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Use of Modeling to Characterize Phenology and Associated Traits Among Wheat Cultivars

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Abbreviations

ATT	Accumulated Thermal Time
CERES	Crop Environment Resource Synthesis
CIMMYT	International Maize and Wheat Improvement Centre
CSY	China Statistical Yearbook
DSSAT	Decision Support System Agrotechnology Transfer
EPS	Earliness *per se*
FAO	Food and Agriculture Organization of the United Nations
FLN	Final Leaf Number
GDD	Growing Degree Days
GPC	Grain Protein Content
ha	Hectar
IPCC	Intergovernmental Panel on Climate Change
IRTG	International Research Training Group
IWIS	International Wheat Information System
kg	Kilogram
m	Meter
N	Nitrogen
NNFI	Non-normed Fit Index
N_{min}	Soil Available Mineral Nitrogen
P_{123}	Earliness Factor Based on Model Parameters
RMSE	Root Mean Square Error
VD	Vernalization Days
WUE	Water Use Efficiency

1 General Introduction

1.1 The Importance of Predicting Wheat Phenology

Wheat (*Triticum* spp.) is cultivated throughout the major agro-climatic zones of the world and arguably, is found in a wider range of environments than any other crop (Nuttonson, 1955). To maximize yield potential in any environment, it is required that the wheat plant optimizes the use of resources such as water and radiant energy and avoids stress conditions during the growth cycle. The timing of the phases of the life cycle is therefore a priority for improving crop production, whether through breeding or crop management. Reasonable adjustments to the different phases can avoid e.g. winter damage from cold temperatures or escape drought and high temperatures in the summer months.

Understanding crop development (phenology) allows targeting of germplasm to specific environments. It reduces the risk of crop failure and enables an accurate timing of pesticides, fungicides and fertilizers (Hodges, 1991b). The ability to estimate the time required to pass through the stages of development is also important for accurate modeling of morphogenesis and yield components in wheat (Shaykewich, 1995). For the development of crop growth models, the understanding of timing of crop growth processes helps to predict physiological responses more realistic and allows targeting of inputs to ensure maximum production (Appleton and Haggar, 1985). Plant breeders are well aware that yield potential is affected by differences in the plant life cycle, and prediction of wheat phenology is important to them, too. To breed cultivars of wheat adapted to specific environmental conditions, it is fundamental that their life cycle is adjusted so that important developmental stages occur at the most appropriate times.

Change in global climate, especially to regional spatial temperature patterns from increased atmospheric concentrations of greenhous gases, is expected to have major consequences for crop production (IPCC, 2001). Since the start of the 20th century, the global mean temperature increased about 0.6°C (Nicholls et al., 1996). One effect is that springtime phenological events have become earlier by an average of 2.3 days per decade (Parmesan and Yohe, 2003). In Europe, warmer spring temperatures have advanced flowering dates of native trees by 4 days per °C (Fitter et al., 1995). For Asia, the rate of increase in growing-season length for crops was 4.5 d °C^{-1} (Zhang et al., 2004). Studies of the effect of changes in mean annual temperature on agricultural crops have advanced understanding of the effects of climate changes on wheat production (Houghton et al., 1996). Investigations from 1981 to 2001 at various locations in China found that

with increasing maximum and minimum temperatures wheat planting, anthesis and maturity dates became earlier and that yield decreased slightly (Tao et al., 2006). Another trend, examined over the 20th century, was the global increase of areas of excessive wetness or drought (Dai et al., 1998). In many wheat-growing regions, growth must occur between periods of heat or drought (Stapper and Harris, 1989). In Hungary, droughts have increased, whereas wet spells have decreased (Szinell et al., 1998). For China, an increasing area of droughts mainly caused by a decreasing mean precipitation has been observed (Ye, 1996). If the observed trends of global climate change continue, farmers, plant breeders as well as researchers must seek solutions to the arising problems. As a consequence, it is imperative to improve our ability to predict crop phenology in order to maximize wheat yield and maintain grain quality while protecting the environment.

1.1.1 The Importance of Predicting Wheat Phenology in China

After rice, wheat is the most important cereal crop in China, with a total farming area of around 22 million ha and a production in 2003 of 86 million t (CSY, 2004). Wheat cultivation in China extends over an ecologically diverse area from about 18° N to about 50° N, from below sea level to 4.000 m above sea level. Chinas wheat areas can be divided into ten major agro-ecological production zones that are based on wheat types, cultivar reactions to temperature, photoperiod, moisture, biotic and abiotic stresses, and wheat growing seasons (Jin, 1983; He and Chen, 1991; Figure 1). In the northern zones dry, hot winds in the late growth stages limit the growing season, but in other zones growing-season duration is mainly a function of the cropping system. Depending on the climatic conditions and the regional crop patterns wheat is part of many different cropping systems. The ellipses in Figure 1 indicate the regions within the wheat production zones where wheat is a main component of the predominant cropping system.
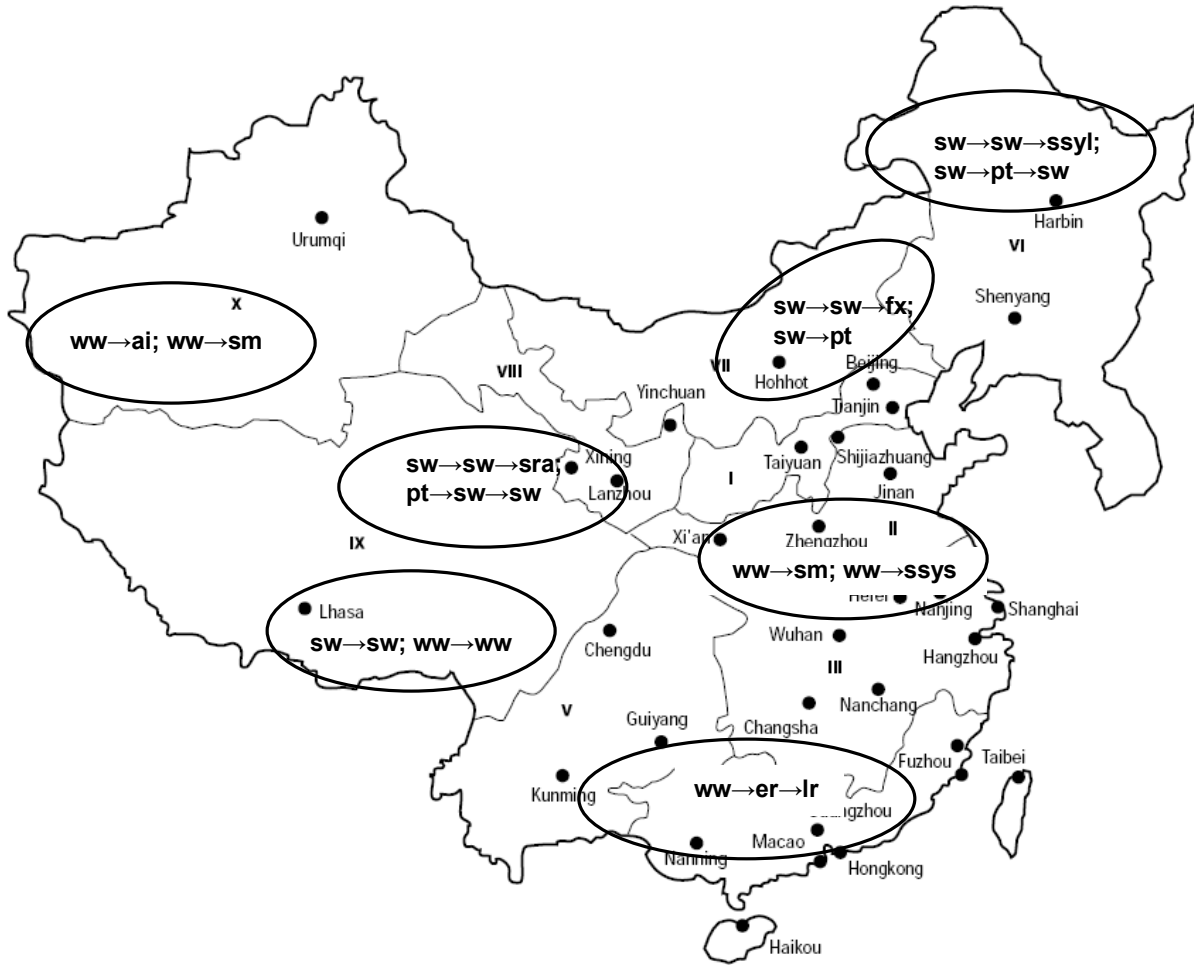
ai	alfalfa	pt	potato	ssys	summer soybean
er	early planted rice	sm	summer maize	sw	spring planted wheat
fx	lineseed	sra	spring rapeseed	ww	autumn planted wheat
lr	late planted rice	ssyl	spring soybean		

Figure 1. Wheat production zones of China. I Northern Winter Wheat Zone; II Yellow and Huai River Valleys Facultative Wheat Zone; III Middle and Low Yangtze Valleys Autumn-Sown Spring Wheat Zone; IV Southwestern Autumn-Sown Spring Wheat Zone; V Southern Autumn-Sown Spring Wheat Zone; VI Northeastern Spring Wheat Zone; VII Northern Spring Wheat Zone; VIII Northwestern Spring Wheat Zone; IX Qinghai-Tibetan Plateau Spring-Winter Wheat Zone; X Xinjiang Winter-Spring Wheat Zone. The ellipses indicate specific regions within the zones where wheat is part of the cropping system.

In Zone I and II mainly autumn planted facultative and winter habit wheats are cultivated which enable in many areas the winter wheat → summer maize or winter wheat → summer soybean cropping system. In Zone III, IV and V the climate is warm enough to plant spring wheat

in autumn which is a precondition for the winter wheat → early rice → late rice cropping system in a lot of areas. Cropping systems containing spring habit wheats such as spring wheat → potato, spring wheat → spring wheat → soybean or spring wheat → lineseed are often established due to dry climate and are practiced in some areas of Zones VI, VII, and VIII. Both spring and winter habit wheats are grown in some areas of zone IX and X, where winter wheat is cultivated before alfalfa, summer maize, after common pea and as monoculture. Spring wheat is grown before spring rapeseed or as monoculture (FAO, 1994).

The distribution of the cropping systems containing wheat all over China shows once again the excellent adaptability of wheat to a wide range of agro-climatic zones. The ability to adapt phenology offers wheat the opportunity to be a partner of many divers arable crops in the cropping systems. To maximize yield over a cropping system, knowledge about wheat phenology is indispensable. Chinese farmers need understanding of wheat phenology to adapt phenology to the demands of the cropping system by e.g. adjusting planting dates or using appropriate cultivars. For plant breeders knowledge about phenology helps to adjust wheat phenology in order to enhance total yield of improved or new cropping systems.

1.1.2 The Importance of Predicting Wheat Phenology in the North China Plain

The North China Plain (NCP) contributes 41% of the total wheat production and is the most important wheat growing region in China. The NCP is located in the eastern part of China between 114°-121°E and 32°- 40°N and includes the plains of Hebei Province, Beijing and Tianjin, and the northern parts of plains in Shandong and Henan Provinces. The climate is semi-arid, and water deficits occur mainly during spring. Irrigation is required in this period for winter wheat, which is cultivated with summer maize in the well established double cropping system. However, together with increased water use in urban areas, the extraction of groundwater for irrigation has led to a water shortage in many regions of the NCP (Kendy et al., 2003). To attain optimal and high wheat yields as requested by Chinese policy, while saving water, research has suggested multiple solutions. Recently, Binder et al. (in review) showed in a model based analysis of the cropping systems scenarios the considerable potential for reducing the irrigation amount while maintaining high yield by improving the irrigation schedule and by a reduction of irrigation applications to winter wheat from six to five or four times. A study of Zhang et al. (2005) indicated a serious capability to save water by using wheat cultivars that are optimized regarding

water use efficiency. The reduction of irrigation to save water by alternating the double cropping system to a single crop without high yield losses was investigated by Binder et al. (2007).

The increase of the average wheat yield per hectare of about 26 % in the last two decades is despite other changed factors like enhanced use of pesticides, machinery and improved varieties mainly caused by an increased amount of mineral N-fertilizer (Binder et al., 2007). The rate of application of N-fertilizers in the NCP has increased rapidly, up to around 200 kg N ha^{-1}(Cai et al., 2002). This raise led to an increase in yield during the last decades, but at the same time yield per unit mineral fertilizer decreased for wheat (Binder et al., 2007). The main reason for the reduced efficiency is high losses of nitrogen to the environment. Field studies of Zhang et al. (1992) and Cai et al. (1998) showed that the loss through ammonia volatilization was in the range of 1-9% of applied N for wheat, while the corresponding apparent denitrification loss was 13–29%. To reduce these nitrogen losses numerous studies proposed suggestions. Zhao et al. (2006) indicated that the optimized N-fertilization by an improved N_{min} method shows high potential of reducing nitrogen losses in the root zone. A placement of urea below the soil surface to reduce ammonia volatilization was suggested by Cai et al. (2002).

A key aspect for the specified approaches, both to save water and increase nitrogen fertilizer efficiency successfully in practice, is to match water and nitrogen supply with the phenology of the plant. The understanding of wheat phenology helps Chinese farmers to time the irrigation and N-fertilization accurately and to match N-application and irrigation to the actual water and N-demand of the plant. Furthermore, respecting the phenology supports them in adapting cropping systems according to the resources of the environment. Plant breeders benefit from understanding phenology because this improves their ability to adjust cultivars to constraints of target environments.

1.2 Phenology of Wheat

Phenology concerns the development, differentiation and initiation of organs (Hodges, 1991a). Lieth (1974) defined phenology as the study of the timing of biological events, the causes of their timing with regard to biotic and abiotic forces, and the interrelation among phases. The main abiotic factors affecting wheat phenology are temperature and photoperiod, although water and nutrient deficits also may have an affect (Penning de Vries et al., 1989). Biotic factors, in this context, means the genetic control of the physiological traits which interact with abiotic factors during development.

Numerous studies have described development stages for wheat and proposed formal scales for evaluating development (Bonnett, 1935; Haun, 1973; Zadoks et al., 1974; Kirby and Appleyard, 1984). The wheat plant in its growth from germination to physiological maturity passes through two main phases of development: the vegetative phase and the reproductive phase. In the first phase the stem remains short, leaf initials are produced by the growing point and tiller development occurs. Indicated by the appearance of double ridges (DR), axillary buds are first visible above leaf primordia, the beginning of the reproductive phase is marked. During the reproductive phase spikelet parts differentiate and increase in size and the internodes of the stem elongate. Terminal spikelet (TS) assigns that all spikelets have been initiated and the stem begins to elongate. Other important key markers of development are heading (Hd), when the head has completely emerged, but not yet started to flower, anthesis (At, flowering) and finally physiological maturity (PM, seed attains its maximum weight).

Various systems exist for describing wheat development through stages. The Zadoks system is most used (Zadoks et al., 1974). The stages in this system are easy to identify and are more detailed than in other systems. The first digit of this two-digit code refers to the principal stage of development beginning with germination (stage 0) and ending with kernel ripening (stage 9). The second digit between 0 and 9 subdivides each principal growth stage. For example, in seedling growth, the second digit refers to the number of emerged leaves. A scale that is mainly based on the Zadoks system and commonly used in Germany is the extended BBCH-scale (Hack et al., 1992). The abbreviation BBCH derives from the team that established this scale (Biologische Bundesanstalt, Bundessortenamt and the CHemical industry). The BBCH-scale allows the comparison of individual codes only within one principal growth stage: an arithmetically greater code indicates a plant at a later growth stage. The number of expanded leaves on the main shoot as a criterion of development was described by Haun (1973). The Feekes-large system (Large, 1954) is frequently used to identify optimum stages for chemical treatments and recognizes eleven major growth stages starting with seedling emergence and ending with grain ripening. During the last decades, it became less popular because it lacks the details of the Zadoks and Haun systems.

To show the effects of environmental and genetic factors on development, the approach of using an arbritary time scale and the apex as delimiter of phases is appropriate (Slafer and Rawson, 1994). Figure 2 shows in a simplified overview how development stages in this scale are defined and the general response of the phasic development of wheat to temperature *per se* (to

drive the growth and differentiation associated with development), low temperature (to satisfy the vernalization response) and photoperiod.
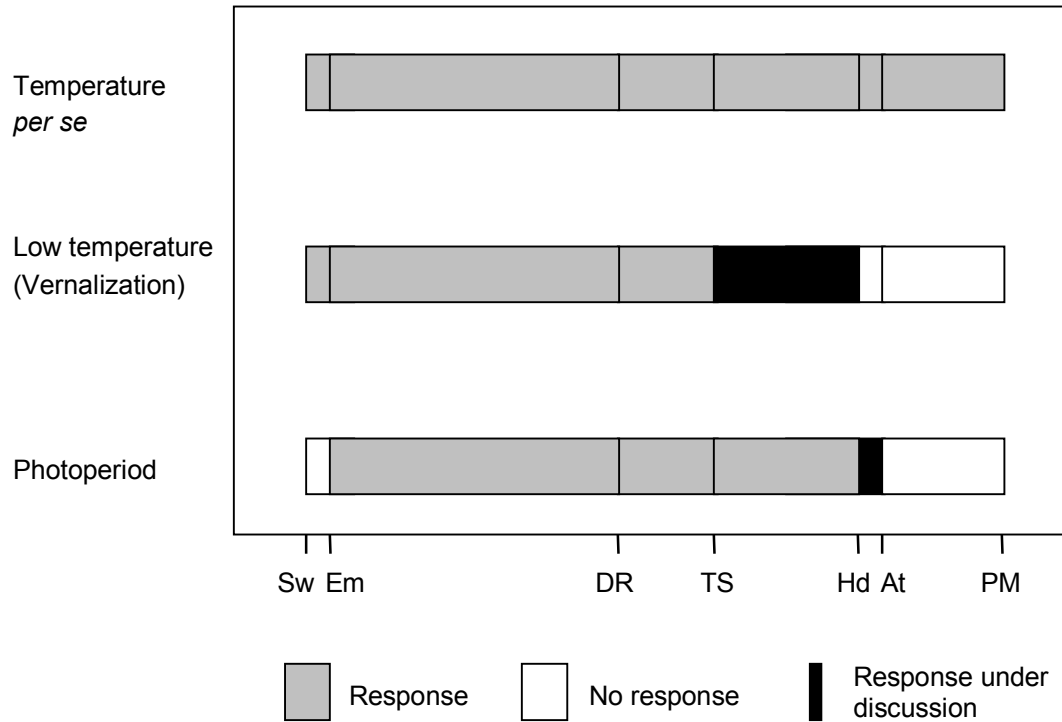
Figure 2. Schematic diagram of wheat development showing the stages of sowing (Sw), emergence (Em), first double ridge appearance (DR), terminal spikelet appearance (TS), heading (Hd), anthesis (At), physiological maturity (PM) and the response of phasic development to temperature *per se*, low temperature (vernalization) and photoperiod.

Numerous studies have indicated that photoperiod interacts with vernalization to determine the response of the plant to temperature, which is the basic driving force of development from emergence to anthesis (e.g. Safer and Rawson, 1994). The impact of these abiotic factors on rate of development is discussed in the following sections.

