Earliness per se and its dependence upon temperature in diploid wheat lines differing in the major gene *Eps-A^m1* alleles

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SUMMARY

Differences in development among wheat cultivars are not only restricted to photoperiod and vernalization responses. When both requirements are fully satisfied differences may still arise due to earliness per se. It is not clear at present to what extent this trait is 'intrinsically' expressed (a constitutive trait) independently of the environmental conditions so that it might be selected under any thermal condition or if it may be altered to the extent of showing a crossover interaction with temperature in which the ranking of wheat genotypes may be altered. The present study assessed the influence of temperature on the intrinsic earliness for lines of diploid wheat characterized for their differences in a major gene for intrinsic earliness, but also possibly differing in their genetic background for other factors controlling this polygenic trait. To do so the lines were grown individually in two temperature regimes (16 and 23 °C) under long days having previously been fully vernalized. Multiple comparisons analyses were carried out among lines of the same allelic group for the *Eps-A^m1* gene. Results indicated that within each group there were lines that did not differ in their earliness per se, others differed but without exhibiting any line × temperature interaction and finally different types of interaction were shown, including cases where the ranking of lines was altered depending on the growing temperature. It is thus possible that the selection of a genotype based on its earliness per se in an environment might not represent the same performance in another location where temperature varied significantly.

INTRODUCTION

Differences in developmental patterns among wheats (*Triticum aestivum*, L.) are essential for improving adaptation (Slafer & Whitechurch 2001) and yield potential (Slafer *et al*. 1999). Understanding the genetic and physiological bases of these developmental patterns is critical for their rational use in breeding (either conventionally or assisted by molecular biology tools). In wheat the main environmental factors affecting development are photoperiod, vernalization

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and temperature (Pirasteh & Welsh 1980; Fischer 1984; Hay & Kirby 1991; Slafer & Rawson 1994). Major differences in time to heading among cultivars are ascribed to their responses to these factors. The largest differences are mainly attributed to different sensitivities to photoperiod and vernalization (Miralles & Slafer 1999). Consequently, both the genetics and physiology of these responses have been extensively studied in hexaploid wheat (Flood & Halloran 1986; Law 1987; Slafer & Rawson 1994; Worland 1996; Slafer & Whitechurch 2001; Snape *et al*. 2001). However, the differences between cultivars are not restricted by any means to these two sensitivities: even after all vernalization and photoperiod requirements are fully satisfied, there is still variation in time to heading (Slafer & Rawson 1994). These differences

in development between cultivars have been termed earliness per se or intrinsic earliness (Hoogendoorn 1985; Masle *et al.* 1989; Penrose *et al.* 1991; Worland *et al.* 1994; Slafer 1996), and both terms will be used interchangeably hereafter. Although it has been shown that there is a wealth of variation in earliness per se in different geographical regions of Europe or America (Worland *et al.* 1994; Appendino *et al.* 2003), there are several genetic and physiological aspects that remain unexplained for this trait. To gain a better understanding of these aspects may be instrumental in fine-tuning developmental patterns for a particular photoperiod and vernalization responsiveness.

As part of our lack of physiological knowledge of this trait (see Slafer 1996 for a detailed description of non-validated assumptions), it has not been clearly established to what degree the intrinsic earliness/lateness of a genotype is actually '*intrinsic*'. This means that we do not know whether it is a constitutive trait expressed independently of the environment (Hoogendoorn 1985; Worland *et al.* 1994) or if it can be modified by the growing temperature (Slafer & Rawson 1995*a*). Broadly speaking, there are two possible major types of genotype × temperature interaction: in one of them the magnitude of differences among cultivars would change with the thermal conditions, but their ranking in earliness would not be affected. The other case represents a cross-over interaction in which the ranking of genotypes may be altered. For instance, in the most extreme case, a genotype known to be 'intrinsically early' in a particular condition may become 'intrinsically late' in a different condition (Slafer 1996). Similarly, and again for the extreme cases of the possible interactions, a genetic factor conferring intrinsic earliness may be expressed as a genetic factor for intrinsic lateness in a different environment.

As the screenings for intrinsic earliness require to be conducted with full satisfaction of the photoperiod and vernalization requirements, they are mostly (virtually always) conducted under controlled conditions, in which for practical and economic reasons temperatures are substantially higher than those actually experienced in the field by the crop. In this context, it seems quite relevant to elucidate whether the growing temperature may alter the expression of intrinsic earliness in wheat.

