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Field-based evaluation of vernalization requirement, photoperiod response and earliness *per se* in bread wheat (*Triticum aestivum* L.)

Markus Herndl [a,*], Jeffrey W. White [b], L.A. Hunt [c], Simone Graeff [a], Wilhelm Claupein [a]

[a] *Institute of Crop Production and Grassland Research (340), University of Hohenheim, Fruwirthstr. 23, D-70599 Stuttgart, Germany*

[b] *U.S. Arid Land Agricultural Research Center, USDA-ARS, 21881 N. Cardon Lane, Maricopa, AZ 85239, USA*

[c] *Department of Plant Agriculture, Crop Science Building, University of Guelph, Guelph, Ontario, Canada N1G 2W1*

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Abstract

Vernalization requirement, photoperiod response and earliness *per se* (EPS) of bread wheat cultivars are often determined using controlled environments. However, use of non-field conditions may reduce the applicability of results for predicting field performance as well as increase the cost of evaluations. This research was undertaken, therefore, to determine whether field experiments could replace controlled environment studies and provide accurate characterization of these three traits among winter wheat cultivars. Twenty-six cultivars were evaluated under field conditions using two natural photoperiod regimes (from different transplanting dates) and vernalization pre-treatments. Relative responses to vernalization (RRV_{GDD}) and photoperiod (RRP_{GDD}) were quantified using the reciprocal of thermal time to end of ear emergence, whereas earliness *per se* was estimated by calculating thermal time from seedling emergence until end of ear emergence for fully vernalized and lately planted material. An additional index based on final leaf numbers was also calculated to characterize response to vernalization (RRV_{FLN}). To test whether the obtained indices have predictive power, results were compared with cultivar parameters estimated for the CSM-Cropsim-CERES-Wheat model Version 4.0.2.0. For vernalization requirement, RRV_{GDD} was compared with the vernalization parameter P1V, for photoperiod (RRP_{GDD}), with P1D, and for earliness *per se*, EPS was compared with the sum of the component phase durations. Allowing for variation in EPS in the calibration improved the relation between observed versus simulated data substantially: correlations of RRP_{GDD} with P1D increased from $r^2 = .34$ ($p < .01$), to .82 ($p < .001$), and of RRV_{GDD} with P1V, from $r^2 = .88$ ($p < .001$), to .94 ($p < .001$). In comparisons of observed versus simulated anthesis dates for independent field experiments, the estimated model coefficients resulted in an r^2 of .98 ($p < .001$) and root mean square error of 1*d*. Overall, the results indicated that combining planting dates with vernalization pre-treatments can permit reliable, quantitative characterization of vernalization requirement, photoperiod response and EPS of wheat cultivars. Furthermore, emphasize the need for further study to clarify aspects that determine EPS, including whether measured EPS varies with temperature or other factors.
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Keywords: Earliness *per se*; Anthesis; Modeling; Photoperiod; Vernalization

1. Introduction

Cultivars of bread wheat (*Triticum aestivum* L.) vary considerably in when specific development stages and finally anthesis are attained. This variation is largely determined by groups of genes that affect requirement for vernalization (*Vrn* genes), sensitivity to photoperiod (*Ppd* genes) and earliness *per se* (*Eps* genes). The response to vernalization is mainly controlled by homologous genes located on the 5A, 5B and 5D chromosomes, namely *Vrn-A1*, *Vrn-B1*, *Vrn-D1* (Law et al., 1976; Worland et al., 1987). Genes primarily controlling sensitivity to photoperiod are *Ppd-A1*, *Ppd-B1* and *Ppd-D1*, located on group 2 chromosomes (Welsh et al., 1973; Law et al., 1978). A third proposed genetic factor influencing rate of development is earliness *per se* (EPS). The inheritance of EPS is less clear but involves the locus *Eps-2B*, located on chromosome 2B (Scarth and Law, 1983) and additional loci on the chromosomes 3A, 4A, 4B and 6B (Hoogendoorn, 1985; Miura and Worland, 1994). The effect of vernalization and photoperiod loci may vary with developmental stage (Slafer

Abbreviations: EPS, earliness *per se*; FLN, final leaf number; GDD, growing degree days; VD, vernalization days.

* Corresponding author. Tel.: +49 711 459 22372; fax: +49 711 459 24344.
E-mail address: m-herndl@uni-hohenheim.de (M. Herndl).

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and Rawson, 1994; Slafer and Whitechurch, 2001), and additional genes may modify the main temperature response of development (Slafer, 1996; van Beem et al., 2005).

