Influence of ‘historic’ photoperiod during stem elongation on the number of fertile florets in wheat

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SUMMARY

Extending the duration of the late reproductive phase in wheat has been proposed as a possible avenue to improve spike fertility. There is a positive correlation between the number of fertile florets and the duration of the stem elongation phase when this phase is varied by extended photoperiod. Photoperiod treatments imposed during the vegetative period also influence the duration of stem elongation. The present study analysed the effect of long photoperiod (19 h) of different duration (10, 12, 14, 18 or 22 d) imposed before the onset of stem elongation on floret fertility in wheat. It was found that the length of the stem elongation phase was modified by earlier ‘historic’ photoperiod treatments imposed during previous phases. However, neither the number of fertile florets per spike nor the spikelet fertility was affected significantly by these historic treatments. The results of the study therefore showed that an increased duration of the late reproductive phase was ineffective in increasing the number of fertile florets, unless the length of that phase was directly altered by current photoperiod.

INTRODUCTION

Wheat plants produce a large number of floret primordia but only a small proportion survive and complete their development to produce a fertile floret (Langer & Hanif 1973; Miralles et al. 1998). The survival of floret primordia is critical as this process is a determinant of grain number per unit area, the most important yield component in wheat. The final number of fertile florets at anthesis has been clearly related to the amount of assimilate allocated to the spikes, either as a result of changes in crop growth rates during the pre-anthesis spike growth period (Fischer 1985; Thorne & Wood 1987; Savin & Slafer 1991; Abbate et al. 1995) or by changes in dry matter partitioning to the spikes (Siddique et al. 1989; Slafer & Andrade 1993; Miralles et al. 1998). Slafer & Rawson (1994) have speculated that modifying the length of the spike growth phase may produce similar changes in floret survival (i.e. the longer the phase the greater the survival and the number of fertile florets).

The fact that (i) photoperiod sensitivity can alter the duration of both vegetative and reproductive phases in wheat (Rawson 1970; Kernich et al. 1996; Slafer & Rawson 1996) and that (ii) a differential photoperiod sensitivity has been reported as development progresses (Slafer & Rawson 1996), suggests the possibility of independently selecting varieties which differ in the duration of different phases (Halloran & Pennell 1982). It also suggests that this could be achieved without changing flowering time (Slafer & Rawson 1996).

Miralles et al. (2000), in a phytotron study using reciprocally interchanged photoperiod treatments at the terminal spikelet stage, altered the duration of the stem elongation phase independently of the duration of the earlier phases. That study demonstrated that an increased duration of the late reproductive phase from terminal spikelet to anthesis in wheat resulted in more fertile florets per spike. Thus, when duration of the late reproductive phase was directly altered by the current photoperiod (treatments actually imposed during the spike growth phase) the number of fertile florets changed in parallel. Field studies have confirmed the phytotron studies (Slafer et al. 2001; Gonzalez et al. 2002). However, photoperiod effects

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on the duration of a particular phase are not restricted to those observed when the treatment is imposed. There may also be a ‘memorized’ or ‘historic’ effect on the duration of a particular phase produced by photoperiod changes occurring well before the onset of this phase (Slafers & Rawson 1995). Miralles et al. (2003) observed in plants grown in a phytotron and exposed to long days for different period of time that some of the treatments produced a clear effect on the duration of the terminal spikelet to anthesis phase without altering the previous phases, even though the treatments were always imposed before terminal spikelet (see Fig. 2 in Miralles et al. 2003). However, there is no evidence of the effect of photoperiod modifying the late reproductive phase on the number of fertile florets. That information would contribute to understanding whether the changes observed in the number of fertile florets due to manipulations of late reproductive phase are mediated by the duration of the phase or as a consequence of a direct effect of photoperiod.

The aim of the present study was to determine whether the duration of the late reproductive phase, when influenced exclusively by historic photoperiod acting during previous phases, affects the number of fertile florets per spike in the same way as when that phase is altered by a current photoperiod.

MATERIALS AND METHODS

A semi-dwarf bread wheat (Triticum aestivum L. cv. UQ 189) with strong photoperiod sensitivity but almost insensitive to vernalization was grown in naturally lit temperature- and photoperiod-regulated growth cabinets at CSIRO (Canberra). Cabinets were naturally lit for 9 h (between 08.00 and 17.00 h). Mean temperature in the growth cabinets was 13 °C achieved as a sinusoidal daily cycle between extremes of 17 (day) and 9 °C (night). Plants were supplied with complete Hoagland’s nutrient solution each morning and with water each afternoon. On 16 February 1998, two wheat seeds were sown per 100 × 150 mm pot, filled with an equiproportional mixture (by volume) of perlite and vermiculite.