Part of the lack of knowledge on the likely genotype × temperature interaction in intrinsic earliness may be due to the complexity of the hexaploid genome of bread wheat in which this trait has been mostly studied. Using simple, diploid wheat may help to better understand the nature of this interaction. Another reason may be the quantitative nature of the trait, with many genetic factors controlling it located on different chromosomes (Scarth & Law 1983; Miura & Worland 1994; Laurie *et al.* 1995; Suárez *et al.* 1995; Worland 1996; Kato *et al.* 1999; Snape *et al.* 2001; Bullrich *et al.* 2002). This evidences a complex genetic base for this trait. Analysing the genotype × temperature interaction for intrinsic earliness in a set of diploid lines built up to strongly differ in the constitution of one of these genes (but with variation among lines for the constitution of other possible intrinsic earliness genes) may provide material better suited to investigate to what degree the thermal condition of the growing plants may alter their intrinsic earliness.

In a previous study aimed to locate a particular vernalization gene (Dubcovsky *et al.* 1998), two genotypes of *Triticum monococcum* (the spring type DV92 and the winter type G3116) showed a behaviour suggesting they might strongly differ in their intrinsic earliness. The objectives of the present study were (i) to illustrate the actual difference in intrinsic earliness between two lines of *Triticum monococcum* known to strongly differ in their responsiveness to vernalization and (ii) to assess the influence of temperature on the intrinsic earliness for lines of diploid wheat characterized for their differences in a major gene for intrinsic earliness, but also differing in their genetic background for other factors controlling this polygenic trait.

MATERIALS AND METHODS

An initial experiment was conducted to elucidate whether the apparent differences between the two accessions of diploid wheat, *Triticum monococcum* DV92 and G3116, were in fact due to their differences in intrinsic earliness. One of the accessions, DV92, is a cultivated spring wheat that carries recessive alleles at the vernalization loci $vrn\text{-}A^m1$ and $vrn\text{-}A^m2$ (Dubcovsky *et al.* 1998) and the other, G3116, is a wild winter wheat that carries dominant $Vrn\text{-}A^m2$ and recessive $vrn\text{-}A^m1$ alleles (Dubcovsky *et al.* 1998).

Plants of these lines were grown in a glasshouse experiment (average temperature *c*. 20 °C) at the Department of Applied Biology, University of Buenos Aires, Argentina, under the factorial combination of two photoperiods and two vernalization treatments. Ten individual plants per cultivar for each combination of photoperiod and vernalization were grown. Vernalization treatments consisted of unvernalized controls and seedlings vernalized for 6 weeks at 10 °C in the dark. For this purpose, seeds of the unvernalized control were sown around the time when the seedlings of the vernalized treatment were already 5 weeks old in the vernalization room, and when both (vernalized and unvernalized seedlings) were at the same stage, individual plantlets were transplanted in mid June to pots 13·5 cm tall and 9 cm in diameter and distributed in the two photoperiod regimes. Photoperiods were either short days (8 h natural light) or continuous light (photoperiod extended to
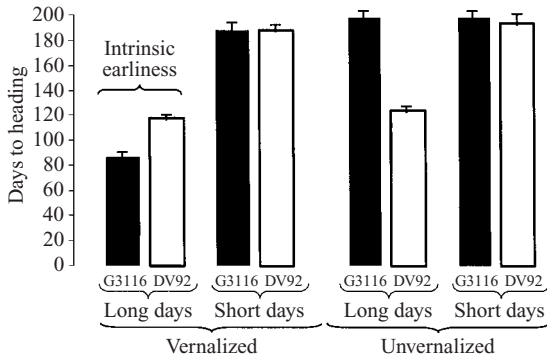
Fig. 1. Duration of time to heading in the two lines of *T. monococcum*, DV92 and G3116, grown under the factorial combination of two photoperiods (8 h natural photoperiod or continuous light) and two vernalization treatments (unvernalized or vernalized for 6 weeks at 10 °C). Time to heading under the most inductive conditions represents the intrinsic earliness for the thermal conditions of the study. Segments correspond to the standard error of the means.

24 h with incandescent lamps of low intensity) during the first 40 days after transplant. Pots were irrigated in order to avoid drought stress.

The second experiment was designed to study the genotype × temperature interaction on intrinsic earliness. Thirty-two single seed descendant (SSD) homozygous lines from the cross DV92 × G3116 were used, together with the parental lines, in the present study. These lines were previously evaluated to map a gene for earliness per se, *Eps-A^m1* (Bullrich *et al.* 2002).

The SSD lines included all possible combination of spring and winter types with the two alleles of the *Eps-A^m1* locus based on a linked RFLP marker (Bullrich *et al.* 2002). Among the spring SSD lines, six were *Eps-A^m1*-late and 10 were *Eps-A^m1*-early. Among the winter SSD lines five were *Eps-A^m1*-late and 11 were *Eps-A^m1*-early.