1.2.1 Abiotic Factors Influencing Wheat Development

Temperature

Temperature is the main abiotic factor determining rates of development because all metabolic processes are temperature sensitive (Midmore et al., 1982; Frank et al., 1987). In general, development accelerates with increasing termperature. Many authors have reported a nearly linear relation between rate of development (reciprocal of the development duration) and mean air temperature (Gallagher, 1979; Rickmann et al., 1983; Slaver and Savin, 1991). Ritchie and Ne Smith (1991) reviewed the effect of temperature on crop development. Below a base temperature (T_{base}), no development occurs. Above T_{base}, the rate of development increases up to the optimum temperature (T_{opt}). The optimum may mark the onset of a range of temperatures where the rate is constant and maximal (a plateau response) or the rate may decline immediately above T_{opt} (Salisbury and Ross, 1978). If a plateau is believed to occur, the optimum is usually defined as having two values (lower, T_{opt1}, and upper, T_{opt2}). Above a maximum temperature (T_{max}), development is assumed to cease. Often, T_{max} is not estimable because plant death occurs first. This suite of temperatures represents the cardinal temperatures for development. These may vary with growth stage as well as genotype. Furthermore, the values will differ depending on whether the time scale is daily or hourly (Frank et al., 1987; Ritchie and Ne Smith, 1991).

Temperature sensitivity of wheat varies between plant components and during the course of development (Slafer and Savin, 1991). In general, base and optimum temperature thresholds increase with development and wheat is more temperature sensitive during the reproductive phase and less sensitive during its vegetative phase (Figure 3; Entz and Fowler, 1988). The phase between sowing and emergence shows a high sensitivity to temperature. Angus et al. (1981) and Addae and Pearson (1992) found a linear relation between the rate of development and temperature with important cultivar differences. Investigations of development phases such as spikelet initiation phase (DR-TS), stem elongation phase (TS-At) and grain filling phase (beginn grain filling-PM) regarding response to temperature led to the conclusion that though genotypic variation occurs at any stage of development, the response to temperature is weaker in the spikelet initiation phase than in any other development phase (Slafter and Rawson, 1994).
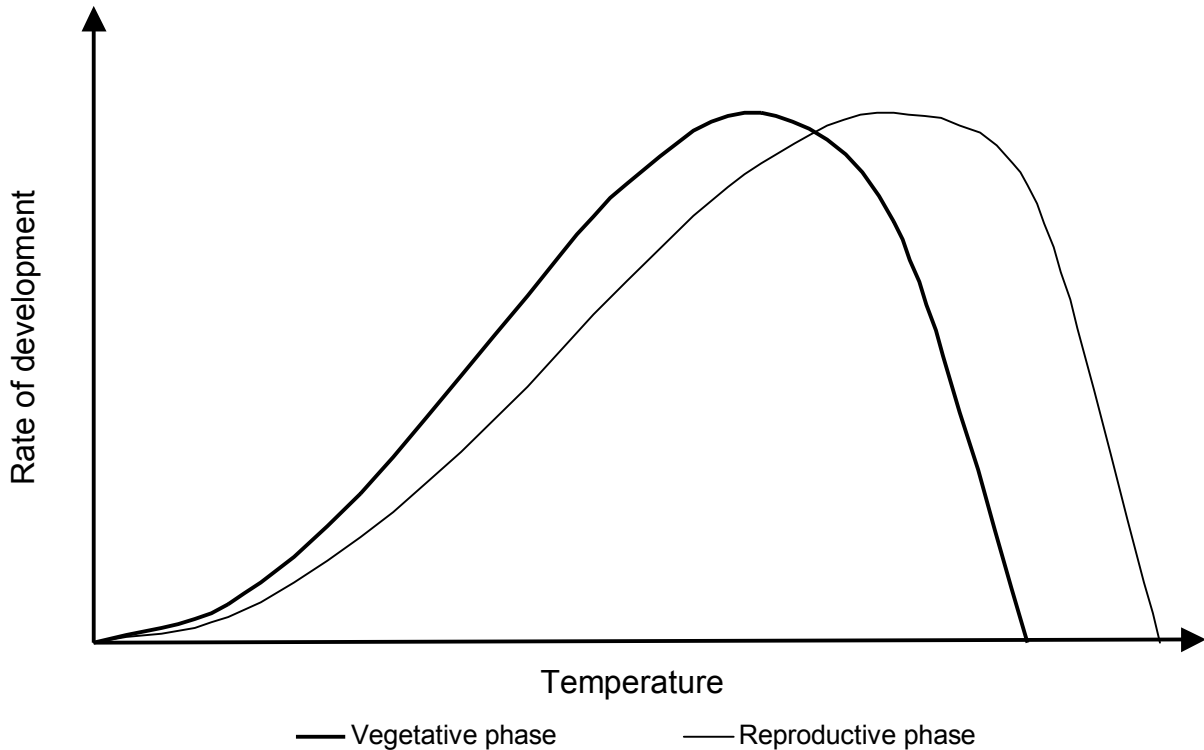
Figure 3. Schematic diagram of temperature response of development rate in vegetative and reproductive phase. Response functions according to Wang and Engel (1998). (Curve parameters: T_{base} vegetative phase/reproductive phase = 0°C; T_{opt} vegetative phase = 25°C, reproductive phase 30°C; T_{max} vegetative phase = 35°C, reproductive phase = 40°C).

In the phases beginning with germination and ending with floral initiation, wheat responds to exposure to low (nonfreezing) temperatures by increasing the rate of development. This cold requirement, called vernalization, must be met before spikelet formation can begin (Ritchie, 1991). Commonly, these assumption is accepted but there are studies where vernalization can affect rate of development beyond these phase. Griffiths and Lyndon (1985) found that the effect of vernalization was greatest up to double ridges, but that about 10% of the effect occurred from double ridge to ear emergence.

Spring wheats show a much lower response to vernalization, but there is also a wide range of senstitivity to vernalization among winter wheat cultivars (Rahman, 1980).

Photoperiod

Wheat is a long-day plant (Garner and Allard, 1923) as evidenced by the rate of development increasing under long photoperiods (Slafer and Rawson, 1996). While other species such as maize or sunflower have a juvenile phase (a phase where the plant cannot respond to photoperiod), wheat reportedly lacks a juvenile period and responds to photoperiod from seedling emergence to anthesis (Marcellos and Single, 1972; Kiniry et al., 1983; Villalobos et al., 1990).

Photoperiod mainly affects the rate of development in the early stages of wheat development whereas some authors showed contrary results. Studies of Rawson (1971) showed that the hastening effect of longer days was greater prior to double ridge stage than the hastening effect after double ridge stage. Studies of Allison and Daynard (1976) and Rahman and Wilson (1977) showed that the rate of development is mostly affected by photoperiod in the spikelet initiation phase (DR-TS), followed by the stem elongation phase (TS-At), and the vegetative phase (Em-DR).

Various functions have been used to describe the effect of photoperiod on developmental rate. Similar to the thermal time accumulation, there are parameters affecting the response. Major (1980) and Slafer and Rawson (1995) proposed that the slope between P_o (optimum photoperiod) and P_c (critical photoperiod) is the photoperiodic sensitivity. Most cultivars delay their development until lengthening days (photoperiod sensitive cultivars), though some cultivars behave as a short-long day plants (photoperiod insensitive cultivars; Evans, 1987).

According to Slafer and Rawson (1996) rate of development in all vegetative phenophases is modified by temperature, photoperiod, cultivar and their interactions. An interaction of photoperiod and temperature was also reported by Cao and Moss (1989b). A recent study of genetic control of flowering in wheat suggested that photoperiod may interact with vernalization (Trevaskis et al., 2007).

1.2.2 Genetic Factors Influencing Wheat Development

Genotypic variation in wheat development is mainly determined by groups of genes that affect sensitivity to requirement for vernalization (*Vrn* genes), photoperiod (*Ppd* genes), and earliness *per se* (*Eps* genes).

Vernalization

In general, regarding vernalization requirement wheat can be subdivided into winter types, where vernalization is required to promote flowering and spring types, which do less or not (Snape, 2001). The response to vernalization is mainly controlled by homologous loci located on the 5A, 5B and 5D chromosomes, namely *Vrn-A1* (formerly *VRN1*), *Vrn-B1* (formerly *VRN2*), *Vrn-D1* (formerly *VRN3*; Law et al., 1976; Worland et al., 1987). In addition to these major vernalization loci, loci with minor effects have been reported on chromosome 7B (*Vrn-B4*; Law, 1966). Recently, Trevaskis et al. (2007) reported that these loci have shown to regulate not only the vernalization response but also the promotion of flowering by long days. *Vrn-A1* accelerates the transition to reproductive development at the shoot apex and is induced by vernalization. *Vrn-B1* integrates vernalization and day-length responses by repressing *Vrn-D1* until plants are vernalized. *Vrn-D1* is induced by long days and further accelerates reproductive apex development.

If the allele at a *Vrn* locus is dominant, the vernalization requirement is greatly reduced but not eliminated. Studies of Snape et al. (1976) showed that the *Vrn-A1* locus is predominant in reducing the vernalization requirement. Adjusting this allele allows to design facultative, spring or winter wheat.

Photoperiod

Three homologous loci located on group 2 chromosomes, *Ppd-A1* (formerly PPD3), *Ppd-B1* (formerly PPD2) and *Ppd-D1* (formerly PPD1), determine photoperiod sensitivity (Welsh et al., 1973; Law, 1978), with the dominant alleles reducing sensitivity. Field studies by Worland and Sayers (1996) have shown that *Ppd-D1* and *Ppd-B1* are important in accelerating or delaying flowering time in spring after vernalization requirement has been satisfied. Most modern European wheat varieties have low daylength sensitivity because they carry the dominant allele of *Ppd-D1* (Worland and Sayers, 1996). A study conducted in the major wheat growing regions in

Europe showed that *Ppd-D1* reduced flowering time by 6-14 days, depending on season (Worland and Sayers, 1995). Photoperiod sensitivity (allele at the *Ppd* locus recessive) means that floral initiation is delayed until lengthening days satisfy their photoperiod requirements (Worland and Sayers, 1996)

Earliness per se

Wheat plants do not flower immediately after they emerge from soil, even when they are grown under temperature and photoperiod conditions that allow a maximal rate of development up to flowering. The so called basic development rate is the rate of development towards flowering as measured when the responses to photoperiod and vernalisation are removed (i.e. under very long photoperiod and after long vernalisation duration (Major, 1980; Flood and Halloran, 1984). The reciprocal of the basic development rate is the total duration of phases up to anthesis, if vernalization and photoperiod requirements are fully satisfied, and is commonly termed 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), as well as other loci (Miura and Worland, 1994). The effect of these loci may vary with developmental stage (Slafer 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).

1.2.3 Leaf Development in Wheat

The interval between seedling emergence to anthesis is closely related to the interval between initiation of leaf primordia (plastochron) and the interval between the appearance of two successive leaves (phyllochron; Kiniry et al., 1991). With increasing temperature above T_{base}, both the plastochron and phyllochron decrease until T_{opt} is attained. For wheat, plastochron and phyllochron indicated the base temperature is 0°C and the optimum 15°C (Kirby, 1985; Baker et al., 1986). Observed phyllochron intervals range from 50 growing degree days (GDD) for a spring wheat to 125 GDD for an early planted winter wheat (Rickman and Klepper, 1991). Double ridge stage will occur for winter wheat about one phyllochron after single ridge and jointing about two phyllochrons later. Development stages later than jointing are dependent upon the flag leaf number. Anthesis is expected from the completion of heading to about one half of one phyllochron after heading stage (Rickmann and Klepper, 1991). Some researchers found that

phyllochron was not constant throughout crop development and therefore affected by environmental conditions (Peterson et al., 1989; Hunt and Chapleau, 1986; Cao and Moss, 1989a). Other authors reported a constant phyllochron interval during crop development fixed by environmental conditions at seedling emergence (Kirby and Perry, 1987; Bauer et al., 1984).

However, to determine the duration of the leaf growth period, final leaf number produced on the main stem (FLN) must be counted. FLN ranges for field grown wheat from five to over 14 depending on genotype and environmental conditions (Kirby and Perry, 1987; Stapper and Fischer, 1990). Baker et al. (1980) examined a correlation between rate of change of daylength and rate of leaf emergence at the time of emergence of the first leaf. Increasing the duration of vernalization decreases the number of primordia that become leaves i.e. a decrease of FLN for responsive varieties (Berry et al., 1980). To take FLN as a rate to quantify genetic variability in vernalization response is still under debate, but had relevance in a lot of studies (e.g. Rawson et al., 1998).

1.3 Modeling Phenology

Any crop growth model that considers partitioning to different organs over time must consider the timing of crop growth processes. Accurate prediction of phenology is essential to the prediction of physiological responses under varying conditions and without accurate prediction of growth stages, the model will simulate growth processes occurring at different times than they actually do (Hodges, 1991b).

Attempts to predict phenology date back to the 18th century (Shaykewich, 1995). Using temperature sums instead of calendar days to quantify the time required for plants to complete a development stage was suggested by Reaumur (1735). This approach is rather simple, but in principle it is included in most models estimating phenological development.

The basis of every phenological model is mathematical algorithms that describe variation in rates of development over time. For wheat, various equations have been used to describe the interaction of environmental factors and physiological traits during phenological development, especially toward flowering (Ritchie et al., 1991; Wang and Engel, 1998).

Current wheat simulation models use different combinations of algorithms to describe the environmental influence on progress toward flowering. CERES-Wheat (Ritchie, 1991) calculates daily vernalization and photoperiod response from emergence until terminal spikelet and adjusts the daily flowering progress based on the least favourable factor. AFRCWHEAT (Weir et al.,

1984) modifies thermal time from emergence to double ridge by a factor derived from the multiplication of daily vernalization and photoperiod effects. Between double ridge and heading, only photoperiod response is considered to affect progress towards flowering (Weir et al, 1984). Other models only use vernalization degree-days (Craigon et al., 1995) or photoperiod response (Miglietta, 1991) to predict development rate prior to heading but do not combine these two processes.

1.3.1 Factors Affecting Phasic Development in Cropsim-CERES-Wheat

Cropsim-CERES-Wheat is a simulation model for wheat growth and is mainly based on CERES-Wheat (Ritchie, 1991), but as in the CROPSIM-wheat model (Hunt and Pararajasingham, 1995) most variables are extracted and placed in external files. The plant growth module of Cropsim-CERES-Wheat is used in the Cropping Systems Model (Jones et al., 2003) which is incorporated in DSSAT 4.0 (Hoogenboom et al., 2004a).

In Cropsim-CERES-Wheat, nine growth stages are defined (Hoogenboom et al., 2004a). Vegetative growth occurs in the first four stages, whereas grain filling and time from physiological maturity to harvest of crop are represented through stages five and six (Table 1).

Table 1. Growth stages of wheat as defined in CSM-Cropsim-CERES-Wheat model version 4.0.2.0 (Hoogenboom et al., 2004a).

Stage	Event	Plant Parts Growing
1	Emergence to terminal spikelet initiation	Roots, leaves
2	Terminal spikelet to end of leaf growth and beginning of ear growth	Roots, leaves, stems
3	End of leaf growth and beginning of ear growth to end of pre-anthesis ear growth	Roots, leaves, ear
4	End of pre-anthesis ear growth to beginning of grain filling	Roots, stems
5	Grain filling	Roots, stems, grain
6	End of grain filling to harvest	-
7	Fallow or presowing	-
8	Sowing to germination	-
9	Germination to emergence	Roots, coleoptile

A growth stage in the simulation is reached when the accumulation of thermal development units (TDU) attains pre-determined levels as specified by ecotype or genotype coefficients. The rate of development during the whole plant life cycle is assumed to vary with temperature *per se* and is modified by vernalization and photoperiod during the period from seedling emergence to terminal spikelet.

Temperature

On the basis of daily thermal time units (DTT), which are computed from daily maximum, minimum air temperatures and cardinal temperatures, the progress through growth stages is driven. Cardinal temperatures recognized in the model are: base temperature (T_{base}), a lower optimum temperature (T_{opt1}), an upper optimum (T_{opt2}), and a maximum temperature (T_{max}) above which development terminates. In Cropsim-CERES-Wheat, the values of the cardinal temperatures depend on the process and the growth stage that is simulated and are specified in the species file (Table 2).

Table 2. Temperature response (°C) of simulated processes in CSM-Cropsim-CERES-Wheat model version 4.0.2.0. Cardinal temperature recognized in the model: Base temperature (T_{base}), lower optimum temperature (T_{opt1}), upper optimum (T_{opt2}), and maximum temperature (T_{max}).

	Develop-ment 1[a]	Develop-ment 2[b]	Leaf growth	Photo-synthesis	Vernali-zation	Lethal temperature hardening	Grain filling, dry weight	Grain filling, nitrogen	Grain number
T_{base}	0	0	0	0	-5	-5	0	0	0
T_{opt1}	26	30	10	10	0	0	16	16	16
T_{opt2}	50	50	20	25	7	5	35	35	35
T_{max}	60	60	35	35	15	10	45	45	45

[a] pre-grain filling period

[b] grain filling period

Vernalization

To account for the effect of vernalization on the rate of development, a vernalization factor is used. It is the relative development rate when unvernalized, plus the ratio of the accumulated vernalization-days to required vernalization-days (P1V). P1V is the cultivar specific coefficient that considers the genetic variability in sensitivity to vernalization. By expressing the differences

in vernalization through this coefficient, cultivars which have a low sensitivity to vernalization (spring wheat cultivars) and winter wheat cultivars can be incorporated in a single model. Vernalization in the model is assumed to occur between –5°C to 15°C and can be reversed if maximum air temperature is higher than 30°C.

Photoperiod

In the period from seedling emergence to terminal spikelet, photoperiod is also assumed to affect the rate of development. The determining parameter is daylength or civil twilight which is computed from day of the year and latitude and is referenced to when the sun is 6° below the horizon. Photoperiods shorter than 20 h slow the rate of development through a day-length factor that decreases from 1 to 0 as photoperiods shorten. The delay depends on the photoperiod sensitivity of the cultivar being used, which is expressed in the cultivar specific coefficient P1D.

Earliness per se

Variation in earliness *per se* is accounted for by the sum of three parameters: P1 (duration of phase end juvenile to double ridges), P2 (duration of phase double ridges to end leaf growth) and P3 (duration of phase end leaf growth to end spike growth). The parameters are presented in the CSM ecotype file, implying that their values are relatively constant among groups of cultivars of similar adaptation or genetic background (Hoogenboom et al., 2004a).

Leaf development

The phyllochron term PHINT in Cropsim-CERES-Wheat is defined as the interval of time between appearance of successive main stem leaf tips. A phyllochron is assumed to require a constant number of degree days. If the sowing date for a crop is about the same time each year, the PHINT value should be constant from year to year. Furthermore, time from terminal spikelet initiation to anthesis is under temperature control and is assumed to take approximately three phyllochrons until the end of leaf growth and two additional phyllochrons until anthesis.

1.3.2 Integration of Genetic Information into Crop Models

Advances in characterizing plant genomes and the resulting understanding of physiological processes suggests the possibility of improving model descriptions of crop growth and development (White and Hoogenboom, 2003). New methods developed to identify genomic locations associated with plant traits by gene mapping technologies (e.g. Syvänen, 2001) or monitoring metabolite concentrations (Weckwerth, 2003) allow the use of genetic information for crop models. According to Messina (2006a), the integration of gene information into a crop model requires three steps:

(1) Measuring traits for known genotypes in a field trial

(2) Estimating the genotypic model coefficients for these traits

(3) Developing a parameter model that estimates the genotypic model coefficients using genetic information across all genotypes

The plant material for the field trials should be selected depending on the availability of information about their allelic makeup at loci with known effects on physiological processes. Near isogenic lines are common to identify and test for epistatic and pleiotropic effects. Recombinant inbred lines are mainly used for quantitative trait loci (QTL) studies and are suitable to identify additive effects. At the molecular level, allelic information at given loci or QTL-associated makers are identified for each genotype by laboratory techniques. Relationships between gene combinations and genotypic model coefficients are developed by parameter models. When using molecular markers as inputs to predict the genotypic model coefficients, the genotypic model coefficients are mapped in the genome and QTL are estimated as a part of the same procedure (Wang et al., 2003). Genotypic model coefficients in Genegro, developed by White and Hoogenboom (1996), were based on the allelic information at given loci and linear models estimated using regression. However, up to now there are many gene-based approaches to simulate plant growth and development such as Yin et al. (2003), using QTL information for barley; Messina (2003), using allelic information for soybean and Welch et al. (2003) using genetic information of gene mutation for *Arabidopsis thaliana*.

