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Post-flowering photoperiod and radiation interaction in soybean yield determination: Direct and indirect photoperiodic effects

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ABSTRACT

Soybean (*Glycine max* (L.) Merrill) exposure to long days during the post-flowering phase increases total biomass, nodes, pods and seeds per plant, and also the post-flowering duration, increasing the radiation offer. This work aims to identify the main mechanisms responsible for yield increases in response to long days, separating direct photoperiodic effects on yield determination, from the indirect effect associated with changes in cumulative radiation when the crop cycle is modified by photoperiod. Two field experiments were conducted with an indeterminate soybean cultivar. A factorial combination of two radiation levels (unshaded and shaded), and two or three photoperiod regimes (control, extended 1.5 and 3 h) was imposed from flowering to maturity. Yield tended to be reduced by shade and increased by extended photoperiod mainly through their effects on nodes per m^2, and thereby affecting pods and seeds per m^2. Photoperiod extension increased node number due to both increased cumulative radiation (indirect effect) and delayed reproductive development (direct effect). As a result, more pods were established per unit of cumulative radiation under extended photoperiod. The results suggest that photoperiod extension enhanced yield radiation use efficiency due to the alleviation of intra-nodal interferences. The direct post-flowering photoperiodic effect on node number and the resultant effects on pod and seed number, provide evidence of direct photoperiodic effects on soybean yield determination.

1. Introduction

Soybean yield is mainly determined during the post-flowering phase (R1 stage onwards; Fehr and Caviness, 1977), throughout flowering, pod setting and seed filling (Board et al., 1995; Egli, 2010a; Jiang and Egli, 1993, 1995). During that period, often called 'critical period' due to its importance for yield determination (Egli, 1998), limitations in daily assimilate supply caused by shading, defoliation or water stress, reduce seed number per unit area, which is the main yield component (Egli and Yu, 1991; Jiang and Egli, 1995). As a consequence, a positive relationship between seed number or yield and plant or crop growth rate during post-flowering phases has been widely found in the literature (Board et al., 1995; De Bruin and Pedersen, 2009; Egli, 1998; Egli and Yu, 1991; Jiang and Egli, 1995).

Post-flowering photoperiodic effects on soybean seed number and yield have been previously proved evident in experiments that manipulated day length during different reproductive subphases using growth chambers (Board and Settimi, 1986; Cober et al., 1996), night interruptions (Cure et al., 1982; Guiamet and Nakayama, 1984a, 1984b; Morandi et al., 1988; Raper and Thomas, 1978; Thomas and Raper, 1976, 1983) and day length extensions (Han et al., 2006; Kantolic and Slafer, 2001, 2005, 2007; Kumudini et al., 2007). Previous studies found that long photoperiods during the post-flowering phase increase total biomass and nodes, pods and seeds per plant, irrespective of the experimental procedure applied to manipulate photoperiod (Guiamet and Nakayama, 1984a; Morandi et al., 1988; Kantolic and Slafer, 2001; Kantolic et al., 2013).

Abbreviations: iPAR, daily incident photosynthetically active radiation; PAR_{R1-R7}, cumulative photosynthetically active radiation intercepted during post-flowering; PAR_{VE-R6}, cumulative photosynthetically active radiation intercepted from emergence to full seed stage; $RUE_{Y,PAR}$, photosynthetically active radiation use efficiency to produce yield.

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Photoperiodic effects on soybean yield and its components are accompanied by the well-known developmental response to photoperiod during post-flowering (Guiamet and Nakayama, 1984b; Summerfield et al., 1998; Thomas and Raper, 1976). Long days delay reproductive development and physiological maturity, extending the post-flowering phase and the duration of the critical period. A positive relationship has been found between the duration of the critical period and yield (Dunphy et al., 1979) or seed number per unit area (Egli and Bruening, 2000; Kantolic and Slafer, 2001, 2005, 2007). Although the mechanisms controlling these relationships are not completely understood, the exposure of the plant community to a prolonged incident radiation offer should result in more growth during the phase when pods and seeds are produced (Kantolic and Slafer, 2005). Therefore, the post-flowering photoperiodic effect on yield could be an indirect effect associated only to the increase in cumulative incident radiation resulting from the extended post-flowering phase, as the direct environmental factor controlling yield would be the photosynthetically active radiation available for growth. However, Egli and Bruening (2000) had previously suggested that most of the benefit of the longer period should not come from simply exposing the plant community to more incident radiation and that both crop growth and phase length may have some independent effect on seed number.

