PHASIC DEVELOPMENT AND PHYLLOCHRON RESPONSES TO EXTENDED PHOTOPERIODS AND SOWING DATE

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Abstract

Spring and late summer sowings of five sunflower genotypes (inbred lines and hybrids) were subjected to natural and extended photoperiods (E Ph) and the effects of these treatments on the duration of the emergence-floral initiation, floral initiation-bud visible and bud-visible anthesis phases monitored. Final leaf number, phyllochron and the duration of the interval between the appearance of the last leaf and anthesis (LLA) were also noted. In spring-sown crops, E Ph affected the duration of the floral initiation-bud visible phase, phyllochron, and LLA, as well as producing the well known shortening of the emergence-floral initiation phase in three of the five genotypes tested. Several of these responses were markedly altered in the summer sowing, indicating a strong time of sowing/photoperiod interaction. We conclude that simple models of sunflower development need to be improved by the incorporation of the hitherto unaccounted for effects of photoperiod on the duration of the floral initiation-bud visible phase, on phyllochron and on LLA. We also suggest that photoperiod responses in sunflower may have a temperature-dependent component.

Introduction

The most relevant environmental factors controlling crop development are temperature and photoperiod, and their relative significance depends on species or cultivar sensitivity to these factors during each developmental phase. Rawson and Hindmarsh (1982) found that sunflower behaves as a long-day (LDP) or day-neutral (DNP) plant in the emergence to floral initiation (E-FI) phase, and may exhibit short-day (SDP) or DNP responses from floral initiation to anthesis (FI-R5.1), determining an overall (E-R5.1) DNP or SDP response. Lack, in the literature, of detailed studies of photoperiod effects on developmental processes within each of the E-R5.1 subphases in sunflower led Villalobos et al. (1996, see also Sadras and Villalobos, 1993) to assume, in their sunflower crop model, that the crop exhibited a cultivar-

dependent LDP or DNP response in the E-FI phase, that later phases were insensitive to photoperiod, and that any effects of photoperiod on the FI-R5.1 phase were mediated by changes in the total number of leaves initiated at FI (a consequence of the thermal time duration of the E-FI phase). These authors further assumed that phyllochron was insensitive to photoperiod. Results obtained by de la Vega (2001) and Balbi (2002) and others in experiments involving the use of artificially extended photoperiods and summer sowings (in contrast to the usual spring sowing dates used in the central and southern sunflower cropping areas in Argentina) suggested that a re-examination of the species responses to photoperiod and the simplifications incorporated into the Villalobos et al. (1996) model (including that of a constant phyllochron) was needed.

Here we present the results of experiments directed at examining the effects of natural and artificially extended photoperiods on the phyllochron, final leaf number and the duration of E-FI, FI-R1 and R1-R5.1 phases of five selected sunflower genotypes sown in spring or summer. The selected genotypes were assumed to cover a range of known responses of sunflower to changes in sowing date (de la Vega, pers. comm.).

Materials and Methods

Field experiments were sown on February 25, 2000 (Balbi, 2002) and August 20, 2002, at Buenos Aires, Argentina (34º39'S). Two treatments were applied: natural (N Ph) and extended (E Ph) photoperiods (Figure 1), using a split-plot design with three replicates, with the photoperiod treatment as the main plot and the five sunflower genotypes as subplots. Photoperiod extensions were made using supplementary low intensity light provided by fluorescent tubes and incandescent lamps (between 20 and 40 μmol/m sq./s PAR, and a close to sunlight red/far red ratio of 1.15).

Apex development was followed by periodic harvests and dissection of apices, using the Marc and Palmer (1981) scale of floral stages (FS) to categorize apex status from floral initiation (FI = FS1.3) through the end of floret bract initiation (FS10, which coincides with the bud-visible stage [R.1 on the Schneiter and Miller (1981) scale]). Timing of FS1.3 was estimated by adjusting an inverse regression between FS and thermal time (degree C/day, base temperature 4C) after removal of all observations prior to the first observation of FS 1.3 and after the first observation of FS10. Leaf numbers (leaves longer than 4 cm) were counted on plants harvested for apex dissection. In the second experiment, and after bud-visible had been achieved, leaf number and further development of the crop were followed on six tagged plants per plot until the end of anthesis (R6). Final leaf number (FLN) was recorded in both experiments and in the second experiment the time interval between the appearance of the last leaf and first anthesis (LLA) was also registered for the tagged plants. Timing of 50% achievement of R1, R5.1, R6 and LLA in each plot was derived from these observations. Phyllochron values were estimated as the inverse of the slope of a linear regression fitted to the leaf number/thermal time from crop emergence relationship. Data for all leaves above Leaf 5 (cotyledons =0) were used for this purpose in the spring-sown experiment, and data for leaf number of plants harvested between FS1.3 and FS8 in the summer-sown experiment.