1.4 Research Context

The research of the present dissertation was conducted in the context of the "International Research Training Group Sustainable Resource Use in North China" that was established in 2004 by the Deutsche Forschungsgemeinschaft (DFG), the Chinese Ministry of Education, the University of Hohenheim (Stuttgart) and the Chinese Agricultural University (Beijing). The research idea of the International Research Training Group (IRTG) is the quantification of material flows as a consequence of changes in cropping systems. The overall objective is to analyse flows and systems and to assess resource detraction and changes in cropping systems at different levels (IRTG, 2007).

Projects within the training group comprise different disciplines and range from soil science, plant nutrition, ecology, physics, biogeophysic, crop production and plant breeding to agricultural economics, agricultural informatics and rural development policy. To ensure the linkage between projects, most of them work collaborative in a main field experiment whereas all of them are cross-linked by using jointly modeling approaches. Projects are divided into 3 subgroups in which subprojects within group 1 describe, analyse and model material flows and pollution levels in soil and air; subprojects within group 2 analyse, model and optimize cropping systems with special emphasis to breeding potentials. The modeling and assessment of corresponding sustainable production systems at different levels (farm, region, sector) is part of subproject 3.

The research of this dissertation is embedded in subproject 2.1b and comprises a close cooperation between the partners of plant breeding (2.2) and optimizing cropping systems (2.1a). The overall objective of subproject 2.1b was to explore limits and possibilities for designing high yielding ideotypes by the use of crop models and underlying genetic information. To develop basic approaches, datasets from field trials distributed over a wide range of environments were used. To test approaches in a local scale, two locations in the NCP were selected. The fact that wheat is one of the most important crops in the NCP and the importance of predicting phenology, especially for this region, led to the goal of the dissertation.

1.5 Goal of the Present Dissertation

Since the prediction of wheat phenology becomes more important under varying conditions caused e.g. by climate change, the research of this dissertation focused on underlying determinants of variation in phenology. Combining modeling and modern genetics opens exciting options for optimizing phenology, with emphasis on predicting differences among cultivars. The overall objective was to characterize and test the impact of wheat phenology on agronomic traits by the use of a crop model and underlying genetic information. To achieve this goal, the specific objectives were:

- to characterize vernalization and photoperiod responses of wheat cultivars using field-based assessments and compare these with genotypic model parameters that are also used to characterize genotypic differences in development,
- to determine whether a gene-based approach of modeling phenology of wheat grown over a wide range of wheat production environments can provide useful predictions of flowering time,
- to highlight how a simulation analysis with parameters influencing wheat phenology can be used to describe traits and their behaviour in environments in the North China Plain,
- to test whether model-based characterizations of parameters affecting wheat phenology are predictive for cultivar differences in grain protein content.

1.6 Formal Structure and Introduction to the Chapters

This dissertation is based on four Chapters containing manuscripts that were submitted to peer reviewed journals (Chapter 2, 3, 4, 5). One Chapter provides basic information associated with the articles (Chapter 1) and Chapter 6 contains the general discussion.

Chapter 1 comprises a literature review of phenology in wheat and phenological modeling. The Chapter provides basic information on factors that affect phenology in wheat (environmental, genotypic) and how these factors are considered in modeling phenology.

Chapter 2 consists of the article "Field-based evaluation of vernalization requirement, photoperiod response and earliness *per se* in bread wheat (*Triticum aestivum* L.)" submitted to *Field Crops*

Research, accepted in October 2007. Cultivar variation in vernalization requirement, photoperiod response and earliness *per se* of wheat is usually estimated using controlled environments such as glasshouses or growth chambers. By the use of pre-planting vernalization treatments and two different planting dates an approach was developed to characterize vernalization requirement, photoperiod response and earliness *per se* among wheat cultivars in the field. The accuracy of the obtained responses was evaluated by comparing the field results with cultivar parameters estimated for the CSM-Cropsim-CERES-Wheat model Version 4.0.2.0.

Chapter 3 consists of the article "Simulation-Based Analysis of Effects of *Vrn* and *Ppd* Loci on Flowering in Wheat" submitted to *Crop Science*, accepted in September 2007. Model parameters influencing wheat phenology are usually estimated from genotypes by comparing field with simulation results. Through integrating effects of *Ppd* and *Vrn* loci, the estimation of the model coefficients P1V (vernalization requirement) and P1D (photoperiod response) was effective for predicting flowering date over a wide range of environments.

Chapter 4 comprises the article "A model-based ideotyping approach for wheat under different environmental conditions in the North China Plain" submitted to *Agricultural Science in China*, accepted in June 2007. Designing a wheat-ideotype means to specify traits and their importance in determining yield. The performance of model input parameters and their corresponding traits were tested by the use of the simulation model CMS-Cropsim-CERES-Wheat. In ideotyping sequences, input parameters were varied, and the model was run for two locations in the North China Plain, considering dry and wet growing seasons for each location.

Chapter 5 consists of an approach resulting in the article "The impact of vernalization requirement, photoperiod sensitivity and earliness *per se* on grain protein content of bread wheat (*Triticum aestivum* L)" submitted to *Euphytica,* accepted in Februar 2008. Early anthesis combined with long grain filling duration is reported to increase grain protein content in wheat. By the use of a long term performance nursery, firstly the impact of genotype, environment and their interactions on grain protein content was pointed out and secondly in a closer examination the impact of vernalization requirement, photoperiod sensitivity and earliness *per se* on grain protein content was investigated.

Chapter 6 completes the dissertation by containing the general discussion where firstly findings across chapters are displayed and classified according to the goal of the dissertation and secondly, discussed together to highlight consequences for present applications. The last section presents how findings can contribute to adapt cropping systems to climate change trends in China and to ensure a sustainable resource use in the North China Plain. Future perspectives and a brief summary complete the manuscript.

2 Field-based Evaluation of Vernalization Requirement, Photoperiod Response and Earliness *per se* in Bread Wheat (*Triticum aestivum* L.)
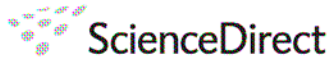
Field-based evaluation of vernalization requirement, photoperiod response and earliness *per se* in bread wheat (*Triticum aestivum* L.)

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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 $1d$. 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

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

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
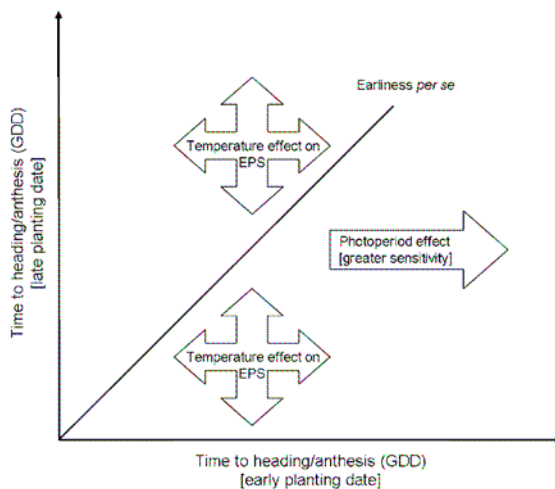

Fig. 1. Scheme of expected effects of photoperiod and temperature on wheat development for two planting dates assuming different photoperiod regimes.

Table 1
Origin, classification of the *Ppd-D1* locus, final leaf number (FLN), and growing degree days from seedling emergence until end of ear emergence (GDD) of cultivars used in the study

Cultivar	Origin[a]	*Ppd-D1* locus[b]	FLN (TD1, 0VD[c])	FLN (TD1, 60VD[d])	GDD (TD1, 60VD)	GDD (EPS[e]) (TD2, 60VD)	GDD (TD1, 0VD)
Balkan	Yugoslavia	Dominant	13	5	699	696	1444
Bezostaya	USSR	Dominant	14	6	703	701	1413
Biscay	Germany	–	–	6	825	761	dne[f]
Bounty	England	Recessive	13	6	809	774	1476
Bussard	Germany			6	825	761	dne
Capelle Desprez	France	Recessive	13	6	809	749	1146
Contra	Germany	–	–	6	812	736	1551
Dekan	Germany	–	13	6	800	736	1425
Dream	Germany	–		7	851	803	1488
Drifter	Germany	–	14	6	812	761	1473
Dwarf Bezostaya	USSR	Dominant	12	5	694	690	1399
Enorm	Germany	–	13	6	772	666	1300
Excellent	Germany	–	13	6	825	736	1257
Hybnos 2b	Germany	–	12	6	800	720	1233
Ludwig	Austria	–	–	6	800	788	dne
Magnus	Germany	–	–	6	812	774	dne
Mandub	Germany	–	11	7	825	720	1041
Maris Templar	England	Recessive	13	6	812	717	1444
Mironovskaya 808	USSR	Recessive	–	6	763	692	1602
Odesskaya 51	USSR	Dominant	–	6	734	729	1414
Opus	Germany	–	–	6	825	774	dne
Renan	France	–	13	6	772	679	1488
Terrier	Germany	–	13	6	812	761	1397
Tiger	Germany	–	–	7	800	774	dne
Tommie	Germany	–	–	6	812	749	dne
Vakka	Finland	Recessive	–	7	869	774	1516
S.E.d			1.20	0.46	11.38	29.56	67.24

[a] Origin of the non-German cultivars as reported in the International Winter Wheat Performance Nursery (e.g. Kuhr et al., 1984).
[b] Genetic makeup was determined through the online database of Martynov et al. (2006).
[c] Transplanting date 3 April 2006; no vernalization pre-treatment.
[d] Transplanting date 3 April 2006; vernalization pre-treatment of 60 vernalization days (VD).
[e] Earliness *per se*.
[f] Did not reach ear emergence stage before end of growing season.

was derived from their genetic makeup as reported in the online database of Martynov et al. (2006). As there were no reported differences in *Vrn* loci among the cultivars, all cultivars were assumed to require vernalization. Cultivars carrying a dominant allele at the *Ppd-D1* locus were assumed photoperiod insensitive, and ones carrying a recessive allele at the *ppd-D1* locus were considered photoperiod sensitive. To examine the influence of EPS and vernalization on development more precisely, 17 cultivars which are commonly cultivated in Germany were also included, although no genetic data were available (Table 1).

2.2. Vernalization treatments

Vernalization treatments used the method of restricted water proposed by Purvis and Gregory (1952). First, seed were imbibed, sterilized and placed on filter papers in petri dishes. Seed moisture content was then adjusted to 50% of dry weight, and the petri dishes were maintained in a germination cabinet for 60 vernalization days (VD; Streck et al., 2003). Cabinets were maintained at a temperature of 4 °C and kept dark. Twice weekly, water content was adjusted to 50–55% of dry weight by spraying distilled water on the petri dishes. After vernalization,

seedlings measuring 10–20 mm in length were selected for transplanting to the field to ensure that seedlings from different cultivars were at similar stages of development (van Beem et al., 2005). Ninety seedlings per cultivar were transplanted first into small pots, which were kept in a semi-enclosed greenhouse maintained at ambient temperature and photoperiod until they had reached emergence, defined as Haun stage 0.5 (Haun, 1973). Seedlings were transplanted into the field plots within 2 days of emergence.

2.3. Field activities

The field work carried out at the research station Ihinger Hof (48°44′N; 8°56′E; 450 m elevation, 693 mm annual precipitation, 8.1 °C mean annual temperature) of the University of Hohenheim, Germany. The major soil type according to the former German soil classification (Boden, 1982) is Parabraunerde, which is equivalent to the WRB classification (FAO, 1998) as a Haplic Luvisol. The texture is mainly silty clay.

Cultivars were subjected to two photoperiod and temperature regimes through use of two dates of transplanting, 3 April 2006 (TD1) and 5 May 2006 (TD2), and a fully vernalized (60VD) and a non-vernalized (0VD) treatment. The experi-
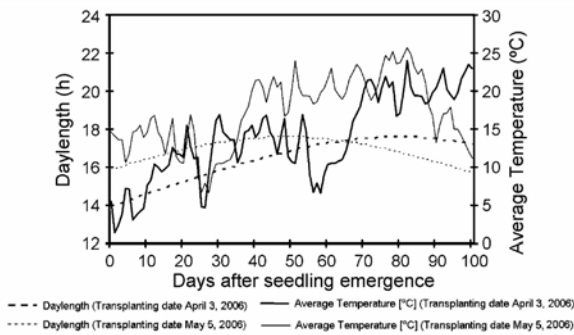
Fig. 2. Daylength and average air temperature during the growth period of transplanting dates 3 April 2006 (TD1) and 5 May 2006 (TD2).

mental design was a split plot design with three replicates. Transplanting dates were main plots, and cultivars by vernalization treatments were in a factorial arrangement allocated in three incomplete blocks per replicate. Seedlings were transplanted in two rows with 30 plants per 2 m row. TD1 was expected to provide a photoperiod regime where cultivar differences in response would be expressed, whereas the longer initial daylength for TD2 should have minimized effects of photoperiod (Fig. 2). To quantify the reaction to vernalization and photoperiod, two traits were recorded: date of end of ear emergence and final leaf number on the main stem (FLN). End of ear emergence was considered to be reached when at least 50% of the plants had attained the respective stage.

To evaluate the effectiveness of using a cultivar-dependent value of EPS, data on time of anthesis were obtained from two trials involving nine of the German cultivars (Table 2). The trials were designed to provide data on crop growth and development and were conducted at Ihinger Hof in 2005 and 2006 (Herndl et al., submitted). Plots were sown the preceding October, following recommended practices for winter wheat. Fertilizer and weed management were similar to the 2006 characterization trial.

2.4. Rates of development

Relative responses to vernalization (RRV_{GDD}) and photo-period (RRP_{GDD}) were computed as suggested by White and Laing (1989). The indices were calculated using rates of development (R), defined as

$$R = \frac{1}{F} \tag{1}$$

where F is GDD (°C) from seedling emergence to end of ear emergence. The relative response to vernalization was estimated as

$$RRV_{GDD} = 1 - \frac{R_{NV}}{R_{FV}} \tag{2}$$

where R_{NV} was defined for plants from non-vernalized (0VD) seed transplanted on the first date (TD1) and R_{FV} is the rate for fully vernalization (60VD) seed transplanted on the first date. Similarly, the photoperiod response (RRP_{GDD}) was calculated

according to

$$RRP_{GDD} = 1 - \frac{R_P}{R_{FV}} \tag{3}$$

where R_P is the rate of development for fully vernalized seed (60VD) transplanted on the second date (TD2) and R_{FV} is the rate for fully vernalization (60VD) seed transplanted on the second date.

To provide an additional estimate of vernalization requirement, a relative response based on final leaf numbers was calculated as

$$RRV_{FLN} = 1 - \frac{FLN_{FV}}{FLN_{NV}} \tag{4}$$

where FLN_{FV} is the final leaf number obtained under full vernalization, first planting date (60VD, TD1) and FLN_{NV} is the final leaf number without vernalization for the same date (0VD, TD1). EPS was estimated as GDD (°C) between seedling emergence and end of ear emergence for the second transplanting of fully vernalized material.

2.5. Simulation model

Models to predict time of anthesis of wheat as influenced by vernalization requirement, photoperiod response and earliness are well explored and applied in several simulation models (Ritchie, 1991; Hunt and Pararajasingham, 1995; Wang and Engel, 1998). The Cropping Systems Model-Cropsim-CERES-Wheat model version 4.0.2.0 (CSM; Jones et al., 2003) parameterizes these effects in species, cultivar and ecotype files. Days at optimum vernalizing temperature that are required to complete vernalization are specified by a parameter P1V, and the percentage reduction in development rate in a photoperiod 10 h shorter than the optimum photoperiod relative to the rate at the optimum is specified by P1D (Hoogenboom et al., 2004). Variation in EPS is accounted for through the sum of the component phase durations from germination to the end of spike growth (P_{123}). The individual phase durations (P1, P2 and P3 defined in Table 2) are represented in the CSM wheat ecotype file, implying that their values are relatively constant among groups of cultivars of similar adaptation or genetic background.

Initial testing with CSM indicated that the optimal photoperiod (specified as 20 h by the model parameter P1DT) was too short to accurately differentiate genotypic differences in photoperiod responses. Data in Cao and Moss (1989a) and Slafer (1996) indicated that some cultivars responded to photoperiods greater than 20 h, so P1DT was increased to 23 h.

The parameters P1V and P1D were estimated from the characterization data in a multi-step procedure. For treatments that had been pre-vernalized, progress in development from seedling emergence until end of ear emergence was assumed to vary mainly with temperature and the cultivar-specific photoperiod sensitivity for the first transplanting date (TD1). Thus, to estimate P1D, P1V was set to zero, and P1D values were varied to obtain a simulated end of ear

Table 2

Relative response to vernalization based on final leaf number (RRV$_{FLN}$), rate of relative response to vernalization (RRV$_{GDD}$), rate of relative response to photoperiod (RRP$_{GDD}$) and calibrated phase durations of cultivars used in this study

Cultivar	RRV$_{FLN}$	RRV$_{GDD}$	RRP$_{GDD}$	P1[a] (GDD)	P2[b] (GDD)	P3[c] (GDD)
Balkan	0.62	0.52	0.00	190	250	256
Bezostaya	0.59	0.590	0.00	290	250	161
Biscay	–	dne[d]	0.08	290	250	221
Bounty	0.56	0.45	0.04	290	250	234
Bussard		dne	0.08	290	250	221
Capelle Desprez	0.50	0.29	0.07	290	250	209
Contra[e]	--	0.48	0.09	290	250	196
Dekan	0.52	0.44	0.08	290	250	196
Dream[e]		0.43	0.06	380	250	173
Drifter[e]	0.55	0.45	0.06	290	250	221
Dwarf Bezostaya	0.58	0.580	0.01	190	250	250
Enorm[e]	0.56	0.41	0.14	290	250	126
Excellent[e]	0.55	0.34	0.11	290	250	196
Hybnos 2b[e]	0.48	0.35	0.10	290	250	180
Ludwig	–	dne	0.02	290	250	248
Magnus	–	dne	0.05	290	250	234
Mandub[e]	0.39	0.21	0.13	380	250	90
Maris Templar	0.54	0.44	0.12	290	250	177
Mironovskaya 808	–	0.52	0.09	290	250	152
Odesskaya 51	–	0.48	0.01	290	250	189
Opus	–	dne	0.06	290	250	234
Renan[e]	0.58	0.48	0.12	290	250	139
Terrier[e]	0.55	0.42	0.06	290	250	221
Tiger	–	dne	0.03	380	250	144
Tommie	–	dne	0.08	290	250	209
Vakka	–	0.43	0.11	380	250	144
S.E.d	0.05	0.03	0.04	–	–	–

[a] Duration of phase from end juvenile to terminal spikelet, which therefore affects leaf numbers (thermal units).

[b] Duration of phase from terminal spikelet to end leaf growth (thermal units).

[c] Duration of phase from end leaf growth to end spike growth (thermal units).