For each line 30 seedlings were fully vernalized by subjecting them, after seed imbibitions at room temperature, to vernalizing growing conditions: 5 °C for 8 weeks under short days. When fully vernalized, the seedlings of each line were transferred to growth chambers under continuous light at the Institute of Biological Resources, INTA, Buenos Aires. Half of the seedlings were grown at 16 °C and the other half at 23 °C. The pots, 13·5 cm tall and 9 cm in diameter, to which single plantlets were transplanted were arranged within each chamber in a completely randomized design.

The date of heading of each line was registered from daily inspections of the plants. Statistical analyses (Tukey *post-hoc* test for the variable mean days to heading) among lines with a same *Eps-A^m1* allele were made in order to detect the effect of
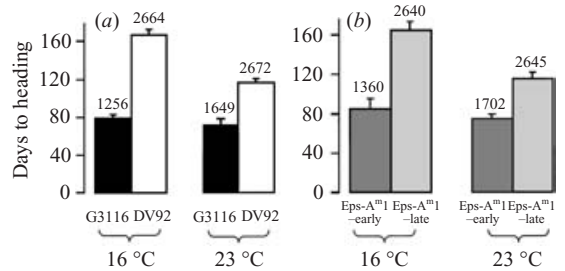

Fig. 2. Time to heading, of plants grown under either 16 or 23 °C in continuous light after being vernalized for 8 weeks at 5 °C. (*a*) the lines G3116 and DV92 of *T. monococcum*, and (*b*) the SSD lines carrying the allele *Eps-A^m1* for earliness or lateness (from G3116 and DV92, respectively). Figures on top of bars in (*a*) stand for the corresponding thermal time (see text). Segments correspond to the standard error of the means.

changing temperatures on other possible genetic factors in the background of the lines controlling earliness per se.

RESULTS

The first experiment not only confirmed the known response to vernalization of the spring (DV92) and winter (G3116) lines (Dubcovsky *et al.* 1998), but also demonstrated that time to heading differed in these lines by 30 days (equivalent to *c.* 600 °C; Fig. 1) when grown under long days after being vernalized. The demonstration that these lines do greatly differ in earliness per se confirmed their suitability as material for the study of the sensitivity to temperature of the intrinsic earliness of wheat.

No association was found with the genetic constitution of the lines for *Vrn-A^m1* and *Vrn-A^m2* loci and the individual performance of the lines among a class for *Eps-A^m1* allele. It must be also considered that the lines were fully vernalized so this interaction was independent of the winter or spring habit of the lines.

The effect of temperature on the different *Eps-A^m1* alleles was evidenced on heading date when growing conditions varied between 23 and 16 °C. At the warmest temperature, in agreement with the first experiment, both parental lines (DV92 and G3116) differed in time to heading by *c.* 40 days, but at the lowest temperature the difference was much larger, due to their differential sensitivity to temperature (Fig. 2*a*). All the derived SSD lines that carried the *Eps-A^m1* alleles from them followed the same general behaviour. Thus, lines possessing the early *Eps-A^m1* allele (from the winter parent, G3116) headed on average earlier than those possessing the late *Eps-A^m1* allele (from the spring parent, DV92) exhibiting the same interaction of *Eps-A^m1* genotype × temperature
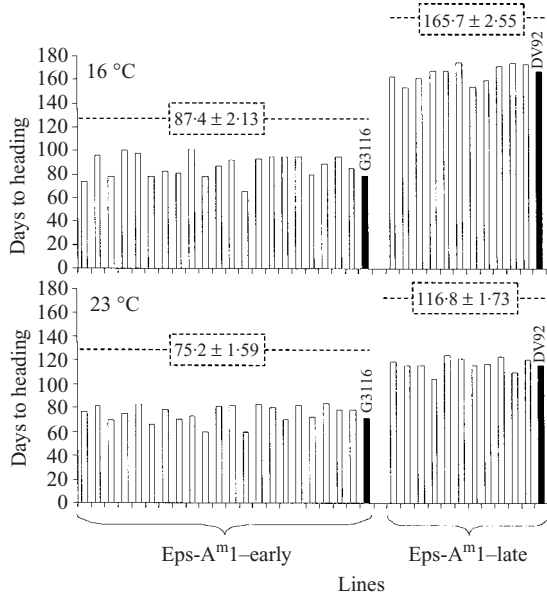
Fig. 3. Time to heading of F_6 homozygous SSD lines of *T. monococcum* derived from the cross between lines G3116 and DV92 grown at 16 (top panel) and 23 °C (bottom panel). The lines are separated for their allelic condition for the *Eps-A^{m}1* gene: the early allele is that belonging to G3116 and the late allele to DV92 (closed bars represent the parent lines). Figures on top of each group of lines stand for the average time to heading ($\pm$ S.E.M.) for those lines.