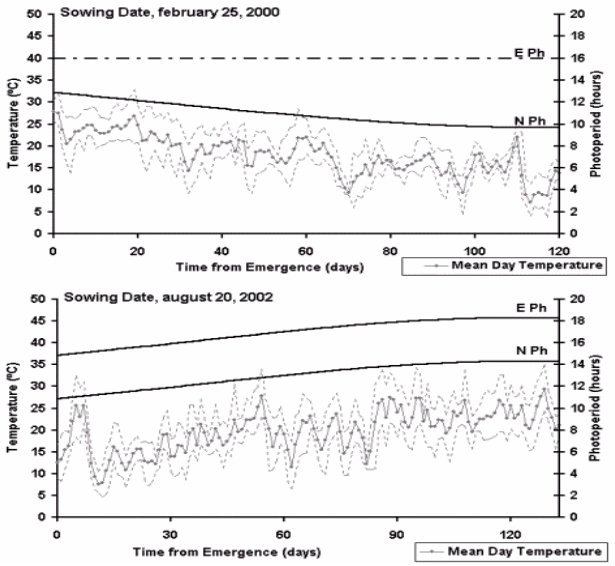

Figure 1. Temperature and photoperiod during the sowing to anthesis periods of both experiments (N Ph, natural photoperiod; E Ph, extended photoperiod). Top, sown in late summer (February 25, 2000) and bottom, sown in spring (August 20, 2002).

Air temperature was logged hourly with a Campbell automatic meteorological station located 10 m from the experimental field; and thermal time calculated using the cardinal temperatures of Villalobos and Ritchie (1992) (i.e., Tbase = 4C, Topt = 28C and Tmax = 40C). Statistical analyses were performed using the SAS software (SAS system for Windows 8.2).

Results

Phasic Development. The five sunflower genotypes studied here exhibited a variety of responses to treatment and sowing date across the developmental phases studied in these experiments (Figure 2). In spring sowing, four genotypes exhibited an LDP response for the duration of the E-FS1.3 phase, and the remaining one a DNP response. Thus, in this sowing, genotype behaviour was consistent with the findings of Rawson and Hindmarsh (1982). By contrast, in summer sowing there was no effect of photoperiod on the duration of this phase and, interestingly, the thermal time duration of the phase increased considerably in one genotype under E Ph. The duration of the FS1.3-R1 phase in the spring sowing was altered by E Ph in four out of five genotypes, and in three of these four the type of response was similar to that of the E-FS1.3 phase (Figure 2). In summer sowing, the response type for the FS1.3-FS8 phase was reversed (i.e., from LDP to SDP response) or became nonsignificant in three genotypes that had exhibited an LDP response to E Ph in the spring sowing. Taken as a whole, these results indicate that photoperiod and sowing date can affect the thermal time duration of post-floral initiation phases of development. The duration of the R1-R5.1 phase was only slightly, or not at all, modified by E Ph, and when this occurred the effect was in the same direction as that of the FS1.3-R1 phase duration (data not shown), with the exception of

Paraíso 20 in the late summer sowing. When the overall (E-R5.1) response was considered we found examples of SDP or DNP response types in late summer sowing and LDP or DNP in spring sowing, with Morgan734 and HA89 changing from an SDP response in late summer sowing to an LDP response in spring sowing (data not shown).