[d] Did not reach ear emergence stage before end of growing season on transplanting date 3 April 2006; no vernalization pre-treatment.

[e] Cultivars evaluated in the study conducted at the research station Ihinger Hof in 2005 and 2006, Germany (Herndl et al., submitted).

emergence date that matched the values observed from the field. To obtain P1V, these estimates of P1D were then used under the assumption that the development progress in the model would now predominantly be influenced by the vernalization requirement, and P1V values were varied until simulated and observed end of ear emergence matched.

To examine the effect of P_{123} in the model, P1V and P1D were set to zero, and values of P_{123} were varied while simulating conditions for TD1 and TD2 conditions. Two approaches were used to quantify the influence of EPS on the calibration of P1V and P1D. First, a constant value of P_{123} (770 GDD), which corresponded to a value used to characterize many wheat cultivars in CSM, was tested. In the second approach, the parameter P1, which defines the duration from the end of the juvenile phase to terminal spikelet and therefore affects leaf numbers (Hoogenboom et al., 2004), was varied according to the leaf numbers observed for TD1 with full vernalization (Table 1). In addition, P3 (duration of from end of leaf growth to end of spike growth) was adjusted to match EPS values estimated from the field experiment. P2 (duration of from terminal spikelet to end of leaf growth) was assumed constant at 250 GDD (Table 2).

2.6. Evaluation of the adapted P_{123} approach

To provide an independent evaluation of the need for cultivar-dependent P_{123} values instead of a constant P_{123}, an independent dataset for a subset of the German cultivars (Table 2) was consulted. The cultivar-dependent values and corresponding cultivar coefficients in the model as obtained from the characterization trial were inserted and the model was run with management and weather data obtained from the 2005 and 2006 trials at Ihinger Hof. By comparing observed versus simulated days to anthesis, the quality of the characterization of P1V, P1D and mainly the cultivar-dependent P_{123} was tested.

2.7. Statistical analyses

Within the split plot design an incomplete block structure was arranged. Due to missing values, the incomplete blocks structure was no longer valid, so this blocking was ignored. The plots within groups of incomplete blocks were still randomized, so they were consider as complete blocs. The SAS Generalized Linear Models procedure (GLM) was used to estimate treatment means (SAS Institute, 2000). Linear regressions were performed with Excel.

3. Results

3.1. Observed field data

With no vernalization pre-treatment, 19 of the 26 cultivars reached ear emergence and flag leaf stage in the first transplanting, whereas in the second transplanting date no cultivar attained these stages. With the pre-treatment all cultivars in both transplanting dates reached these stages (Table 1). Due to foliar diseases and technical problems, final leaf number data from only 14 of the 19 cultivars were recorded. Based on values of RRV$_{GDD}$ (Table 2), the cultivars Capelle Desprez and Mandub stood out for their relatively low vernalization requirements while cultivars which did not reach emergence stage before the end of the growing season stood out as having an unfulfilled vernalization requirement. RRV$_{FLN}$, which provided an alternate assessment of vernalization requirement, showed good agreement with RRV$_{GDD}$ (r^2 = .82; Fig. 3).

Cultivars carrying *Ppd-D1* had values of RRP$_{GDD}$ close to zero, whereas most of the other cultivars (including the known *ppd-D1* carriers) showed higher values (Table 2). Cultivars varied in EPS from 666 to 774 GDD (Table 1).

3.2. Variation in EPS

In comparisons of GDD to end of ear emergence for the two planting dates, cultivars dominant for *Ppd-D1* were closer to the EPS line predicted with the CSM model whereas the other cultivars, including known carriers of *ppd-D1*, fell to the right of the EPS line (Fig. 4), in agreement with the arguments illustrated in Fig. 1. No obvious groupings for EPS were suggested by Fig. 4, raising doubts whether EPS can be considered constant among groups of cultivars as implied by the use of ecotype parameters in CSM.

Given the apparent variability in EPS, the model parameters P1V and P1D were re-estimated for each cultivar, allowing P1 and P3 to vary according to data on final leaf number and observed EPS. These coefficients showed much stronger
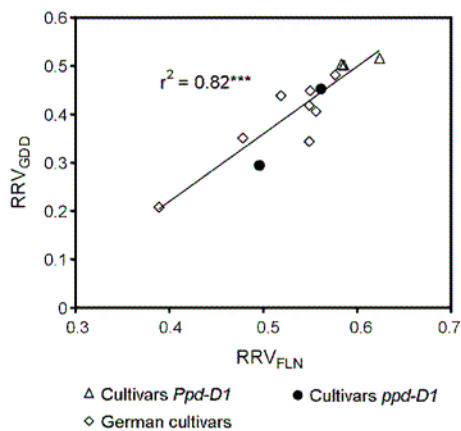

Fig. 3. Relation between rate of relative response to vernalization (RRV$_{GDD}$) and rate of relative response to final leaf number (RRV$_{FLN}$).
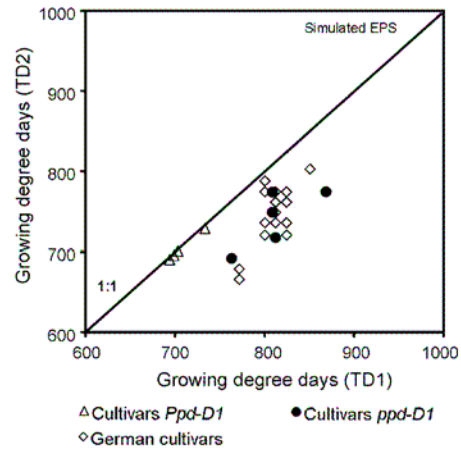
Fig. 4. Comparison of time to end of ear emergence expressed as GDD for 26 cultivars transplanted at two dates to provide different photoperiod and temperature regimes. The curve indicates the predicted relation in the absence of a photoperiod effect.

associations with RRV$_{GDD}$ and RRP$_{GDD}$. For vernalization, the correlation between P1V and RRV$_{GDD}$ increased from r^2 = .88 to .94 (Figs. 5A and 6A), and for photoperiod, the correlation between P1D and RRP$_{GDD}$ increased from r^2 = .34 to .82 (Figs. 5B and 6B). P1V and RRV$_{FLN}$ were also highly correlated (Fig. 7).

3.3. Evaluation

In simulations using the values of P1V and P1D estimated while allowing P_{123} to vary, days to anthesis showed good agreement with observations from field trials conducted in 2005 and 2006 (Fig. 8). The root mean square error (RMSE) was 1d, and the regression line had a slope of 1.05 (S.E. of 1.0).

4. Discussion

The overall results confirmed that field evaluations combined with vernalization pre-treatments are an effective mean for characterizing vernalization requirements and photoperiod response of wheat cultivars. It is especially encouraging that the model parameters P1V and P1D allowed prediction of phenology for independent sets of data with a RMSE of 1d (Fig. 8) and that the evaluations were consistent with available data on cultivar differences at the *Ppd-D1* locus. The results also confirm the importance of considering variation in EPS in estimating vernalization requirements and photoperiod response.

The main difficulty encountered with the evaluations was the failure to obtain reliable data for cultivars that did not reach end of ear emergence in the absence of a vernalization pre-treatment. Possible solutions include attempting an even earlier transplanting date, transplanting the materials to a site with a longer but cooler growing season, using multiple partial vernalization treatments and extrapolating the response. Evaluating development based on inspection of the shoot apex
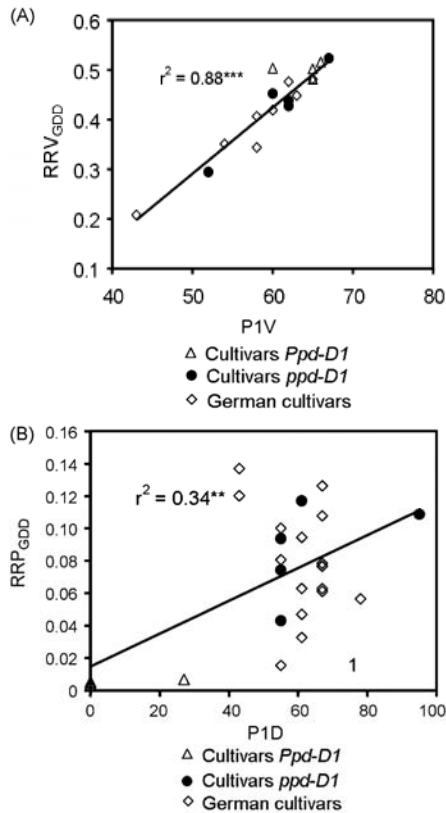
Fig. 5. Comparison of indices of vernalization requirement and photoperiod response with the model parameters P1V and P1D and assuming a constant value of 280 GDD for the CSM parameter P1. (A) Relative response to vernalization (RRV$_{GDD}$) and P1V. (B) Relative response to photoperiod (RRP$_{GDD}$) and P1D.
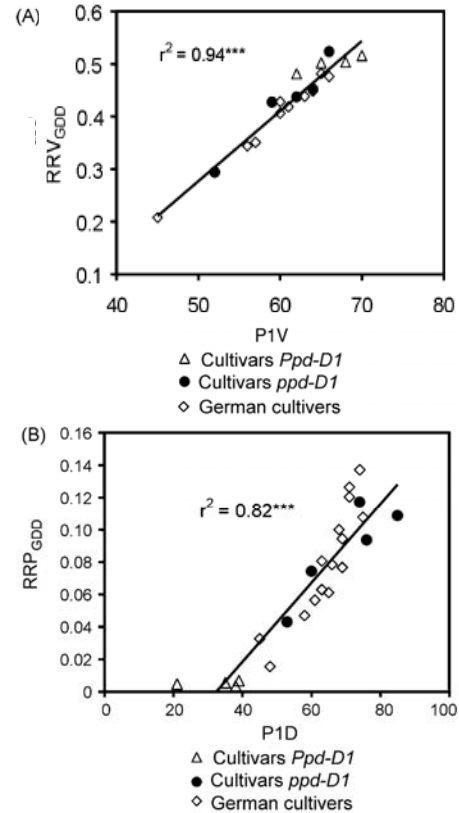
Fig. 6. Relation between relative responses to vernalization and to photoperiod and calibrated coefficients of CSM assuming variation in EPS. (A) RRV$_{GDD}$ and P1V. (B) RRP$_{GDD}$ and P1D.

is another possible solution, but before this approach could be used, it would be important to determine whether the effects of incomplete vernalization are the same throughout early development.

As a group, the German cultivars were more photoperiod sensitive and later than the other cultivars. Capelle Desprez and Mandub showed a slightly lower vernalization requirement compared to the other cultivars. Cultivars which did not reach end of ear emergence before the end of the growing season with no vernalization pre-treatment might have the highest vernalization requirement, but in this study they were not able to fulfill their requirement during the provided growing season. Other authors reported substantial variation in vernalization requirement among winter types (Davidson et al., 1985; Worland et al., 1994a,b; Košner and Pánková, 2002). Considering that there could be interactions between vernalization and photoperiod and that cultivars are able to flower without vernalization (Rahman, 1980; Davidson et al., 1985; Trevaskis et al., 2007) the response data should not be interpreted as absolute values but rather as indicators of cultivar differences.

Cultivars carrying the dominant allele at the *Ppd-D1* locus had lower values of RRP$_{GDD}$, confirming their relatively neutral

response to photoperiod (TD2). Worland et al. (1988) reported that under European conditions, photoperiod sensitive genotypes show a delay of 4–10 days to flowering relative to insensitive materials.
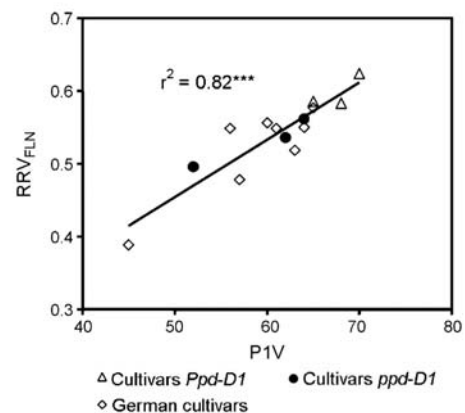
Fig. 7. Relation between the relative response of final leaf number (RRV$_{FLN}$) and the model coefficient P1V calibrated by using cultivar-dependent phase durations estimated as the EPS (GDD) recorded in the characterization trial.
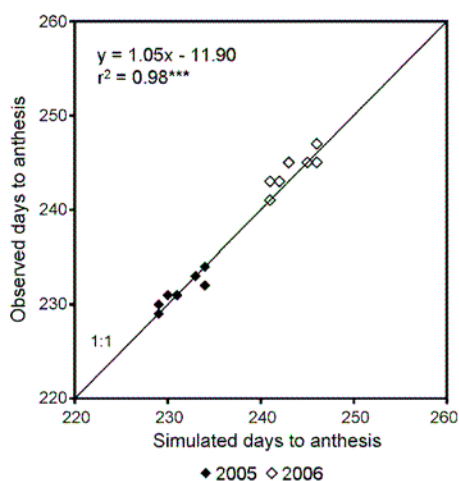
Fig. 8. Relation between observed days to anthesis for nine cultivars grown in 2005 and 2006 at the research station Ihinger Hof, Germany (Herndl et al., submitted) and days to anthesis simulated using P1V, PID and P_{123} estimated from the characterization trial.

The results highlighted the importance of variation in EPS, currently represented in the variables P1, P2, and P3. By adapting these values to individual cultivars, the estimates of effects of photoperiod response and vernalization requirement are improved. The comparison with an independent dataset emphasized the relevance of P_{123} on the accurate calibration of P1V and P1D in the model.

Other factors that might improve model accuracy are allowing photoperiod to affect development after terminal spikelet initiation (Ritchie, 1991; Slafer and Rawson, 1994; Slafer and Whitechurch, 2001), accounting for possible interactions between temperature regime and photoperiod sensitivity (Cao and Moss, 1989b), and less clearly, allowing photoperiod sensitivity to increase in later developmental phases (Slafer, 1996). Accounting for differential response to temperature (Slafer, 1996; van Beem et al., 2005), which could result in apparent differences in EPS, could also be investigated when considering possible model improvements.

5. Conclusions

To characterize vernalization requirement, photoperiod response and EPS among wheat cultivars, field experiments combined with vernalization pre-treatments can provide a useful alternative to controlled environment studies. Field-based results appear to provide reliable data for predicting phenology using simulation models such as CSM. We suggest that model parameters such as P1V and P1D be used to supplement indices such as RRV_{GDD} and RRP_{GDD} in routine descriptions of wheat germplasm. Presumably being closer to underlying genetic characteristics of cultivars (Baenziger et al., 2004; White, 2006), model parameters should be more comparable across studies providing different photoperiod and temperature regimes. Furthermore, rigorous and reproducible characterizations should provide a better understanding of

more complex genetic systems that may underlie EPS or more complex responses such as possible interactions of temperature with photoperiod sensitivity.

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In the previous chapter it was shown that genetic variability in vernalization requirement, photoperiod response and earliness *per se* of wheat can be accurately represented by corresponding **cultivar parameters** in the CSM-Cropsim-CERES-Wheat model.

One constraint of using model parameters for description of wheat phenology is the estimation procedure of the genotypic model parameters. To improve and simplify the linkage between genotypic model parameters and traits influencing wheat phenology, one possibility could be to define a relationship between gene combinations influencing wheat phenology and genotypic model parameters by field research. This approach is implemented in the next chapter.

3 Simulation-Based Analysis of Effects of V*rn* and *Ppd* loci on Flowering in Wheat

Simulation–Based Analysis of Effects of *Vrn* and *Ppd* Loci on Flowering in Wheat

Jeffrey W. White,* Markus Herndl, L. A. Hunt, Thomas S. Payne, and Gerrit Hoogenboom

ABSTRACT

Cereal production is strongly influenced by flowering date. Wheat (*Triticum aestivum* L.) models simulate days to flower by assuming that development is modified by vernalization and photoperiodism. Cultivar differences are parameterized by vernalization requirement, photoperiod sensitivity, and earliness per se. The parameters are usually estimated by comparing simulations with field observations but appear estimable from genetic information. For wheat, the *Vrn* and *Ppd* loci, which affect vernalization and photoperiodism, were logical candidates for estimating parameters in the model CSM-Cropsim-CERES. Two parameters were estimated conventionally and then re-estimated with linear effects of *Vrn* and *Ppd*. Flowering data were obtained for 29 cultivars from international nurseries and divided into calibration (14 locations) and evaluation (34 locations) sets. Simulations with a generic cultivar explained 95% of variation in flowering for calibration data (10 d RMSE) and 89% for evaluation data (10 d RMSE), indicating the large effect of environment. Nonetheless, for the calibration data, the gene-based model explained 29% of remaining variation, and the conventional model, 54%. For the evaluation data, the gene-based model explained 17% of remaining variation, and the conventional model, 27%. Gene-based prediction of wheat phenology appears feasible, but more extensive genetic characterization of cultivars is needed.

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Abbreviations: CIMMYT, International Maize and Wheat Improvement Centre; IWIS, International Wheat Information System; IWWPN, International Winter Wheat Performance Nurseries; QTL, quantitative trait loci; SS, sum of squares.

T IMING OF FLOWERING is a critical determinant of the adaptation of a grain or seed crop to a given production environment and set of management practices. In bread wheat (*Triticum aestivum* L.), the *Vrn* and *Ppd* families of loci exert major influences on flowering by modifying the sensitivity of reproductive development to vernalization and photoperiod, respectively (Flood and Halloran, 1986; Worland, 1996; Laurie et al., 2004; van Beem et al., 2005; Iqbal et al., 2007). Although wheat researchers recognize the importance of these loci, attempts to quantitatively predict the effects of different loci under variable environment conditions are rare. A robust, quantitative methodology for interpreting interacting effects of specific loci and the environment

should permit a much more mechanistic understanding of genotype by environment interactions for phenology, grain yield, and other economically important traits.

Process-based ecophysiological models can integrate the effects of environment, crop management, and cultivar to predict crop growth and development. Cultivar differences in phenology are usually embodied through parameters that modify sensitivity to factors such as vernalization temperatures or photoperiod regimes (e.g., Ritchie, 1991). Cultivar differences in earliness per se may also be represented through minimum durations of specific developmental phases. Often labeled "genetic coefficients" to reflect their use in specifying cultivar differences, the cultivar parameters nonetheless are estimated primarily using phenotypic data obtained from field trials (White and Hoogenboom, 1996; Baenziger et al., 2004). This process is often slow and expensive since obtaining reliable calibrations may require conducting field trials at multiple locations or over several cropping seasons. The process also is often considered prone to over-calibration for local conditions, which can inflate the apparent validity of a model, hinder detection of problematic assumptions or errors in other model inputs, and reduce the reliability of model-based predictions.

Recognizing the problems inherent in use of cultivar-specific model parameters, various researchers have pursued strategies to replace the parameters with data for genetic loci. The GeneGro model for common bean (*Phaseolus vulgaris* L.) used data for seven loci and predicted phenology, yield, and grain size as well as the parent model using conventionally estimated cultivar parameters (White and Hoogenboom, 1996; Hoogenboom et al., 1997, 2004b; Hoogenboom and White, 2003). Messina et al. (2006) successfully modeled phenology in soybean using the same approach. Efforts to use data for quantitative trait loci (QTL) instead of Mendelian loci have shown promise for modeling specific traits (e.g., Reymond et al., 2003; Nakagawa et al., 2005). Attempts to parameterize inputs for whole plant models using QTL appear somewhat less encouraging (Yin et al., 2000). The problems encountered may reflect difficulties inherent in accurately phenotyping the large numbers of lines required for QTL analyses and in identifying true QTL through appropriate statistical analysis (Edmeades et al., 2004). Recently, several papers have argued for more mechanistic approaches for integrating genomics with modeling (e.g., Minorsky, 2003; Tardieu, 2003; White and Hoogenboom, 2003; Hammer et al., 2004; Struik et al., 2005; Wollenweber et al., 2005; Yin et al., 2004; White, 2006). Actual applications of such approaches are few. Among promising examples are efforts to model gene networks for flowering at a simplified level (Welch et al., 2003).