An approach combining two radiation scenarios and contrasting photoperiods has shed some light on the comparison of these two environmental factors' effects on wheat yield (Gonzalez et al., 2005), and more recently on soybean (Kantolic et al., 2013). Kantolic et al. (2013) showed that seed number was closely related to radiation accumulated during pod setting (from stage R3 to R6; Fehr and Caviness, 1977), irrespective of the factor that increased cumulative radiation (higher daily radiation or longer phase duration). These results suggest that long photoperiod increased pods and seeds established per unit land area, mainly through increasing resource availability during part of a phase that is critical for yield determination. Nevertheless, more detailed observations revealed that photoperiodic and radiation effects were not alike at individual nodes: while shading reduced pod number in all plant positions, long photoperiod increased pods per node only in those nodes that flowered after treatment initiation (Kantolic et al., 2013). The authors suggest that long photoperiod failed to promote pod setting at nodes that flowered before treatment initiation (under short photoperiod) because some hierarchical relationships between pods might have already been established. This is relevant, given the fact that age-related interferences among pods within a node seem to be stronger than those among pods produced on different nodes (Egli and Bruening, 2002a, 2002b, 2006a, 2006b).

At the same time, long days or photoperiod extension induce other changes in plant development that may also be directly associated with yield increases. Pod number is related to the number of flowers (Egli, 2005; Jiang and Egli, 1993) and nodes (Egli, 2013). A long flowering period increases flower production and the duration of that period is under control of photoperiod (Guiamet and Nakayama, 1984b; Summerfield et al., 1998) and is rather independent of the assimilate availability (Dybing, 1994). Additionally, biomass partitioning to reproductive structures may be also altered by photoperiod (Cure et al., 1982; Raper and Thomas, 1978). All these effects, and perhaps some additional ones, can be considered "direct effects", as they require the perception of photoperiod and are, at least partially, independent of photosynthetically active radiation.

Mechanisms that increase yield in a way not related to cumulative radiation enhance the efficiency with which radiation is used to produce yield. Thus, identifying these mechanisms and understanding their interaction with other yield-forming traits is of great interest to increase crop yield potential. As soybean post-flowering photoperiod sensitivity is under control of a relatively low number of genes (Cober et al., 1996; Summerfield et al., 1998), direct post-flowering photoperiodic effects that increase yield could be traits that can be rapidly introduced in breeding programs.

In the present work we further analyse soybean yield determination in response to photoperiod extension under contrasting incident radiation scenarios to understand the interaction between photoperiod and radiation effects on yield when the whole post-flowering phase is lengthened. The objective of the present work was to identify the mechanisms responsible for increasing yield under extended photoperiod, separating indirect photoperiodic effects (i.e. those associated with the increase in cumulative radiation caused by the prolongation of the reproductive phase) from the direct effects (i.e. those independent of increases in cumulative radiation and dependent on photoperiod induced changes in crop structure and function).

2. Materials and methods

2.1. Culture

The commercial indeterminate soybean cultivar NA 5009 RG (Nidera Argentina) was grown under field conditions at the experimental field of the School of Agronomy, University of Buenos Aires (34°35′S, 58°29′W) during the 2008/09 (Exp1) and 2009/10 (Exp2) growing seasons. Sowing dates were January 25th and October 25th in Exp1 and Exp2, respectively. Seeds were inoculated with *Bradyrhizobium* liquid inoculant and sown at a high-planting rate in field plots. When the unifoliate leaves were expanded, the plots were hand-thinned to obtain a uniform plant population of 40 plants per m^2. Plots consisted of six rows, 2.5 m long, with 0.35 m row spacing. Weeds, pests and diseases were chemically controlled as needed following local agronomic practices. Rainfall was complemented throughout the crop cycle with a drip system. When necessary, plants were tied up to avoid lodging.

2.2. Treatments

Treatments consisted of the factorial combination of different shade and photoperiod levels applied from the beginning-bloom stage (R1, as described by Fehr and Caviness, 1977) to beginning-maturity stage (R7). In both experiments shading treatments were achieved by installing commercial shade nets (35% radiation reduction) over the plots to reduce canopy photosynthesis (called "shaded" throughout the text). The shade nets changed photosynthetic photon flux density without changing the spectral composition of light. Control plots were maintained without the shading nets ("unshaded"). In Exp1, two photoperiod treatments were imposed: (i) plots were either kept under natural photoperiod ("control") or (ii) exposed to artificially 3.0 h-extended photoperiod in relation to natural photoperiod ("3 h") (Kantolic and Slafer, 2001). In Exp2, an intermediate photoperiod treatment extended by 1.5 h in relation to natural photoperiod was added ("1.5 h"). To extend photoperiod in the field plots, portable lighting structures were used. Each structure combined incandescent and fluorescent lamps that provided an extremely low photosynthetic photon flux density (400–700 nm) of 4 $\mu mol\, m^{-2}\, s^{-1}$ (measured on top of the canopy using a LI-COR Inc. quantum sensor) and a red to far-red ratio of 1.17 (measured using a SKR 110 660/730 sensor, Skye Instruments Ltd.). Lights were automatically switched-on before sunset and switched-off at the required time depending on the length of extension. Lighting structures and shade nets were always kept 20–30 cm above the canopy.