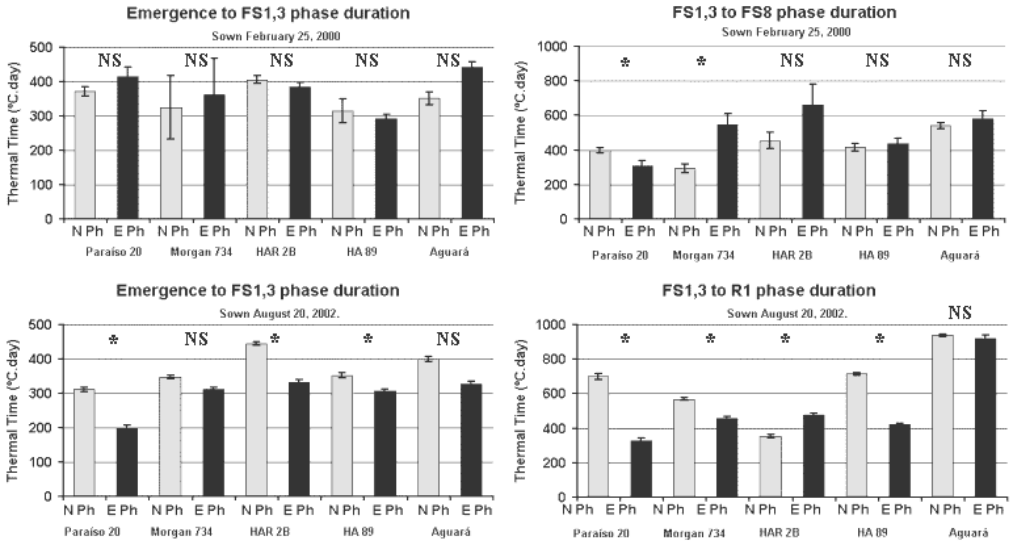

Figure 2. Contrasts, for five genotypes, between experiments sown in late summer (top) or spring (bottom), showing the thermal time intervals between emergence and floral initiation (left) and between floral initiation and bud-visible (R1) or FS8 (right). Grey columns represent the natural photoperiod (N Ph) treatment and the black columns the extended photoperiod (E Ph) treatment. Significant differences ($p < 0.05$) are indicated by the symbol *, and nonsignificant differences with NS.

Morphological Development. Final leaf number was significantly ($p < 0.05$) reduced under E Ph in two genotypes in the spring-sown experiment, and there was a tendency for FLN to change in the same direction in two others (Figure 3, top). In the late summer-sown experiment there was no significant ($p>0.1$) effect of E Ph on FLN. This overall response pattern is consistent with the effects of photoperiod and genotype on the duration of the E-FS1.3 phase (Figure 2), as a shorter E-FS1.3 phase should reduce the number of leaf primordia differentiated (e.g., Sadras and Villalobos, 1993).

In the spring-sown experiment we found no evidence of any change in phyllochron with level of leaf insertion for leaves above leaf five (cotyledons = 0), (data not shown), so mean phyllochron values are presented. Significant ($p<0,05$), and in the case of one genotype a very strong, reductions in phyllochron in response to E Ph were found in three genotypes of the spring-sown experiment, while in another genotype it increased (Fig. 3, middle). In the late summer-sown experiment E Ph increased phyllochron with, again, no evidence of change in phyllochron with level of leaf insertion (data not shown). This response of phyllochron to E Ph, sowing date and genotype differs from the insensitivity of this attribute to these factors that is often assumed (e.g. Sadras and Villalobos, 1993; Villalobos et al., 1996). Photoperiod effects on phyllochron were associated with changes in the duration of the FS1.3-R.1 phase in both experiments with the exception of Paraíso 20 when sown in late summer.

A further unexpected finding was that the duration of LLA in the spring-sown experiment varied among genotypes and could, in some genotypes, respond to photoperiod (Figure 3, bottom). Because the values of this variable can be quite important (minimum values are in the order of two to three phyllochrons), attention should be paid to it when modelling sunflower development.