Over 40 Mendelian loci have been described as affecting physiological traits in wheat (White, 2006). Of these,

perhaps 30 affect traits that are readily modeled. Thus, it appears that there is sufficient genetic information to initiate work on a gene-based wheat model. Experience with GeneGro (White and Hoogenboom, 1996) suggested that the linear regressions used to estimate effects of genes on model parameters could be programmed external to the model code. Given the large number of wheat models available (e.g., Grant et al., 2001; Jamieson et al., 1998; Asseng et al., 2002), it seemed desirable to develop a gene-based estimator of cultivar-specific model parameters, rather than a single gene-based wheat model (White, 2006). If successful, this would facilitate direct transfer of results to alternative wheat models.

The goal of this study was to test the practicability of using a gene-based procedure to estimate model parameters for predicting phenology. The main objective was to determine how well gene-based parameters performed relative to conventionally estimated parameters, testing the results with simulations of flowering time of diverse bread wheats grown over a wide range of wheat production environments.

MATERIALS AND METHODS
Data Sources

Data on crop management and phenology were obtained from the International Winter Wheat Performance Nurseries (IWWPN) from 1969 to 1981. This series of replicated trials was distributed to over 30 countries globally by the University of Nebraska and USDA-ARS with support from the U.S. Agency for International Development. In total, 168 cultivars were tested in the IWWPN. Each year, 30 cultivars or breeding lines were grown, and most cultivars were included for at least 2 yr. Trials were grown at 85 locations, which predominantly represented traditional winter wheat production areas but included spring wheat areas. Results of the IWWPN were published in 13 reports of the Research Bulletin of the Nebraska Agricultural Experiment Station (e.g., Kuhr et al., 1984). Phenotypic data and management summaries were digitized from the reports and stored in the International Wheat Information System (IWIS; Payne et al., 2002) at the International Maize and Wheat Improvement Centre (CIMMYT). Various minor errors such as in reporting of geographic coordinates of locations, year of sowing, and the reference date for time of flowering were corrected, so the data in IWIS differed slightly from that in the published reports. There was possible confusion over reporting of "time of flowering." Although this term is logically associated with time of anthesis, most wheat programs only record heading date. Thus, the reported data may have referred to heading or anthesis. To permit meaningful comparisons across locations, all flowering data were re-expressed as days after sowing.

Although 168 cultivars were tested in the 13 cycles of the nurseries, only 29 cultivars were used (Table 1) due to limited availability of information on their genetic makeup. Alleles present at the *Ppd* and *Vrn* loci were determined through various sources. The online database (Martynov et al., 2006) provided

Table 1. Habit, origin, pedigree, mean observed days to anthesis, assumed genotypes, and estimated model parameters for cultivars used in the study.[†]

Cultivar	Habit	Origin	Pedigree	Days to anthesis		Locus				Model parameters	
				Mean	No. values[‡]	*Vrn-A1*	*Vrn-B1*	*Vrn-D1*	*Ppd-D1*	P1V	P1D
				d						d	%
INIA 66	S	Mexico	Lerma Rojo 64/Somora 64	181	15	1	1	0	1	18	29
Super X	S	Mexico	Penjamo-62(SIB)/Gabo-55	208	86	1	1	0	1	44	32
Lerma Rojo 64	S	Mexico	Yaqui-50//Norin-10/Brevor/3/ Lerma 52/4/2*Lerma Rojo	200	202	0	1	1	1	29	35
Bastion	S	Netherlands	Halle-12//Halle-35/Mara	220	64	0	1	0	1	48	48
Irnerio	S	Italy	Produttore/Manitoba	208	62	0	0	1	1	48	27
Aurora	W	USSR	Hard Federation/Cleveland//Sands	213	58	0	0	0	1	71	21
Balkan	W	Yugoslavia	Backa/Bezostaya-1// Mironovskaya-808/3/NS-433/4/ Skorospelka-35	214	37	0	0	0	1	62	21
Bezostaya 1	W	USSR	(S) Bezostaya-4	214	348	0	0	0	1	58	25
Biserka	W	Yugoslavia	Fortunato*2/(CI-13170)Redcoat	212	65	0	0	0	1	53	26
Dwarf Bezostaya	W	USSR	(S) Bezostaya	211	57	0	0	0	1	68	21
Jugoslavija	W	Yugoslavia	NS-646/Bezostaja 1//Aurora	214	38	0	0	0	1	62	31
Moslavka	W	Yugoslavia	ZG-3814-65/TP-114-1965-A// ZG-3814-65.Sanja	209	35	0	0	0	1	53	20
Odesskaya 51	W	USSR	Odesskaya-16/Bezostaya-1	218	72	0	0	0	1	65	18
Partizanka	W	Yugoslavia	Bezostaya-1/NS-116	215	71	0	0	0	1	62	15
Phoenix	W	Australia	WW-15*2/WW-80	205	38	0	0	0	1	55	17
San Pastore	W	Italy	Balilla/Villa Glori	194	42	0	0	0	1	50	17
Sanja	W	Yugoslavia	ZG-414–57/Leonardo	209	60	0	0	0	1	54	31
Sava	W	Yugoslavia	Fortunato*2/(CI-13170)Redcoat	211	58	0	0	0	1	37	37
Talent	W	France	Champlein/3/Thatcher/ Vilmorin-27//Fortunato	215	68	0	0	0	1	57	28
Zlatna dolina	W	Yugoslavia	ZG-414-57/Leonardo	209	65	0	0	0	1	62	24
Zlatoklasa	W	Yugoslavia	Sanja/TP-114-1965-A//Sanja	210	68	0	0	0	1	55	25
Bounty	W	England	Maris Ploughman/Durin	224	36	0	0	0	0	59	49
Cappelle Desprez	W	France	Vilmorin-27/Hybride du-Joncquois	216	23	0	0	0	0	68	31
Maris Huntsman	W	England	CI-12633/5*Cappelle-Desprez//Hybrid-46/Cappelle-D./3/2*Professeur-Marchal	226	67	0	0	0	0	59	48
Maris Mardler	W	England	Maris Ranger/Maris Durin//Maris Huntsman	219	38	0	0	0	0	60	39
Maris Nimrod	W	England	CI-12633/Yeoman//5*Cappelle/3/ Cappelle/Hybrid-46/4/2*Professeur-Marchal	220	67	0	0	0	0	65	38
Maris Templar	W	England	CI-12633/5*Cappelle D.//Hei-nes-110/ Cappelle-D./3/Nord-Desprez/4/Viking	227	67	0	0	0	0	74	39
Mironovskaya 808	W	USSR	(T) Artemovka	219	72	0	0	0	0	72	34
Vakka	W	Finland	Varma/G-5-20-Kehra	222	60	0	0	0	0	57	42

[†]Habit is as reported in the International Winter Wheat Performance Nurseries (IWWPN); S, spring; W, winter. Origins are as reported in the original IWWPN reports and may not reflect current political boundaries. Loci were scored 0 or 1 if the recessive or dominant allele, respectively, is present. Cultivars are ordered from greatest number of dominant alleles within the *Vrn* and *Ppd* loci.

[‡]Number of locations and years used to calculate the mean for a cultivar.

data for many cultivars and also contained information on pedigrees and growth habit. Dencic (2001) and van Beem et al. (2005) contained additional data. Few evaluations for *Ppd* loci were found. Some daylength insensitive cultivars of European origin were classified by assuming that they contained the *Ppd-D1* locus (Worland, 1996; Worland et al., 1998).

Eighty-two locations of the IWWPN provided sufficient crop management data to allow simulating crop growth and development. Daily data for maximum and minimum tempera-

tures (required to simulate crop development) were obtained for 48 locations, representing 362 experiments (Table 2). Weather data sources included online databases (e.g., University of California, Agriculture and Natural Resources, 2005), individual researchers, and the Global Summary of the Day database (Lott, 1998). In several cases, the nearest weather station corresponded to an airport or other nonagricultural source, so elevation, distance from reported locations of experiments, and land use were examined using the Google Earth mapping tool

(Google, Inc., Mountain View, CA). No weather station data were used if the station was located more than 25 km from the experiment or if the pairs of locations differed greatly in elevation or land cover. No attempt was made to link locations to soil profile descriptions as simulations assumed no limitations of water and nutrients.

Phenotypic and management data were extracted from IWIS as spreadsheets and reformatted for use in the model using a structure similar to the standards of the International Consortium for Agricultural Systems Analysis (Hunt et al., 2001, 2006). Phenotypic data were available for days from sowing to flowering and maturity, grain yield, and other traits, but for this study, only flowering data were considered. The set of management data required to simulate an experiment thus was location (latitude), sowing date, and the list of cultivars grown in that trial.

Simulation Model

All simulations were conducted with the CSM-Cropsim-CERES-Wheat model Version 4.0.2.0 (Jones et al., 2003; Hoogenboom et al., 2004a), which incorporated features from Cropsim (Hunt and Pararajasingham, 1995) and CERES-Wheat (Ritchie, 1991; Ritchie et al., 1998). In CSM-Cropsim-CERES-Wheat, vernalization and photoperiod characteristics of different wheat cultivars or lines are specified in species, ecotype, and cultivar parameter files (Table 3). Developmental stages simulated include germination, seedling emergence, terminal spikelet initiation, anthesis, and physiological maturity. Species and ecotype parameters were held constant for all cultivars. The values were set as provided with the model except for the temperature response of vernalization and the critical long photoperiod, which are discussed below.

Rates of development vary with temperature and photoperiod. The model calculates the average daily temperature as the mean of the daily maximum and minimum temperatures, and all cardinal temperatures for development are based on average temperatures. In the absence of vernalization and photoperiod effects, development rates increase linearly at temperatures above a 0°C base temperature to an optimum of 26°C, above which development proceeds at a maximum rate. Occurrences of stages are simulated by integrating the effective temperatures over time, with a particular stage being reached when sufficient progress, quantified as accumulated effective temperature, has accrued.

In the presence of vernalization and/or photoperiod effects, the accumulated effective temperature is replaced by an equivalent temperature obtained by summing the products of daily effective temperature, a daily vernalization factor

Table 2. Locations providing data used for calibration or evaluation of the gene-based model parameters.

Country	Location	Latitude	Longitude	Elevation	Experiments
				m	
Calibration					
Canada	Lethbridge	49.72	−112.80	909	4
Chile	Chillan	−35.47	−71.92	217	5
Chile	Temuco-Carillanca	−37.33	−72.58	332	6
Germany	Weihenstephan	48.40	11.73	467	12
Hungary	Martonvasar	47.35	18.82	150	11
Japan	Morioka Iwate	39.75	141.13	167	8
Mexico	Toluca	19.27	−99.85	2640	3
Netherlands	Wageningen	51.97	5.64	7	13
South Africa	Bethlehem	−27.83	28.30	1631	12
United States	Davis, CA	38.53	−121.75	15	8
United States	Brookston, IN	40.58	−86.93	183	4
United States	Hutchinson, KS	38.05	−97.92	460	5
United States	Ithaca, NY	42.45	−76.45	293	6
United States	Pullman, WA	46.70	−117.13	777	8
Evaluation					
Argentina	Balcarce	−36.25	−58.23	135	8
Argentina	Bordenave	−34.15	−63.02	212	13
Argentina	Pergamino	−32.12	−60.58	68	1
Austria	Vienna	48.20	16.75	147	11
Bulgaria	Dubrodja	43.72	28.18	236	11
Croatia	Zagreb	45.82	15.98	177	12
Czech Republic	Sedlec	50.23	14.50	300	6
Finland	Jokioinen	60.82	23.48	92	3
France	Orgerus	48.83	1.67	100	4
Germany	Monsheim	49.58	8.33	160	11
Hungary	Szeged	46.00	20.00	84	8
Iraq	Sulaimaniya	36.50	46.50	700	6
Iran	Hamadan	34.78	48.50	1200	8
Iran	Karaj	35.78	50.00	1300	9
Italy	Milano	45.22	9.42	68	11
Nepal	Kathmandu	27.67	85.33	1360	2
Romania	Fundulea	44.50	24.17	66	13
Russia	Krasnodar	45.00	38.92	31	8
South Korea	Suwon	36.32	126.98	37	12
Slovakia	Male Ripnany	48.48	17.98	172	7
Sweden	Svalof	55.58	13.10	50	7
Switzerland	Zurich	47.48	8.53	445	8
Turkey	Erzurum	39.97	41.33	1870	8
Turkey	Eskisehir	39.75	31.58	789	5
Ukraine	Mironovski	50.25	31.17	151	2
Ukraine	Odessa	46.45	30.70	42	1
United Kingdom	Cambridge	52.17	0.10	65	6
United States	Akron, CO	40.08	−103.67	1389	1
United States	Ft. Collins, CO	40.58	−105.17	1475	11
United States	Billings, MT	45.80	−108.53	923	6
United States	Mead, NE	41.17	−96.42	360	9
United States	Salisbury, NC	35.70	−80.62	251	9
United States	Stillwater, OK	36.12	−97.07	270	13
United States	Corvallis, OR	44.50	−123.50	68	7

Table 3. Major model parameters affecting time of anthesis and related traits as specified in CSM-Cropsim-CERES-Wheat species, ecotype and cultivar files.[†]

Parameter	Definition	Value(s)	Units
Species file			
P1DT	Optimal long photoperiod, above which there is no additional effect of photoperiod on development.	23[‡]	h
P1VT	Vernalization type. Threshold value used to characterize response to vernalization.	50	day
P2(1)	Duration from terminal spikelet to jointing	80	°C day[§]
P4(1)	Relative duration from end of ear growth to anthesis	0.25	fraction of P4
PECM	Duration from germination to seedling emergence from a 1 cm planting depth.	10	°C day cm^{-1}
PEG	Duration from sowing to germination in the absence of moisture stress.	10	°C day
TRDV1	Temperature response, development 1	(curve)	°C
TRDV2	Temperature response, development 2	(curve)	°C
TRVRN	Temperature response, vernalization	(curve)[†]	°C
TRLTH	Temperature response, lethal temperature hardening	(curve)	°C
WFGEU	Effect of soil water availability on seed germination	0.5	fraction of
Ecotype file			
P1	Duration from end of juvenile phase to double ridge formation	280	°C day
P2	Duration from double ridges to end of leaf growth	250	°C day
P3	Duration from end of leaf growth to end of spike growth	240	°C day
P4	Duration from end of spike growth to end of lag phase for grain filling	300	°C day
Cultivar file			
P1V	Days at optimum vernalizing temperature required to complete vernalization.	16–74	day
P1D	Percentage reduction in development rate in a photoperiod 10 h shorter than the optimum (P1DT) relative to the rate at the optimum photoperiod	15–48	%
PHINT	Phyllochron interval: the interval in thermal time between successive leaf tip appearances.	80	°C day

[†] Values for P1V and P1D are ranges among the 29 cultivars. All other values were constant across cultivars.

[‡] Values were modified from those provided in the official release of the model. See methods section for details.

[§] Degree day.

(ranging from 0 to 1), and a photoperiod factor (also 0 to 1). The required accumulations of equivalent temperature are model parameters (Table 3).

The cultivar-specific vernalization coefficient P1V specifies how many days of vernalization are required in order for flowering to occur, assuming that temperatures for vernalization are optimal. Vernalization was assumed to occur at temperatures from −4 to 15°C, with the maximum rate occurring between 0 and 3°C. These values differ from the cardinal temperatures provided in the official release of the model (Hoogenboom et al., 2004b), which had cardinal temperatures of −5, 0, 7, and 15°C. This change was introduced because initial tests showed that the original cardinal temperatures required allowing values of P1V as high as 95 d, whereas most studies suggest that complete vernalization occurs in less than 60 d (e.g., Davidson et al., 1985). The model also allows for devernalization to occur when less than 10 d of progress toward vernalization have accumulated, and the maximum temperature exceeds 30°C. The daily vernalization rates are accumulated to indicate vernalization status, this value being used to calculate the vernalization factor. The daily photoperiod factor is calculated using a curvilinear response with P1D and P1DT as parameters, and photoperiod as the environmental variable.

Cultivar sensitivity to photoperiod is mainly determined by the parameter P1D, which specifies the reduction in developmental rate in a photoperiod 10 h shorter than the critical long photoperiod, P1DT. The photoperiod is calculated using a criterion of the sun being 6° below the horizon. P1DT was increased from 20 to 23 h for all cultivars to increase responsiveness of the model to the long photoperiods that occurred at high latitude sites.

Model Calibration

Fourteen locations, representing 105 experiments, were used to calibrate the model (Table 2). Each cultivar was calibrated independently starting from initial values of P1V of 60 d and P1D of 50%. These values were alternately modified, and simulations were run over the calibration datasets. Goodness of fit was judged by comparing means of observed vs. simulated values of flowering date, r^2 values, and RMSE. All other species, ecotype, and cultivar parameters (Table 3) were held constant.

Estimation of Genetic Effects

Genetic effects on P1V and P1D were estimated using the calibrated P1V and P1D values, and a linear regression approach similar to the procedure of White and Hoogenboom (1996) in which each locus was coded with a value of 1 for dominant and 0 for recessive. For vernalization, for which evidence from Halloran (1967) suggests that the *Vrn-1* loci have roughly additive effects (White, 2006), the relationship was established was P1V $= 60.0 − 14.5N_{Vrn}$, where N_{Vrn} is the total number of *Vrn-1* loci present (dominant) in a given cultivar ($r^2 = 0.57$, with $P < 0.01$; RMSE = 8.3 d).

For photoperiodism, although three *Ppd* loci have been identified in wheat, sufficient data were only available to estimate the effect of the *Ppd-D1* locus. The resulting linear model

for photoperiod was P1D = 39.9 − 13.9*Ppd-D1*, where *Ppd-D1* was coded with a value of 1 for wheat cultivars that possessed the dominant allele, and a value of 0 for the recessive allele. This regression gave an r^2 value of 0.42 ($P < 0.01$) and a RMSE of 7.5%. The reduction in sensitivity indicated in the equation agrees with expectation that dominant alleles of *Ppd* reduce photoperiod sensitivity (e.g., Worland, 1996).

Model Evaluation

Phenotypic data from 34 locations, representing 257 experiments were used to evaluate model outputs. Since locations used for calibration were independent of those used for evaluation, the evaluation results were expected to have less bias than if data from the same location were used both for calibration and evaluation. Initial evaluations used bivariate regressions of observed vs. simulated values. Multiple regressions were then used to assess the relative predictive capability of cultivar coefficients estimated directly or indirectly using knowledge of the genetic make-up of the cultivars and the equations linking genetic composition to the P1V and P1D coefficients, as in the approach of White et al. (2007). For the assessments, it was of interest to have a baseline value that would represent a generic cultivar. Thus, values of P1V and P1D were estimated for a hypothetical, generic cultivar by calculating mean values for the 29 cultivars. In regressions comparing predictions based on the three types of estimates of P1V and P1D, predicted values were considered fixed effects and were analyzed using the GLM procedure the SAS package (version 9.1, SAS Institute, Cary, NC). For analyses examining remaining sources of variation, locations, years, and cultivars were considered random effects, and variance components were estimated using the restricted maximum likelihood method as implemented for the MIXED procedure of SAS.