In the original experiment (see Miralles et al. 2003) plants were grown at short photoperiod regime (9 h) for c. 20 days after sowing and then transferred to long photoperiods for 0, 2, 4, 8, 10, 12, 14, 18 or 22 days, before being returned to short photoperiod again where they remained until half of the plant population reached complete anthesis. Pots were regrouped each week to remove any positional and edge effects. Plants grown under long photoperiod were triplicated using three separate cabinets (each block consisted of one cabinet). Treatments were arranged in a randomized block design. In the present paper, only the treatments from 10 to 22 days are considered, as treatments shorter than 10 days had only a small effect on the duration of the terminal spikelet-anthesis period.

From seedling emergence to anthesis, plants were monitored regularly to determine the duration of different phenological phases (Zadocks et al. 1974). At anthesis the number of fertile florets (stage 10 in the scale proposed by Waddington et al. 1983) in the main stem of spikes was determined in five plants per block.

RESULTS

When plants were exposed to 10 or more days of long photoperiod 22 days after sowing the duration of the vegetative and early reproductive phases from seedling emergence to the onset of stem elongation was unaltered, as their photoperiod sensitivity was saturated. However, as the plants remained responsive to photoperiod, the late reproductive phase, from terminal spikelet to anthesis, exhibited a consistent shortening (Fig. 1) as plants were exposed to more cycles of long photoperiod. The shortening of the late reproductive phases was observed even though the terminal spikelet stage, and the onset of stem elongation, was reached well after the plants returned to the short photoperiod (even in the 22 long days exposure treatment).

With the exception of exposure to 10 long days in which plants initiated 12 leaves, in the rest of the treatments (exposures from 12 to 22 cycles of long photoperiod) plants initiated c. 10 leaves without any significant differences in this trait between the treatments (Fig. 1). The duration of the TS-AN phase in these same treatments varied by c. 40 days. Similarly, the number of spikelets per spike (fertile and total) did not show significant differences when plants received between 12 to 22 days of long photoperiod days (Fig. 2).
In the present study the duration of the TS-AN phase varied, as a consequence of the effects of historic photoperiod, to the same extent that was observed by Miralles et al. (2000) applying different photoperiod regimes directly during the time course of that phase (Fig. 3a). However, when the stem elongation phase was altered as a consequence of an historic photoperiod effect, the number of fertile florets was not affected by a reduction in the stem elongation phase (Fig. 3b).

**DISCUSSION**

In the present study, the complete variation observed in the stem elongation phase was a consequence of historic photoperiod effects experienced during the previous phases, as described earlier by Slafer & Rawson (1994, 1995) and quantified by Miralles & Richards (2000). Other studies (Jamieson et al. 1998) have developed the idea that the ‘historic’ photoperiod effects would operate only through modifications on the final leaf number. However, in this particular example, differences in length of the stem elongation phase produced by different photoperiod duration imposed before terminal spikelet appearance were not associated with changes in final leaf number. Therefore, the rate of leaf emergence seems to be a response to changes observed in the duration of the late reproductive phase (see Miralles et al. 2003).

Miralles et al. (2000) demonstrated that an increased duration of the late reproductive phase, due to sensitivity to current photoperiod effect in that phase, resulted in more fertile florets per spike. However, in the present study, with the stem elongation phase altered as a consequence of an historic photoperiod effect, the number of fertile florets was not modified. It is important to highlight that the range of variation in the duration of the stem elongation phase in the present study was similar to that observed in an independent study conducted by Miralles et al. (2000). Therefore, the results of the present study showed that changes in duration of the late reproductive phase only increase the number of fertile florets per spike in wheat, if the duration of that phase is directly altered by current photoperiod. This may mean either that photoperiod exerts a direct effect on the survival of floret primordia when imposed during the spike growth period as was reported by Gonzalez et al. (2003), or that the historic photoperiod effect alters the initial much more markedly than the last half of the stem elongation phase. This is possible as stems are growing rapidly during early stem elongation phase whereas the spike, although developing quickly, grows negligibly (Kirby 1988; Gonzalez et al. 2003). Therefore, a lack of effect on the number of fertile florets per spike might be related to a similar lack of effect on the growth of the spikes. Determination
of which the photoperiod genes (Ppd1, 2 or 3) act during the late reproductive phase, modifying the duration of that phase in response to actual photoperiod, could be a possible way for the breeder to change the relative duration of the reproductive and vegetative phases and thereby alter the number of fertile florets.

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