Fig. 4. Difference in time to heading between growing conditions at 16 and 23 °C of F_6 homozygous SSD lines of *T. monococcum* derived from the cross between lines G3116 and DV92. Figures on top of each group of lines stand for the average time to heading ($\pm$ S.E.M.) for those lines (for further details see caption of Fig. 3).

(Fig. 2*b*). Thermal time to heading was calculated for the parental and the recombinant lines. There was no difference between the mean values to heading of the 'intrinsically late' lines while thermal time to heading was significantly longer when the lines with the *Eps-A^{m}1*-early allele were grown at 23 than at 16 °C (Fig. 2).

Although the interaction was significant for the action of the major gene *Eps-A^{m}1* at different temperatures, the early allele was always significantly earlier at both temperatures than the late allele. However, the group of lines possessing the *Eps-A^{m}1*-early or the *Eps-A^{m}1*-late alleles, which exhibited a generalized similar behaviour, also differed significantly, though less markedly in intrinsic earliness (Fig. 3). The two groups of early and late *Eps-A^{m}1* alleles differed in time to heading, more markedly so at the lowest temperature. There was also variability within each group and the response to temperature also varied among lines of the same group. Consequently the variability in time to heading at one temperature did not mimic the behaviour of the lines at the other (Fig. 3).

Plotting the difference in time to heading between plants grown at 16 and at 23 °C clearly showed that minor Eps genes, acting in the genetic background

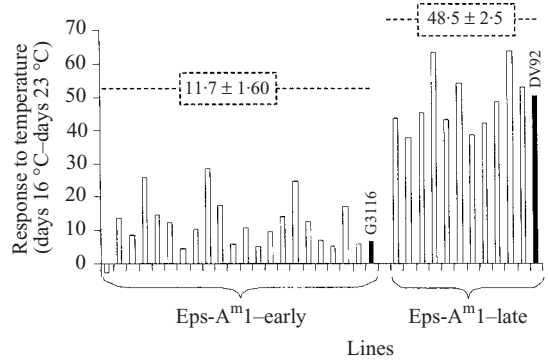within each group of lines with the same major *Eps-A^{m}1* allele, had differential sensitivity to temperature (Fig. 4). Within the group of SSD lines carrying the *Eps-A^{m}1*-early allele, responses to temperature regimes in this study ranged from negligible to 30 days, while responses to temperature within lines carrying the *Eps-A^{m}1*-late allele ranged from 35 and 65 days (Fig. 4). Lines within the same group of the major *Eps-A^{m}1* allele differed less than between groups (compare Fig. 2 and Fig. 3). The differential sensitivity to temperature of the minor Eps genes may well explain the differing rankings at different temperatures.

A Tukey *post-hoc* test was conducted on the variable mean days to heading, in order to contrast all early and late lines within each group. In the group of *Eps-A^{m}1* early lines, 65% of the overall comparisons were not significantly different at either temperature ($P < 0.05$%); 8% differed in their time to heading at the two temperatures but showed no significant line × temperature interactions and finally 27% of the overall comparisons among this early group showed line × temperature interaction in intrinsic earliness. In the late *Eps-A^{m}1* lines, 83% of the overall comparisons showed no significant differences in mean heading date at either temperature and 17% showed a line × temperature interaction.

More detailed comparisons can be made by choosing pairs of lines that showed the four possible combinations of the responses. For instance, no Eps × temperature interaction may be illustrated with the lines represented by the 5th and 6th bars (from left in Fig. 3) and consequently the differences in intrinsic earliness between these two lines remained unchanged by temperature (Fig. 5*a*). In contrast, significant changes in rankings between the two temperatures
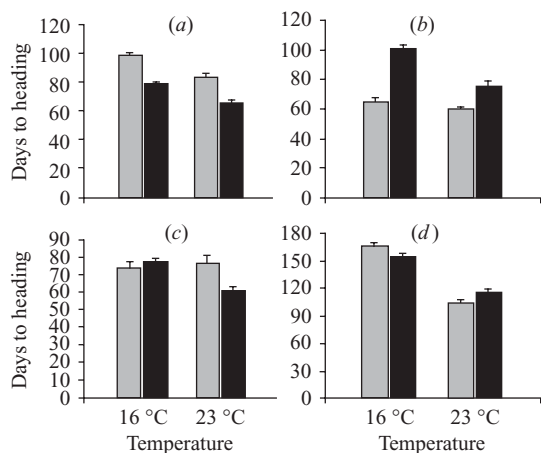
Fig. 5. Examples illustrating four types of interactions between comparisons of selected pairs of lines within the population studied. In all cases it is shown the time to heading at 16 and 23 °C when there was no interaction (*a*), or significant interactions in which the magnitude of the differences among lines was strongly affected but their ranking was either not altered (*b*) or altered so that the significant difference found at one temperature becomes not significant at the other one (*c*) or even the ranking is reversed significantly (*d*). Segments correspond to the standard error of the means.