RESULTS

Simulations using the conventionally estimated coefficients predicted 98% of variation in days to flowering for the calibration dataset and 92% for the evaluation dataset (Table 4 and Fig. 1). The calibration dataset also showed a RMSE of 6.6 vs. 9.0 d for the evaluation data, agreeing with the expected loss of accuracy when dealing with an independent set of data. For single nurseries (years of distribution) of the IWWPN and across all locations, the difference in mean days to flower for the earliest and latest cultivars was typically 18 to 21 d.

Simulations with the gene-based coefficients gave r^2 values of 0.96 for the calibration and 0.90 for the evaluation data, with respective RMSE of 8.6 and 9.9 d. While the results with the gene-based model suggested only moderate loss of accuracy as compared to conventional coefficients, simulations with single values of P1V and P1D, representing the generic cultivar, also gave r^2 values of 0.95 for the calibration data and 0.89 for the evaluation data and RMSE values of 9.7 and 10.4 d, respectively (Table 4).

Regression analysis permitted quantifying whether modeling based on genetic information and relationships linking genetic composition to model coefficients resulted in a significant loss in accuracy. Both the gene-based and conventional coefficients explained large portions ($P < 0.001$) of the variation in the residuals from the regression for simulations with the generic cultivar (Table 5). The remaining variation was estimated as the total sums of squares (SS) less SS attributed to the generic cultivar in Table 5. Thus, for the calibration dataset, the gene-based model explained 29% of remaining variation, and the conventional model, 54%. For the evaluation dataset, the gene-based model explained 17% of remaining variation, and the conventional model, 27%. Comparing the residuals from the regression for simulations with the generic cultivar with the simulations using the other coefficients revealed that this explanatory ability was related to the difference in phenology between spring and winter

Table 4. Summary of comparisons of observed vs. simulated values of days to flowering for conventionally estimated model coefficients, gene-based estimates, and coefficients for a single generic cultivar.†

	Mean	r^2	Slope	Intercept	RMSE
	d				d
Calibration (*n* = 540)‡					
Observed values	208				
Conventional	209	0.98	0.95 (0.01)	10.1 (1.4)	6.6
Gene-based	208	0.96	0.92 (0.01)	16.0 (1.7)	8.6
Generic cultivar	208	0.95	0.95 (0.01)	10.0 (2.0)	9.7
Evaluation (*n* = 1499)					
Observed values	214				
Conventional	213	0.92	1.00 (0.01)	0.6 (1.6)	9.0
Generic cultivar	212	0.90	0.99 (0.01)	5.2 (1.8)	9.9
Mean values	214	0.89	1.02 (0.01)	−2.7 (2.0)	10.4

†Values of r^2 are significant at the 0.001 probability level. Values in parentheses after slopes and intercepts are standard errors.
‡*n* = number of pairs of observed vs. simulated data with no missing values.

Table 5. Analyses of variance for linear regressions examining ability of simulations to account for observed variation in phenology, considering both calibration and evaluation datasets.†

Source	df	Sums of squares (SS)	% SS	F-value	RMSE
					d
Calibration					
Generic cultivar	1	943,086	94.8	21,474	6.6
Gene-based	1	14,812	1.5	337	
Conventional	1	12,926	1.3	294	
Residual	536	23,540	2.4		
Evaluation					
Generic cultivar	1	1,371,807	89.5	17,269	8.9
Gene-based	1	27,452	1.8	346	
Conventional	1	16,442	1.1	207	
Residual	1481	117,649	7.7		

†The ANOVAs are for sequential entry of effects using values of P1V and P1D for the generic cultivar, gene-based estimates, and conventionally estimated values. *F*-values are significant at the 0.001 probability level.
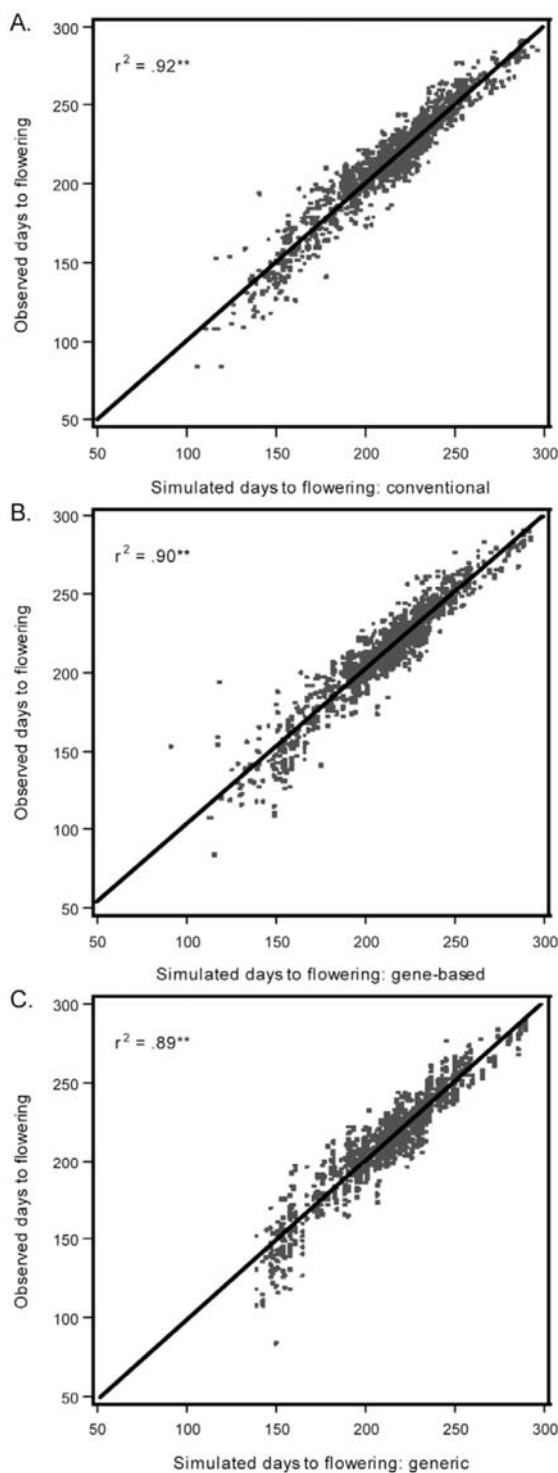
Figure 1. Comparisons of observed vs. simulated days to flowering for the evaluation datasets using different values of the coefficients P1V and P1D for the simulations: (A) conventionally estimated coefficients; (B) gene-based coefficients; (C) coefficients for a single generic cultivar (estimated as means of the conventional estimates). Fitted lines are for linear regressions with slopes and intercepts as given in Table 4.

wheats and the variation within the spring cultivars (Fig. 2, evaluation dataset only).

Complementary information about the performance of the gene-based coefficients was obtained with the data for residuals by first accounting for simulations using the gene-based coefficients, and then testing for effects of location, year within location, cultivar, and simulations using the conventionally determined coefficients (Table 6). When used alone, the gene-based coefficients explained over 90% of the total variation in the evaluation dataset (Table 4), but large portions of variation in the residuals were still associable with effects of location, year, cultivar, and the conventional model (Table 6).

DISCUSSION

The predictive capability of the model using gene-based coefficients confirmed the potential for predicting wheat phenology by combining physiological descriptions with genetic data. For the evaluation dataset, the gene-based model explained 63% of the variation that would be explained by conventionally determined model coefficients (SS of 14,812 for gene-based alone vs. SS of 27,738 for the conventional model), once the generic cultivar effect was considered (Table 5). Furthermore, when flowering date was simulated with the gene-based approach, only 5% of the total variation was unexplained in the calibration dataset and 10% in the evaluation set (Table 4).

The comparisons of conventional and gene-based simulations with residuals from the generic cultivar (Fig. 2) illustrated the impact of the limited availability of data on specific loci. There was no additional predictive power within the winter wheats, where only two genotypes (*Ppd-D1* dominant or recessive) were distinguishable with the available genetic data.

The results arguably present an optimistic view of the potential of gene-based wheat modeling because the set of genotypes and locations is more diverse than routinely dealt with in wheat breeding nurseries. Spring and winter wheats are seldom evaluated together, and experimental sites are often grouped according to similarities in growing environment and germplasm types grown. Nonetheless, first accounting for effects of the generic model should have fully compensated for the bias from considering a wide range of environments.

Conversely, the results may present a conservative impression of the utility of gene-based approaches due to constraints on the accuracy and completeness of the genotypic, phenotypic, and environmental data and of the model calibration. Our ability to ascribe genotypes for *Vrn* and *Ppd* loci should improve with rapid progress in sequencing the loci and understanding how they interact (Yan et al., 2003; Sherman et al., 2004; Turner et al., 2005;). Furthermore, the evidence for multiple alleles of the *Vrn-1* loci (Košner and Pánková, 1998; Sherman et al.,

2004; Yan et al., 2004) and for additional *Vrn* loci (Yan et al., 2006) offers promise for improved discrimination of vernalization response. Similarly, variation for earliness per se (*Eps*) loci (Scarth and Law, 1984; Appendino and Slafer, 2003; Tóth et al., 2003; van Beem et al., 2005) were not considered due to insufficient information on variation in *Eps* loci among cultivars. Incorporating effects of the *Eps* loci not only should improve overall performance of the model, but should allow for more accurate characterization of effects of the *Vrn* and *Ppd* loci.

Evaluations of time to flowering likely were subject to observer bias. In wheat research, "flowering" is most often equated to time of spike emergence, which is also termed "ear emergence" or "heading." However, it can also refer to time of anthesis. Regardless of the reference stage, there also may have been observer bias as to what portion of plants (or tillers) must have individually attained a given stage before a field plot was scored as having reached that stage. Weather data were also problematic. Although considerable effort was made to match reported experiment locations to weather stations, lack of weather data from actual experiment sites undoubtedly introduced additional error. Unlike most assessments of ecophysiological models, the evaluation data were fully independent of the calibration data since the two sets represented geographically separate sets of locations, which furthermore were managed by different research teams at each location.

There is no question of the long-term value of understanding the control of flowering at the level of gene expression and molecular signals, and recent progress is remarkable (Trevaskis et al., 2007). Our positive results emphasize, however, the immediate utility of combining existing ecophysiological models with genetic data. In the case of wheat, progress in interpreting genotype by environment interactions appears readily obtainable by improving characterization of wheat lines for variation in the *Vrn* and *Ppd* loci. Such an approach can benefit from information emerging from molecular studies, but the characterizations should emphasize robust description of ecotypic variation over detailed understanding of molecular mechanisms. Progress in quantitative modeling of phenology will likely reveal areas where research on specific processes will have high payoff. Ecophysiological models thus may provide a valuable tool for priority setting and hypothesis testing in plant biology, echoing arguments of R.S. Loomis and colleagues almost 30 yr ago for appropriate use of models (Loomis et al., 1979).

The strength of the results rest in large part on the availability of the large IWWPN dataset, currently maintained by CIMMYT. Although conducted over 25 yr ago, the experiments provide a unique resource for examining responses of genotype to environment. Combining findings from genomics with the integrative power of ecophysiological models holds potential for increasing our ability to
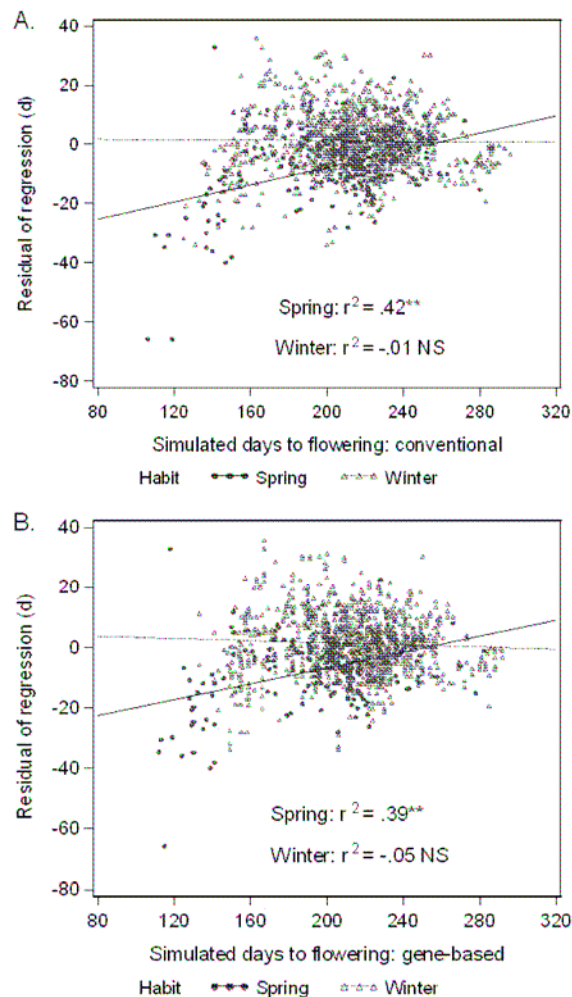
Figure 2. Comparisons of residuals of regression with the generic cultivar vs. simulated days to flowering for the evaluation datasets using different values of the coefficients P1V and P1D for the simulations. Fitted lines are for linear regressions estimated separately for spring or winter types: (A) conventionally estimated coefficients; (B) gene-based coefficients.

predict crop performance as a function of genotypes, management and expected environmental conditions.

CONCLUSIONS

Once expected large effects of location and year were accounted for, simulations using the gene-based approach accounted for 29 and 17% of variation in time to flowering, for the calibration and validation datasets, respectively. In comparison, conventional coefficients explained 54 and 27% of variation for the two datasets. Additional information on genetic makeup of cultivars should further improve the predictive power of the gene-based simulations. This might involve either refinements of linear estimates of gene effects or more mechanistic representations based on emerging information on gene action. Although

Table 6. Restricted maximum likelihood method analysis examining how location, year, cultivar, and model predictions from conventionally estimated coefficients account for residual variation in observed time to flower after allowing for model predictions using gene-based coefficients (regression equations given in Table 4).[†]

Parameter	Calibration dataset			Evaluation dataset		
	Variance component	SE	Z-value	Variance component	SE	Z-value
Location	17.83	8.91	2.00*	171.28	49.68	3.45***
Year (location)	14.89	2.87	5.18***	35.60	3.96	8.98***
Cultivar	1.85	0.80	2.33**	8.56	2.51	3.42***
Residual	15.90	1.14	13.98***	14.25	0.60	23.69***

Fixed effects	Value	SE	df	t	Value	SE	df	t
Intercept	21.36	4.02	13	5.3***	70.99	5.06	28	14.0***
Conventional	0.89	0.02	406	49.7***	0.68	0.02	1210	32.8***

*Significant at the $P = 0.05$ probability level.

**Significant at the $P = 0.01$ probability level.

***Significant at the $P = 0.0001$ probability level.

[†]Location, year within location, and cultivar were considered random effects, and the model predictions as fixed effects.

the focus was on phenology, a gene-based approach should be extensible to traits that more directly affect yield or grain quality. Application to other traits, however, again requires improved genetic characterization of wheat lines. The basic approach also appears readily applicable to other wheat models as well as to other crops.

Acknowledgments

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Results presented in the previous chapter indicated that genetic variability in vernalization requirement and photoperiod of wheat could be represented correctly by **gene-based estimates** of the corresponding cultivar parameters in the CSM-Cropsim-CERES-Wheat model.

What application can be developed out of these findings?

The objective investigated in the next chapter is to use model coefficients for plant breeding purposes through the design of ideotypes for a target population of environments. By the use of sensitivity analyses in the model, the combination of plant traits that maximize yield for a specific environment will be accomplished.

4 A Model-based Ideotyping Approach for Wheat under Different Environmental Conditions in the North China Plain

A Model Based Ideotyping Approach for Wheat Under Different Environmental Conditions in North China Plain

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Abstract

Before starting a breeding program for a specific crop or variety, it can be helpful to know how traits behave in determining yield under different conditions and environments. Crop growth models can be used to generate valuable information on the relevance of specific traits for an environment of interest. In this paper, the simulation model CMS-Cropsim-CERES-Wheat was used to test the performance of input parameters which describe cultivar differences concerning plant development and grain yield. In so-called ideotyping sequences, the specific cultivar parameters were varied and the model was run with the same management information in four different scenarios. The scenarios consisted of two locations, Wuqiao (37.3°N, 116.3°E) and Quzhou (36.5°N, 115°E) in Hebei Province (North China Plain), and a dry and a wet growing season for each location. The input parameter G1 (corresponding trait: kernel number per spike) followed by G2 (corresponding trait: kernel weight) had the biggest influence on yield over all scenarios. The input parameters P1V (corresponding trait: vernalization requirement) and P1D (corresponding trait: photoperiod response) also played an important role in determining yield. In the dry scenarios a low response in vernalization and photoperiod generated a higher yield compared to a high response. The lower responses caused earliness and the period of late water stress was avoided. The last relevant parameter that affected yield was PHINT (corresponding trait: leaf area of first leaf). The simulation showed that with an increasing PHINT, yield was enhanced over all scenarios. Based on the results obtained in this study, plant breeders could carefully select the relevant traits and integrate them in their breeding program for a specific region.

Key words: ideotyping, model, CMS-Cropsim-CERES-Wheat, breeding, North China Plain

INTRODUCTION

Since the early 1950s, the term ideotype was used to characterize ideal plant types. Up to now, ideotypes of crops like wheat, rice, and maize have been described (Donald 1968; Jennings 1964; Mock and Pearce 1975). These ideal plant types should serve as breeding goals and enable breeders to make faster progress than only by selection for yield. Donald (1968) defined the term ideotype breeding as follows: Yield should be enhanced by breeding for individual, mostly morphological traits. He pointed out that the first step of ideotype breeding should be to specify traits and their importance for determining yield. Since knowledge for a lot of traits is available, breeders often use field experiments across different years and sites to evaluate how traits influence yield. However, genetic differences are often masked by genotype × environmental interactions (Allard and Bradshaw 1964), which makes the quantitative pre-

diction of the traits more difficult. To reduce the environmental effects, mean values of a wide range of environmental factors can be used. This approach, however, does not show the physiological background of the observed variations. Another task for breeders to deal with is to know how traits behave under conditions differing from the tested environmental conditions. This needs further field experiments under these specific environmental conditions.

A good possibility to obtain the missing physiological information or to change environmental conditions without a new experiment is by simulation with suitable models. In recent years, simulation models were used to ascertain traits for higher yield. Particularly for rice a lot of studies exist, but also other crops like rape and soybean have been investigated (Dingkuhn *et al.* 1991; Penning de Vries 1991; Habekotte 1997; Messina 2003). Haverkort and Grashoff (2004) used the term ideotyping for tracing the ideal genotype for a target environment. For example, the crop growth model LINTUL-POTATO containing IDEOTYPING POTATO (Haverkort and Grashoff 2004) allows the adaptation of parameters for optimizing yield and gives breeders information about the behaviour of the traits before starting a breeding program in different environments. However, for wheat no ideotyping approach by the use of a simulation model under varying conditions and in different environments exists.

In China, wheat is mainly grown in North China Plain (NCP). The NCP contributes approximately 41% of the total wheat grain yield in China. The annual precipitation ranges between 500 mm in the north to 800 mm in the south, whereas the evapotranspiration is far beyond it. To attain high yields it is therefore necessary to irrigate. Considering that the groundwater level declines in some counties more than 1 m annually (Lu 2003; Kendy *et al.* 2003), it is an important aim to improve water use efficiency (WUE) of wheat varieties grown in the NCP. Besides the option to optimize irrigation schedules, an important water-saving method could be to select or breed new varieties that have a higher tolerance to water stress while maintaining high yields. Experiments at the Luancheng Agro-Eco Experimental Station in China showed that by the introduction of a new wheat variety, grain yield increased by 22% at the same irrigation level. A long term study from 1982 to 2002 indicated that WUE increased by 20% while total water consumption did not change considerably (Zhang *et al.* 2005). As a conclusion, plant breeders should be incited to breed new cultivars with higher WUE as an innovative contribution to save water.

