (Munier-Jolain et al., 1994) and the production of nodes and pods may continue when it has already finished in the mainstem. Describing the plants by taking into account the most usual scale (Fehr and Caviness, 1977),

### Table 6. Correlation coefficient (r) between the final number of seeds and the duration of the R3–R6 phase and the reproductive sub-phases included in it

<table>
<thead>
<tr>
<th>Independent variable</th>
<th>Expt 1</th>
<th>Expt 2</th>
<th>Both experiments</th>
</tr>
</thead>
<tbody>
<tr>
<td>Duration of R3–R4 (d)</td>
<td>0.86***</td>
<td>0.10ns</td>
<td>0.85***</td>
</tr>
<tr>
<td>Duration of R4–R5 (d)</td>
<td>0.63*</td>
<td>0.56m</td>
<td>0.63**</td>
</tr>
<tr>
<td>Duration of R5–R6 (d)</td>
<td>0.26m</td>
<td>0.17ns</td>
<td>0.17ns</td>
</tr>
<tr>
<td>Duration of R3–R6 (d)</td>
<td>0.83***</td>
<td>0.57m</td>
<td>0.85***</td>
</tr>
</tbody>
</table>

Results are presented separately for expts 1 and 2 as well as the data for both experiments together.

* , ** , *** Significant at the 0.05, 0.01 and 0.001 probability levels, respectively; ns, not significant.
that only considers development in the mainstem, fails to
describe the ability of the whole plant to respond to the
photoperiod.

Development responses during R3–R6 were highly
coupled with the production of seeds per unit land area
and this response was not affected by the timing of
exposure to long photoperiods. These results do not com-
pletely agree with those of Asumadu et al. (1998) who con-
cluded that the sensitivity of development to photoperiod in
a number of soybean isolines ended before the end of flow-
ering. In the present study sensitivity to photoperiod was
assessed analysing the moment of occurrence of phenologi-
ical events and responses such as node number and seed pro-
duction. The ability of the plants to perceive photoperiod
and modify their responses seems to remain throughout
the reproductive period although some different processes
may have different windows of sensitivity. From a pro-
ductive point of view it is important to have found that
the sensitivity, defined in terms of seed production per
unit land area, includes the whole critical period. It
allows the development of different agronomic strategies
that may combine cultivars and sowing dates to expose
different parts of the period to a long photoperiod.
Exploring genetic variability in these responses with iso-
lines similar to those assessed by Asumadu et al. (1998)
may help to predict the performance of different genotypes
in different natural photoperiodic environments.

A saturation of the response of seed number to the dur-
atation of R3–R6 was found to occur at approximately
twice the duration of this phase under natural conditions.
In previous experiments it had been found that extending
R3–R6 beyond a 50% increase, clearly reduced the
expected pod addition and growth because of radiation
and temperature constrains (Kantolic and Slafer, 2005).
The data of the present study reinforce the finding that a
lengthened critical period may well result in higher
yields, though an excessive duration of the phase will not
necessarily continue to increase seed number.

In coincidence with previous results from experiments
with manipulations of photoperiod until maturity
(Kantolic and Slafer, 2005), seed filling in plants of T10
took place under noticeably worse environmental con-
ditions than in the control and, under these circumstances,
seed weight tended to be reduced. In the rest of the treat-
ments, although seed growth was delayed and the length
of the R5–maturity phase was reduced, plants which had
been exposed to long photoperiods did not reduce seed
weight and yield was increased virtually in parallel with
changes in number of seeds per unit land area (Fig. 4).
This is an important result, considering that soybean seed
weight is generally source-limited (Egli, 1999; Borrás
et al., 2004) and an increase in seed number without
changes in crop photosynthesis should result in smaller
seeds, as source and sink are usually in balance (Egli and
Bruening, 2001). It has been proposed that the less induc-
tive photoperiod during reproductive phases increases
assimilate availability, as a longer duration results in
greater radiation interception and greater production of
assimilates (Kantolic and Slafer, 2005) and there is some
evidence in wheat to support this hypothesis (González
et al., 2005). If the photoperiod responses are mediating a
mechanism such that seed weight maintains high while
seed number is nearly doubled, manipulating sensitivity
to photoperiod during the critical pod formation phase
may be a means of improving the source:sink ratio
during the critical period, a very potent trait to further
increase soybean yields (Kumudini, 2002).

In conclusion, sensitivity to photoperiod remained high
during most post-flowering phases generating a quantitative
and continuous response to daylength. This response
included historic as well as current effects of photoperiod
and was highly and positively coupled with the processes
of generation of yield in a moderately photoperiodically
sensitive indeterminate soybean.

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