(Fig. 5*d*) are illustrated by the lines represented by the 4th and 7th bars (from left) within the lines having the *Eps-A^{m}1*-late allele (Fig. 3). Intermediate cases can also be easily found provided there is a population with different minor Eps genes in their background (e.g. Fig. 5*b* and *c*).

DISCUSSION

The lack of association with the genetic constitution of the lines for *Vrn-A^{m}1* and *Vrn-A^{m}2* loci and their individual performance among a class for *Eps-A^{m}1* allele confirmed the hypothesis that these two traits are not linked and that it might be possible to combine any sensitivity to vernalization with any earliness per se; a fact that could be seen in Slafer (1996), where a re-analysis of data from Rahman (1980) and Davidson *et al.* (1985) illustrated that differences in intrinsic earliness between cultivars could be found in any combination with sensitivity to photoperiod or vernalization.

The different thermal times for the early and late lines showing no difference between the mean values to heading of the 'intrinsically late' lines and significant differences when the lines with the *Eps-A^{m}1*-early allele were grown at 23 or 16 °C probably implies a different optimum temperature for each allele of this

Eps-A^{m}1 gene; with the optimum temperature likely to be higher than 23 °C for the *Eps-A^{m}1*-late allele (and then thermal time estimated directly as the product of time by mean temperature being the same for both temperature regimes), while it must be lower than 23 °C for the *Eps-A^{m}1*-early allele (Fig. 2). Results from the literature support the hypothesis that genotypic variation for optimum temperature can be found and that a threshold value for temperatures optimizing the rate of crop development may be within the range of those used in the present study (Slafer & Rawson 1995*b*).

Although the temperature × genotype interaction was significant for the action of the major gene *Eps-A^{m}1*, the early allele was always significantly earlier at both temperatures than the late allele. However, the group of lines possessing the *Eps-A^{m}1*-early or the *Eps-A^{m}1*-late alleles which exhibited a generalized similar behaviour also differed significantly, though less markedly, in intrinsic earliness probably due to epistasis with other minor (and unidentified) Eps genes (Fig. 3).

Lines within the early or late group also have differences in their genetic backgrounds as a result of the genetic recombination between parental lines (DV92 and G3116) independently of their particular *Eps-A^{m}1* alleles, and comparisons of heading date between lines within the same *Eps-A^{m}1* allelic group do not necessarily imply the same allelic state for other, minor, Eps alleles. Clearly they differed in some genetic factors controlling earliness per se other than *Eps-A^{m}1*. This assumption is also sustained because some of the lines were earlier and others later than the parents (DV92 and G3116), indicating the possibility of a transgressive segregating genetic background (Fig. 3).

The influence of temperature is highlighted by the results of the present study, and may reflect different optimum temperatures for the different alleles of the *Eps-A^{m}1* gene. It is thus possible that the selection of a genotype based on its earliness per se in an environment might not represent the same performance in another environment (location, sowing date or year), which may be of paramount importance when deciding whether or not to select for this trait when a second generation is achieved in a year (e.g. off-season under thermal conditions markedly different to those of the targeted environments). However, it is evident for the population analysed here that the possibility of sustaining the ranking of heading date between two genotypes is reasonably high, for instance between the set of *Eps-A^{m}1*-early and late lines and particularly among a set of *Eps-A^{m}1* lines.

Based on the above assumptions, the use of precise genetic stocks can help in the detection of each minor or major factor controlling earliness per se. Molecular markers mapping these genes would be valuable tools to gather those alleles that consistently extend or

shorten the minimum time to heading in normal growing temperatures. This would give wheat breeding the possibility of more precise genotypic selection for this trait. As an example, the gathering of lateness alleles for the normal growing temperatures could be valuable to extend the time to heading mainly in photoperiod and vernalization insensitive cultivars, particularly at late sowing date.

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