Numerous reports have characterized vernalization requirement, photoperiod responses and EPS of cultivars in a semi-quantitative manner (Wall and Cartwright, 1974; Midmore, 1976; Davidson et al., 1985; Hoogendoorn, 1985; Miura and Worland, 1994; Ortiz-Ferrara et al., 1998). In most cases, durations (measured in calendar days or thermal time) from seedling emergence or transplanting to heading or anthesis were compared for different vernalization or photoperiod regimes. In some cases, however, the number of primordia that became leaves (FLN) were compared on plants exposed to different cold periods (Chujo, 1966; Hay and Kirby, 1991; Rawson et al., 1998). The data were generally obtained using controlled environments, which may reduce their quantitative reliability and applicability for predicting phenology under field conditions. Furthermore, the use of controlled environment chambers or glasshouses can increase costs of the evaluations.

Field testing is a promising alternative for characterization of vernalization requirement, photoperiod response and EPS, particularly if the results provide a reliable basis to predict phenology. Cultivar differences could be quantified by providing different pre-planting vernalization treatments and then testing the materials under two or more planting dates or locations that differ in photoperiod. In the absence of effects of vernalization and photoperiod, variation in heading or anthesis date would be driven by EPS. Under two different temperature and photoperiod regimes (e.g. from two planting dates), a close relation between observed times to a given growth stage should be observed for a series of genotypes being evaluated (Fig. 1). The same relation should hold for photoperiod insensitive genotypes grown in two environments providing different photoperiods. Photoperiod sensitivity would be evidenced by deviations from the EPS curve, showing slower development in the environment with shorter photoperiod (Fig. 1). Once

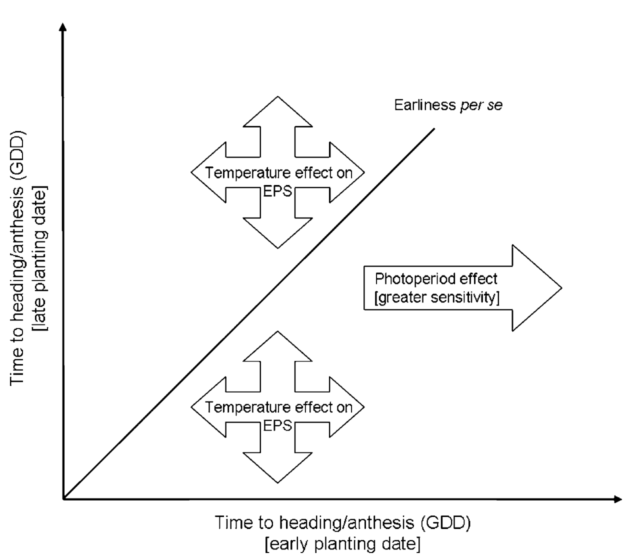

Fig. 1. Scheme of expected effects of photoperiod and temperature on wheat development for two planting dates assuming different photoperiod regimes.

photoperiod sensitivity and EPS have been estimated, vernalization requirements can be assessed by comparison with an unvernalized treatment, where the difference in phenology (expressed as a delay) indicates the vernalization requirement.

In practice, several constraints may reduce the accuracy of responses ascertained under field conditions. Under artificial conditions, an 18 h or 24 h photoperiod is often used with the objective of ensuring that the photoperiod requirement is fully satisfied (Flood and Halloran, 1984; Slafer and Rawson, 1995; van Beem et al., 2005). Under field conditions, natural daylengths at 50° latitude will not exceed 18 h (Košner and Pánková, 2002). EPS also may vary with temperature regime. van Beem et al. (2005) reported poor agreement in EPS for 51 wheats tested under two temperature regimes. Slafer (1996) reported that the optimum photoperiod could vary with developmental stage and between cultivars.

Processed-based wheat simulation models such as the Cropping Systems Model-Cropsim-CERES-Wheat (CSM; Jones et al., 2003) typically quantify the combined effects of temperature, including vernalization if it occurs, and photoperiod on phenology. Although the terminology and parameters considered vary among models, two major types of approaches can be recognized based on whether model equations focus on leaf or apical development (Jamieson et al., 2007). Regardless of which approach is used, a potential rate of development is assumed to be reduced by effects of incomplete vernalization, non-optimal temperatures (independent of the vernalization process), and sub-optimal photoperiods. Cultivar differences in phenology are represented through parameters for vernalization requirement, photoperiod sensitivity, and EPS. The EPS component is often difficult to identify because it is subdivided among developmental time requirements for phases such as from germination to seedling emergence and from double-ridge formation to anthesis. There are clear parallels between how vernalization requirement, photoperiod sensitivity and EPS are characterized in germplasm characterizations and in simulation models, but no attempts appear to have been made to integrate these two approaches in order to improve characterizations of germplasm.

The aim of this paper is to determine whether field experiments combining different vernalization regimes with planting dates can provide accurate characterization of vernalization response, photoperiodism and earliness *per se* among wheat cultivars. Accuracy is best judged through quantitative predictions of field performance, so CSM-Cropsim-CERES-Wheat was used to simulate cultivar differences in phenology as affected by cultivar, daily weather and field management.

2. Materials and methods

2.1. Cultivars

Nine winter wheat cultivars were selected according to their vernalization requirement and sensitivity to photoperiod (Table 1). Information about the response of the cultivars

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