The objective of this study was to highlight how crop growth models, in particular CSM-Cropsim-CERES-Wheat, can be used for ideotyping. Furthermore, the paper points out how CMS-Cropsim-CERES-Wheat can describe traits and their behaviour in different environments in order that plant breeders get information about their physiological background in determining yield and, in further consequence, in affecting WUE.

MATERIALS AND METHODS

The ideotyping approach consisted in using a crop growth model for wheat which was previously calibrated for a common wheat cultivar at two different locations in Hebei Province, China. The influence of traits in determining yield was evaluated by varying a number of parameters in an input file, where cultivar differences were specified. Changing the values of model parameters corresponded to subjecting a genotype with changed properties to a target environment. On the basis of these so-called ideotyping sequences, the influence of the traits on phenology and yield can be evaluated.

Model and model calibration

The crop growth model CMS-Cropsim-CERES-Wheat was used for ideotyping (Ritchie *et al.* 1985). CMS-Cropsim-CERES-Wheat is a part of DSSAT 4.0.1.0 (Decision Support System for Agrotechnology Transfer) which is designed to estimate crop production (Jones *et al.* 2003). CMS-Cropsim-CERES-Wheat has seven cultivar coefficients to characterize cultivar differences (Table 1). To calculate these cultivar coefficients, the following data are required: phenological dates (such as days to anthesis and days to harvest or maturity), yield and yield components (Hunt *et al.* 1993). In con-

trast to DSSAT 3.5, where cultivar coefficients are calculated by an optimization calculation program named GENCALC (Hunt *et al.* 1993), the coefficients in DSSAT 4.0.1.0 are calculated by hand. The procedure to obtain the coefficients comprises three steps: First, the coefficients P1V and P1D which affect days to anthesis have to be calculated. P1V and P1D values were varied to obtain a simulated anthesis date that matched the anthesis date observed from the field. The same procedure follows for the coefficient P5 which affects days to maturity. Finally, the parameters which influence yield and yield parameters (G1, G2, G3, and PHINT) must be calibrated equally (Jones *et al.* 2003).

For ideotyping in different environments, the coefficients are ideally derived from a common cultivar which is widely used in the country or region of interest. In this case, the cultivar coefficients were calibrated based on data across two locations and three years of a common Chinese cultivar named Shijiazhuang 8. The sites for the calibration of the cultivar coefficients were Wuqiao, which is located 250 km south of Beijing, Hebei

Province (37.3°N, 116.3°E) and Quzhou, 400 km southwest of Beijing, Hebei Province (36.5°N, 115°E). Datasets for calibration were field data from the China Agricultural University (CAU) experimental stations at these sites (Table 2).

Description of the simulation environments

Both simulation environments are located in Hebei Province. In this part of the NCP, winter wheat is mainly grown in a double cropping system with summer maize. For this, multiple cropping irrigation is essential, especially for wheat. Soil properties and common management for wheat in these regions are exemplarily shown in Table 2. The long term average temperature and precipitation are 12.6°C/562 mm for Wuqiao and 13.2°C/514 mm for Quzhou.

Fig.1 shows the average temperature and precipitation of the simulation environments of Quzhou and Wuqiao during the growing season for wheat (Oct. 1-Jun. 1) in the years 1996-2005.

Table 1 Cultivar coefficients of CSM-Cropsim-CERES-Wheat (Documentation DSSAT 4.0.1.0)

Cultivar coefficient	Description
P1V	Days at optimum vernalizing temperature required to complete vernalization
P1D	Percentage reduction in development rate in a photoperiod 10 h shorter than that at the optimum
P5	Grain filling (excluding lag) period duration (°Cd)
G1	Kernel number per unit canopy weight at anthesis (1 g^{-1})
G2	Standard kernel size under optimum conditions (mg)
G3	Standard, non-stressed dry weight (total, including grain) of a single tiller at maturity (g)
PHINT	Phylochron interval, the interval in thermal time (°Cd) between successive leaf tip appearances

Table 2 Management and soil data of the simulation environments which are required to calibrate the cultivar coefficients of the Chinese wheat cultivar Shijiazhuang 8

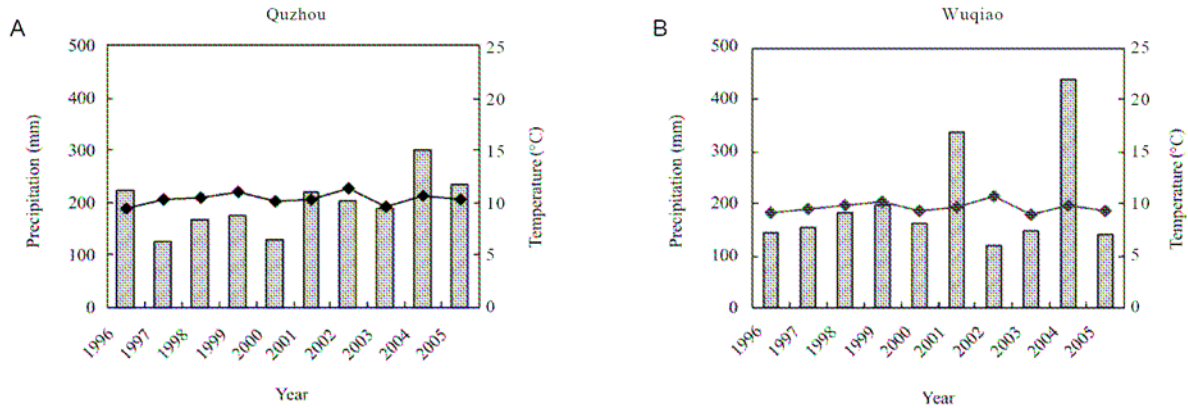|	Quzhou			Wuqiao		
	2003	2004	2005	2002	2003	2004
Soil type	Sandy clay			Silt loam		
Cropping system	Double cropping			Double cropping		
	winter wheat/summer maize			winter wheat/summer maize		
Tillage	No			No		
Planting date	Oct. 11, 2002	Oct. 18, 2003	Oct. 13, 2004	Oct. 7, 2001	Oct. 5, 2002	Oct. 8, 2003
Planting density (plants m^{-2})	450	450	450	450	450	450
Planting depth (cm)	4	4	4	4	4	4
Row spacing (cm)	15	15	15	15	15	15
Date of anthesis	April 21, 2003	April 21, 2004	May 1, 2005	May 9, 2002	May 11, 2003	May 13, 2004
Date of maturity	Jun. 4, 2003	Jun. 4, 2004	Jun. 12, 2005	Jun. 11, 2002	Jun. 13, 2003	Jun. 15, 2004
Grain yield (kg ha^{-1})	5 760	8 492	6 667	7 434	7 584	8 043
Irrigation						
1st application (mm)	Dec.15, 2002, 75	Mar. 24, 2004, 75	Oct. 27, 2004, 75	Mar. 28, 2002, 85	April 1, 2003, 80	April 2, 2004, 78
2nd application (mm)	Mar. 23, 2003, 75	May 9, 2004, 75	May 13, 2005, 75	May 16, 2003, 75	May 16, 2003, 77	May 18, 2005, 75
3rd application (mm)	May 8, 2003, 75					
Fertilization						
1st application (kg ha^{-1})	Oct.15, 2002, 195 N	Oct.9,2004,195N	Oct. 11, 2004, 140 N	Oct. 5, 2002, 70 N	Oct. 3, 2003, 70 N	Oct. 6, 2004, 75 N
	75 P_2O_5	75 P_2O_5	27 P_2O_5	75 P_2O_5	170 P_2O_5	183 P_2O_5
	0 K_2O	0 K_2O	0 K_2O	62 K_2O	70 K_2O	80 K_2O
2nd application (kg ha^{-1})	May 8, 2003, 120 N	May 9, 2004, 120 N	May 13, 2005, 105 N	Mar. 28, 2003, 160 N	Mar. 25, 2003, 180 N	Mar.29, 2004, 193 N

Fig. 1 Long term average temperature (dots) and precipitation (bars) during the growing seasons for wheat (Oct. 1- Jun. 1) in Wuqiao and Quzhou, Hebei Province.

Ideotyping sequences

To use CMS-Cropsim-CERES-Wheat for ideotyping, parameters in the cultivar file were modified (lower, higher and equal to the original cultivar coefficients of Shijiazhuang 8) and the model was run with the management, weather and soil data of the simulation environments. As every coefficient is related to a trait, ideotyping is interesting for breeders, too. The cultivar coefficients and their corresponding traits were arranged in two groups: cultivar coefficients which mainly affect plant development; cultivar coefficients which mainly affect yield components or total yield (Table 3). The extent of variation of the cultivar coefficients occurred according to the following principles: For P1V, the higher value (50 days) represented a winter type whereas the lower value illustrated a Chinese Spring type, which needs about 20 days to achieve vernalization saturation (Fowler *et al*. 1996). Tuning P1D up to 70 should generate sensitivity, a value of 30 should result in insensitivity to photoperiodic response. Varying

P5 by 150°Cd provokes a later or earlier maturity (± 10 days), assuming that the average temperature during grain filling is about 15°Cd above base temperature. A similar approach was used for PHINT, which was set to 90°Cd for the higher and to 70°Cd for the lower requirement. Here the assumption was made that 10°Cd difference results in building approximately 1 leaf more or less.

Kernel numbers per unit canopy weight at anthesis (G1) was set to 30 and 20 according to a study conducted at Luancheng Station, where modern cultivars had around 30 and old varieties about 20 kernels per spike. Correspondingly, the values for G2 were set to 40 for modern and to 30 for older varieties (Zhang *et al*. 2005). The different values for G3 resulted from the variation of other yield-affecting parameters.

In the so-called ideotyping sequences the behaviour of these parameters was tested for four scenarios:

Scenario 1: Quzhou (wet)
Scenario 2: Wuqiao (wet)
Scenario 3: Quzhou (dry)
Scenario 4: Wuqiao (dry)

Dry and wet conditions were selected from the 10 years weather data in two different simulation environments. These were for Quzhou the years 1997 (dry) and 2004 (wet), for Wuqiao the years 2002 (dry) and 2004 (wet) (Fig.1). Management and soil data for these sequences are shown in Table 4.

To minimize the management differences and therefore reduce the simulation to effects of environmental differences, irrigation and fertilization times and amounts were set on equal values for both environments. By

Table 3 Cultivar coefficients and their corresponding physiological traits

Cultivar coefficient	Corresponding traits
Cultivar coefficients which mainly affect plant development	
P1V	Vernalization requirement
P1D	Photoperiod response
P5	Grain filling duration
PHINT	Leaf area of first leaf in vegetative and reproductive stages
Cultivar coefficients which mainly affect yield	
G1	Kernel number per spike
G2	Kernel weight
G3	Stress tolerance

Table 4 Growing conditions, soil properties and management data for wheat in the simulation environments used for the ideotyping sequences

	Quzhou	Wuqiao
Growing condition		
Wet (yr)	2004	2004
Dry (yr)	1997	2002
Soil		
Soil type	Sandy clay	Silt loam
Management		
Planting date	Oct. 10, yr[1]	
Planting density (plants m⁻²)	450	
Planting depth (cm)	4	
Row spacing (cm)	15	
Irrigation		
1st application (mm)	Mar. 1, yr, 75	
2nd application (mm)	May 1, yr, 75	
Fertilization		
1st application (kg ha⁻¹)	Oct. 1, yr, 70 N	
	75 P₂O₅	
	0 K₂O	
2nd application (kg ha⁻¹)	May 1, yr, 160 N	

[1] The corresponding year.

running these sequences, it can be shown how the co-efficients and their corresponding traits behave under varying conditions in different environments.

Statistical analyses

To compare observed with simulated data across different years and locations, root mean squared error (RMSE) and coefficient of determination were calculated. Means of treatments were calculated of all collected field data.

RESULTS AND DISCUSSION

Model calibration

Line 1 in Table 5 shows the values of the calibrated coefficients across three years simulated with the management and soil data from Table 2. The quality of the simulated vs.observed data is exemplarily represented for yield in Fig.2.

Before the behaviour of the coefficients in different environments and growing conditions can be elucidated, the initial differences between the locations from the calibrated values prior to variation have to be explained.

Table 5 shows that under dry growing conditions with the calibrated values in both environments a significant lower yield was achieved. The yield reduction can be accounted to severe water stress between end

of ear growth and end of grain filling. Zhang *et al.* (1999) and Li (1990) reported for wheat in the NCP a sensitivity to water stress from stem elongation to milking. The difference in plant development [later anthesis in Wuqiao (wet) and earlier anthesis in Quzhou (wet) compared to Wuqiao (dry) and Quzhou (dry)] can be explained by differing starting dates of the vegetation periods. Long cold periods till mid of February delayed development in Wuqiao (wet) and Quzhou (dry), in contrast to Wuqiao (dry) and Quzhou (wet), where the earlier start of growth and relatively high spring temperatures accelerated plant phenology.

Modification of cultivar coefficients which mainly affect plant development

Daylength and temperature are the most important environmental variables influencing anthesis date and in further consequence yield components and yield. The cultivar coefficients P1V, P1D, P5 and PHINT which respond to these two environmental variables were varied to test the effect on date of anthesis and maturity, respectively. Environmental constraints like water stress can also affect plant development and yield.

Sequence 1 In sequence 1, the cultivar coefficient P1V was varied to compare the plant development and final yield of ideotypes in the two target environments and growing seasons. For the first run the vernalization requirement was set to 20 days, for the second run to a higher requirement (50 days) compared to the initial value of Shijiazhuang 8 (35 days).

Table 5 shows that the model simulation allowed the lower vernalized ideotype to flower and ripen earlier and generated in three cases a slightly higher grain yield than the calibrated values. The opposite was observed for the higher vernalization requirement where ripening was delayed. Under dry conditions, which are growing seasons with water stress in the late development stages, yield was diminished compared to the calibrated values. Considering the negative effects of water stress from stem elongation to milking on yield, an earlier anthesis and maturity date, caused by a lower vernalization requirement, seems to be a possibility to avoid the period of water stress. However, this only applies if the vegetation period begins early in the year and the lower vernalized type has the advantage of an earlier

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Table 5 Effect of varying cultivar coefficients on plant development and yield in two different simulation environments and under two different growing conditions

	P1V	P1D	P5	G1	G2	G3	PHINT	Quzhou			Wuqiao		
								Anthesis (DAP)	Maturity (DAP)	Yield (kg ha^{-1})	Anthesis (DAP)	Maturity (DAP)	Yield (kg ha^{-1})
Shijiazhuang 8	35	45	650	25	35	1.50	80	196	237	7370	203	244	7400
SEQUENCE 1													
Wet													
Shijiazhuang 8	35	45	650	25	35	1.50	80	195	238	8033	200	243	7853
P1V=20								189	233	8204	193	238	7444
P1V=50								202	243	8300	206	246	8126
Dry													
Shijiazhuang 8	35	45	650	25	35	1.50	80	204	245	6874	196	238	6840
P1V=20								199	241	6914	187	233	7219
P1V=50								210	249	6447	205	243	6584
SEQUENCE 2													
Wet													
Shijiazhuang 8	35	45	650	25	35	1.50	80	195	238	8033	200	243	7853
P1D=30								192	235	8250	195	240	7496
P1D=70								203	244	8187	208	247	8010
Dry													
Shijiazhuang 8	35	45	650	25	35	1.50	80	204	245	6874	196	238	6840
P1D=30								201	243	7064	192	236	7122
P1D=70								211	250	6409	205	243	6584
SEQUENCE 3													
Wet													
Shijiazhuang 8	35	45	650	25	35	1.50	80	195	238	8033	200	243	7853
P5=500								195	231	8016	200	236	7842
P5=800								195	244	8049	200	248	7864
Dry													
Shijiazhuang 8	35	45	650	25	35	1.50	80	204	245	6874	196	238	6840
P5=500								204	239	6874	196	233	6832
P5=800								204	250	6879	196	244	6848
SEQUENCE 4													
Wet													
Shijiazhuang 8	35	45	650	25	35	1.50	80	195	238	8033	200	243	7853
PHINT=70								195	238	7471	200	243	7072
PHINT=90								195	238	8860	200	243	8997
Dry													
Shijiazhuang 8	35	45	650	25	35	1.50	80	204	245	6874	196	238	6840
PHINT=70								204	245	6827	196	238	6071
PHINT=90								204	245	6934	196	238	7533

change from vegetative to generative phase. In Quzhou (dry) the late beginning of the growing season lessened these positive effects slightly.

If there was low water stress like in Quzhou (wet), ideotypes with a higher, as well as with a lower vernalization requirement produced higher yield. This phenomenon is not caused by avoiding water stress in late development stages. It is rather a complex interaction between temperature and photoperiod in different development stages. Conclusively, the higher vernalized ideotype remained longer in the stage of vegetative growth, and as no water stress occurred, it produced more yield components. Rahman *et al.* (1977) reported a positive correlation between the length of the vegetative phase and the number of spikelets per spike. The lower vernalization requirement

caused a shorter vegetative growth and therefore a comparatively longer generative growth with a positive effect on yield. In Wuqiao (wet) a late start of growing season prevented the positive effect of a long vegetative growth. For Quzhou (wet) a comparatively longer generative growth and therefore a yield advantage for an ideotype with a higher vernalization requirement was observed.

Sequence 2 In the next ideotyping sequence, P1D was changed to show how an ideotype with low (30) or high (70) photoperiod response performed concerning development and final yield in the different scenarios. The same pattern as for vernalization requirement could be observed (Table 5). A lower sensitivity, generating an earlier development, created a higher yield compared to a higher sensitivity under dry growing conditions.
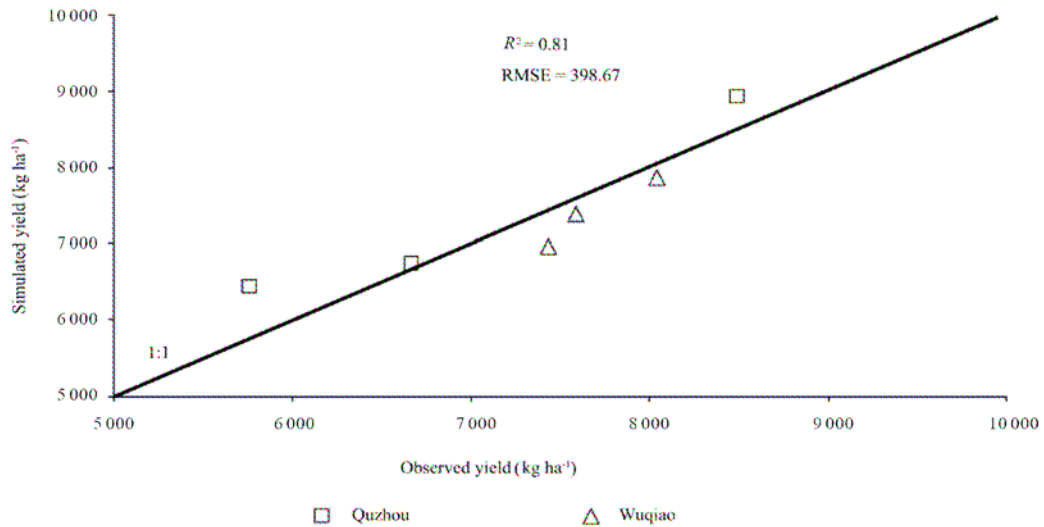
Fig. 2 Simulated vs. observed yield (kg ha⁻¹) for calibration across three years and the two simulations environments Wuqiao and Quzhou.