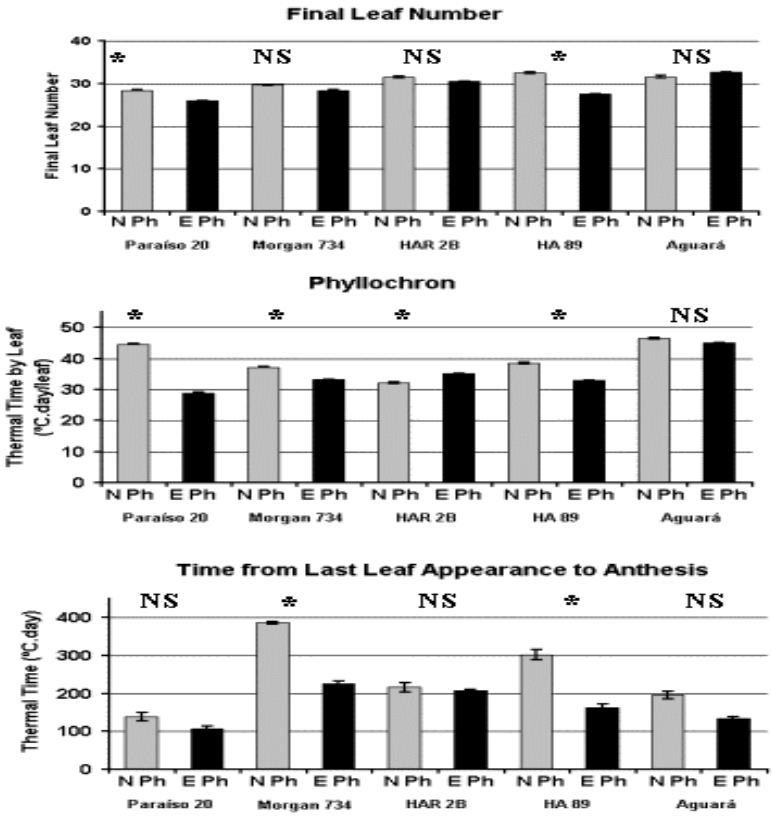

Figure 3. Responses to photoperiod of Final Leaf Number (top), Phyllochron for leaves above the fifth (middle), and the interval from the Appearance of the Last Leaf to Anthesis (bottom) for five spring-sown genotypes. Values for the last two variables are expressed as thermal time (degree C.day, Tb=4C). Grey columns are natural photoperiod (N Ph) and black ones are extended photoperiod (E Ph) treatments. Significant differences ($p<0.05$) are indicated by the symbol *, and nonsignificant differences with NS.

Discussion

The main findings of this work are that thermal time to anthesis in sunflower can be modified by photoperiod and sowing date due to their effects on: i) the duration of the FS1.3-R1 phase, in addition to the previously reported (Rawson and Hindmarsh, 1982) effects on the E-FS1.3 phase; ii) the value of the phyllochron; and iii) the duration of the interval between the appearance of the last leaf and anthesis.

In addition, our results show there can be a strong time of sowing/photoperiod interaction for some of these responses in some genotypes. Taken as a whole, these results

indicate the need for a complete overhaul of simple descriptive frameworks for sunflower development (e.g., Villalobos et al., 1996), which appear to be only approximately true for spring-sown sunflower, and even for those conditions do not incorporate photoperiod effects on either the duration of the FS1.3-R1 phase or on phyllochron, or on changes in LLA.

The fact that the phyllochron responses to photoperiod did not change above Leaf 5, and that photoperiod effects on the duration of E-FS1.3 and FS1.3-R1 tend to be in a common direction for each genotype, suggests that the nature of these responses is established early in development and then persists right up to the appearance of the last leaf.

The photoperiod/time of sowing interactions (Figure 2) for E-FS1.3 and FS1.3-R1 (or FS8) are specially interesting (and puzzling!), as they suggest that sowing date can alter the responsiveness to photoperiod or even (in the case of FS1.3-R1) produce a reversal in response type. It is not clear why this might be so, but an interaction of photoperiod response with temperature may be involved. In *Fragaria* (Guttridge, 1985), in *Linum usitatissimum* (Sorlino, 2002) and in *Arabidopsis thaliana* (Welch et al., 2003) it has been shown that low temperatures can change photoperiod responses qualitatively. Ongoing work in temperature-controlled glasshouses using the present set of sunflower genotypes has produced results which seem consistent with this explanation (data not shown).

Acknowledgements

This work was supported by ANPCyT (PICT 08-01493). RMD held a FONCyT Scholarship during this study. AJH is a member of the Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), the National Research Council of Argentina. Special thanks are due to AdlV for his recommendations on the genotypes used in these experiments.

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