The reasons were the same as explained in Sequence 1. Studies showed that wheat with low photoperiod sensitivity (photoperiod insensitivity) tends to accelerate heading and maturity, and has therefore the advantage, especially in hot regions, to finish grain filling before water stress can affect yield (Worland 1996).

Under wet growing seasons yield improvement or reduction is also caused by development differences and influenced by environmental constraints as mentioned in Sequence 1. Comparable results were found in mainland regions in Europe where a photoinsensitive cultivar carrying the allele at the *Ppd-D1* locus dominant reached about 15% higher yields, in UK no advantages compared to photosensitive cultivars were found (Dyck *et al.* 2004).

Sequence 3 The coefficient P5 was used to compare the effect of a long or a short grain filling duration. The values were set to 800 for a long period and 500 for a short period. The simulation revealed that the extended grain filling period as well as the shortened period had almost no influence on yield (Table 5). The reason was that the calibrated value with 650°Cd represented already a long grain filling duration. Normally, grain filling is finished for Chinese cultivars in these regions between 30-35 d (Chenggang S 2005, personal communication) i.e., 450°Cd. However, in the case of water stress during grain filling, grain weight will be reduced due to a shortening of the period resulting from accelerated senescence (Hochmann 1982).

Sequence 4 In this sequence two different phylochron intervals (PHINT) were compared. The ideotype with a lower PHINT (70°Cd) produced a higher number of final leaves which generated a significantly lower LAI and correspondingly a lower yield in almost all scenarios. The opposite occurred when PHINT was raised up to 90°Cd. The number of final leaves was diminished and LAI increased, which finally resulted in a higher yield (Table 5).

This is true for wet growing seasons in the leaf building stages. In Quzhou (dry), where severe water stress conditions prevailed during early vegetative stages, the final leaf number was also influenced as described above, but LAI and therefore yield varied little between the different diversifications. This was caused by a reduced leaf expansion and correspondingly decreased LAI due to stress conditions. The reduction of leaf expansion by drought stress was also reported by Boyer (1968).

Summing up, the results of this study indicated that P1V (corresponding trait: vernalization requirement) was the most important factor for plant development, and affected yield indirectly. The impact of this parameter varied over environments and growing conditions. As a conclusion, a low or facultative vernalization requirement slightly enhanced yield. An earlier development in dry growing seasons allowed plants to avoid the period of water stress.

Plant development was secondarily influenced by

P1D (corresponding trait: photoperiod response). In nearly all cases, insensitivity resulted in a slightly higher yield. Similar to a low vernalization requirement, photoperiod insensitivity caused earliness and therefore an advantage regarding the avoidance of water stress. PHINT (corresponding trait: leaf area of first leaf) also had an important effect on yield. High LAI on account of few leaves with big area produced the highest yield in almost all scenarios. No influence on plant development was observed. P5 (corresponding trait: grain filling duration) and G3 (corresponding trait: stress tolerance) had no significant effects on yield and in further consequence on WUE in any of the simulated cases.

Modification of cultivar coefficients which mainly affect yield and yield components

Wheat grain yield can be computed by multiplication of the yield components. In this part, only the single impact of a yield component will be accounted. The yield enhancement triggered by yield component compensation was not considered.

Sequence 5 In this sequence, the cultivar coefficient G1 was set to 20 and 30, respectively. Varying kernel number by five kernels resulted in nearly 1.5 t more or less grain yield (compared with the initial value of the calibrated cultivar) for low stressed and around 1.3 t for late stressed plants (Fig.3-A, B). Similar results were also reported in a long term study at the Luancheng Station where an increase of about 6 kernels per spike significantly enhanced yield (Zhang 2005). The effect of this parameter as well as the effect of G2 (Sequence 6) on grain yield must be seen in context of yield component compensation (Adams 1967). Especially in warmer environments, a negative compensatory effect of the number of spikes per square meter on number of kernels per spike and kernel weight existed (Garcia del Moral *et al.* 2003).

Sequence 6 To assume a high or a low standard kernel size under optimum conditions, different values for G2 were compared. The higher kernel size was set to 40, the lower to 30. The same pattern as for varying G1 was achieved, but on a slightly lower level. Values differed by 1.2 t from calibrated yield in wet growing seasons and by 1 t in dry growing

seasons (Fig.4-A, B). As mentioned above, the compensatory effects among yield components should be considered.

Sequence 7 In the last ideotyping sequence the cultivar coefficient G3 was modified. As already mentioned, the variation of G3 results from the variation of G1 and G2. The values are therefore 1.3 for the low and 1.7 for the high response. Within this range no significant reduction or increase of grain yield was found for any scenario (Fig.5-A, B).

The impact of this parameter on yield is limited and therefore only a considerable change would generate a significant difference in yield.

The cultivar coefficient G1 (corresponding trait: kernel number per spike) had a major impact on yield and in further consequence on WUE in all scenarios. G2 (corresponding trait: kernel weight) as the next important factor increased yield in all environments and under all conditions significantly, but not as much as G1. However, possible compensatory effects among yield components must be considered when discussing the yield enhancement caused by these parameters.

In Table 6, the responses of all parameters and their corresponding traits are presented. It gives breeders a short overview of the performance of the traits in different scenarios. With this information, ideotypes for all environments and growing conditions can be created. Furthermore, it shows how the parameters and traits can affect yield.

This ideotyping approach was developed on the basis of one cultivar. Other cultivars may react differently. However, the reaction principles are expected to correspond.

CONCLUSION

The crop growth model CSM-Cropsim-CERES-Wheat is a suitable tool to show the physiological background of traits in determining yield and plant development in different environments and under varying conditions. It allows adapting input parameters which influence plant development, yield components and finally yield. In so-called ideotyping sequences the quantitative impact of these parameters on yield can be simulated by varying them in different simulation environments under different growing conditions. To make it interesting
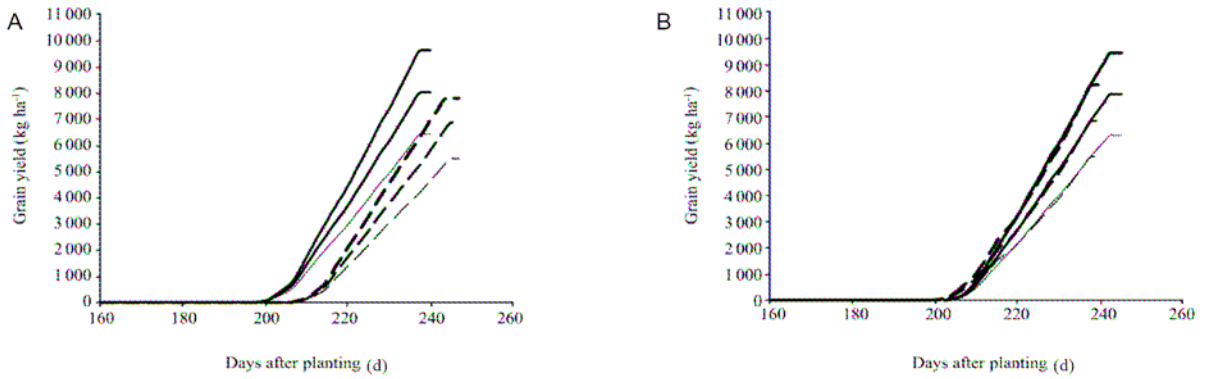
Fig. 3 A, change of yield and plant development in the simulation environment Wuqiao after varying the cultivar coefficient G1. B, change of yield and plant development in the simulation environment Quzhou after varying the cultivar coefficient G1. Dashed lines represent the dry growing season, solid lines the wet season. Increasing thickness of the lines corresponds to the increase of the coefficient from 20 to 25 to 30.

Fig. 4 A, change of yield and plant development in the simulation environment Wuqiao after varying the cultivar coefficient G2; B, change of yield and plant development in the simulation environment Quzhou after varying the cultivar coefficient G2. Dashed lines represent the dry growing season, solid lines the wet season. Increasing thickness of the lines corresponds to the increase of the coefficient from 30 to 35 to 40.
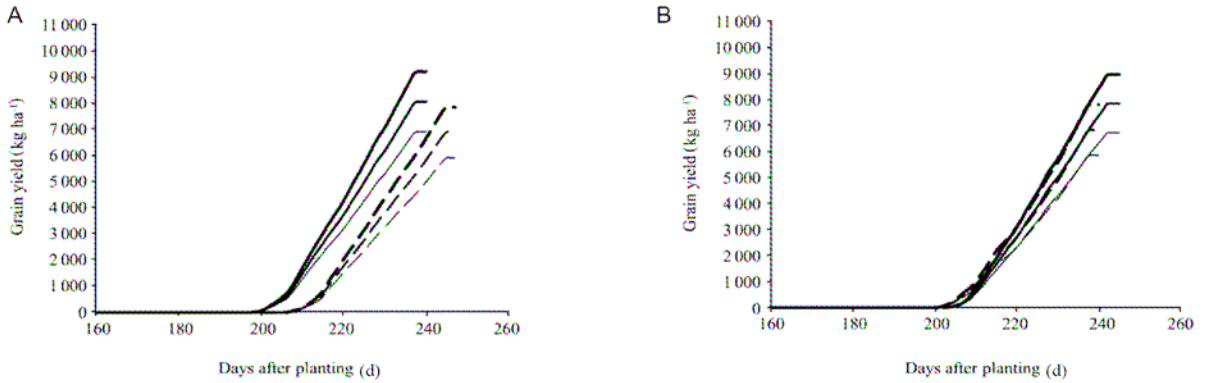

Fig. 5 A, change of yield and plant development in the simulation environment Wuqiao after varying the cultivar coefficient G3; B, change of yield and plant development in the simulation environment Quzhou after varying the cultivar coefficient G3. Dashed lines represent the dry growing season, solid lines the wet season. Increasing thickness of the lines corresponds to the increase of the coefficient from 1.3 to 1.5 to 1.7.
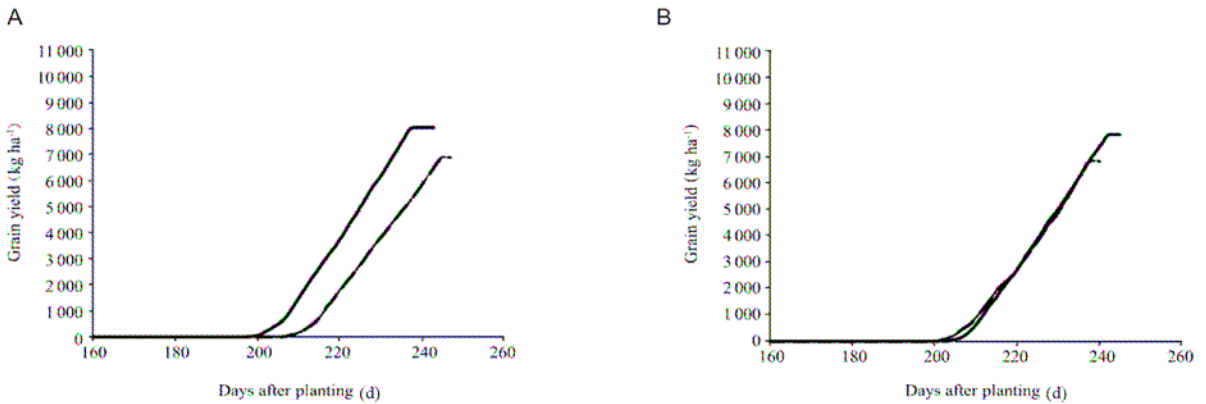
Table 6 Performance of the cultivar coefficients and their corresponding traits concerning yield

Cultivar coefficient	Growing condition	Variation	Quzhou		Wuqiao	
			Response	Proposed breeding goal	Response	Proposed breeding goal
P1V	Wet	Down	+	Facultative vernalization requirement	- -	High vernalization requirement
		Up	+		+	
	Dry	Down	0	Medium vernalization requirement	++	Low vernalization requirement
		Up	- -		-	
P1D	Wet	Down	+	Insensitivity to photoperiod	-	Sensitivity to photoperiod
		Up	0		0	
	Dry	Down	+	Insensitivity to photoperiod	+	Insensitivity to photoperiod
		Up	- -		-	
P5	Wet	Down	0	No response	0	No response
		Up	0		0	
	Dry	Down	0	No response	0	No response
		Up	0		0	
PHINT	Wet	Down	- -	High leaf area of first leaf	- -	High leaf area of first leaf
		Up	++		++	
	Dry	Down	0	No response	- -	High leaf area of first leaf
		Up	0		++	
G1	Wet	Down	- -	High kernel number per spike	- -	High kernel number per spike
		Up	++		++	
	Dry	Down	- -	High kernel number per spike	- -	High kernel number per spike
		Up	++		++	
G2	Wet	Down	- -	High kernel weight (minor effect than G1)	- -	High kernel weight (minor effect than G1)
		Up	++		++	
	Dry	Down	- -	High kernel weight (minor effect than G1)	- -	High kernel weight (minor effect than G1)
		Up	++		++	
G3	Wet	Down	0	No response	0	No response
		Up	0		0	
	Dry	Down	0	No response	0	No response
		Up	0		0	

++/-- 5%, +/- = 5-2%, 0   2% more or less yield after variation.

for breeders, the parameters which are used in the model can be linked with phenological traits. By the use of this ideotyping approach, breeders can see how traits behave in different environments under varying growing conditions. With the information of the physiological background, they can decide whether it makes sense to test a trait in a field experiment under specific environmental conditions. Furthermore it allows breeders to quantify the impact of the variation of a trait in various environments and under different growing conditions.

The approach of testing calibrated parameters in different environments under different conditions by the use of a crop growth model was developed and applied exemplarily. This method can be used for further questions such as the consequences of varying plant phenology on biotic or abiotic stress factors or the effect of climate change.

Acknowledgements

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In the previous chapter, genotypic differences among ideotypes for photoperiod response, vernalization reuqirement translated into differences in potential yield for dry scenarios in two locations in the North China Plain. Results help plant breeder to understand the physiological background before selecting a specific trait.

Enhanced understanding of the underlying physiological processes of past genetic improvement can increase the efficiency of plant breeding programs. The analysis of genetic improvement by statistical means with genotypic model parameters to investigate the coherences between phenology and grain protein content was accomplished in the next Chapter.

5 The Impact of Vernalization Requirement, Photoperiod Sensitivity and Earliness *per se* on Grain Protein Content of Bread Wheat (*Triticum aestivum* L.)

The impact of vernalization requirement, photoperiod sensitivity and earliness per se on grain protein content of bread wheat (*Triticum aestivum* L.)

Markus Herndl · Jeffrey W. White · Simone Graeff · Wilhelm Claupein

Abstract In wheat, a shorter pre-anthesis phase is often associated with increased grain protein content (GPC) but decreased grain yield. Cultivar differences in pre-anthesis development are mainly determined by vernalization requirement, photoperiod sensitivity and earliness per se. This research examines whether cultivar differences in these traits affect GPC, especially whether the three traits can partially explain genotype × environment interactions for GPC. Twenty-four winter wheat and five spring wheat cultivars selected from International Winter Wheat Performance Nursery (IWWPN) trials and 12 winter wheats tested over 2 years in Germany were characterized using the CSM-Cropsim-CERES-Wheat model. The model parameter P1V specifies the cultivar vernalization requirement, P1D the photoperiod response, and P_{123} earliness per se. Covariance analyses of the IWWPN dataset indicated that about 7% of variation in GPC was explained by cultivar, with another 7% attributable to interactions of cultivar with region, site and year. P1V, P1D and P_{123} all influenced GPC, but their effects varied with region, site and year. For example,

for two regions, the effect of P1V on GPC decreased with latitude. Path analyses using the data from Germany confirmed that GPC increased with earlier anthesis, which was influenced by P1D and P_{123}. Lack of an effect of P1V at this location presumably was due to all cultivars being completely vernalized. The results indicate that efforts to improve GPC could target the three traits to specific populations of environments, which should reduce the large influence of environment on GPC.

Abbreviations
GPC   Grain protein content
P_{123} Earliness factor based on model parameters
NNFI   Non-normed fit index

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Introduction

Grain protein concentration (GPC) is a key determinant of grain quality in bread wheat, but improvement of GPC is challenging due to large effects of genotype, environment and their interactions (G × E). The relative importance of these factors varies among experiments and environments (e.g. Cox et al. 1985b; Rao et al. 1993). Baenziger et al. (1985) found that in a set of 22 soft and two hard wheat cultivars, tested in

12 environments, there was a 99 times higher variance component of environment than for cultivar. The effect of environment makes it difficult for breeders to test the influence of single traits on GPC, especially if effects of G × E are large. Major environmental factors influencing GPC include air temperature, soil nitrogen levels, water availability during grain filling, as well as post-anthesis light intensity and photoperiod (Kolderup 1975; Spiertz 1977; Van Herwaarden et al. 1998). Genotypic differences have also been reported for traits influencing GPC, including pre- and post-anthesis N-uptake (Woodruff 1972; Austin et al. 1977; Cox et al. 1985a) and nitrogen harvest index (Flood and Martin 2001).

Interpreting G × E effects on GPC requires understanding of the dynamics of supply and demand relations (the source/sink balance), with the relation between C and N being of special interest. Because C assimilation increases faster than N accumulation, GPC usually decreases with greater grain yield (e.g. Lawlor 2002). Grain N accumulation is mostly source-driven and is determined by N stored in vegetative organs and N-uptake from soil during the post anthesis period. Grain yield is mainly determined during pre-anthesis growth but is also influenced by the duration after anthesis (Richards 2000; Martre et al. 2003; Slafer 2003).

Acuña et al. (2005) showed that a shorter pre-anthesis phase (induced by exposition to long days), resulted in low grain yield and increased GPC. Early anthesis, long grain filling duration, low grain filling rate, and high protein concentration were strongly interrelated in F_1 hybrids of Chinese and U.S. cultivar diallel crosses (Mou et al. 1994). Since date of anthesis is highly heritable (e.g. Hsu and Walton 1970), analyses of variation in GPC might benefit from considering the influence of pre-anthesis development. Emphasis on optimizing phenology has special relevance given growing concerns over climatic risk and global warming, which may induce wheat producers to seek earlier maturing cultivars to reduce risk or conversely to seek cultivars with longer growth cycles to exploit longer growing seasons.

Cultivar differences in pre-anthesis development are mainly determined by vernalization requirement, photoperiod sensitivity and earliness per se. Many reports have provided semi-quantitative descriptions for cultivar differences in these traits, but in most cases, responses were determined using artificial environments

(e.g. Davidson et al. 1985; Hoogendoorn 1985; Kato et al. 2001), and the results appear to be difficult to use for quantitative predictions of phenology. Promising alternatives include characterizing cultivar differences through parameters used in process-based ecophysiological models (Herndl et al. 2008) and using genetic data to characterize these three traits (White et al. 2008). Used as inputs to a process-based model, such parameters can reliably predict crop phenology. Since simulation models can integrate interacting effects of genotypic differences, temperature, photoperiod regimes, and management (mainly time of planting), it seems likely that model-based characterizations of cultivars can help explain G × E interactions for GPC. Another option would be to analyze simulated variation in GPC. However, simulations require detailed characterizations of initial soil nitrogen and organic matter status and of crop management, and such data are seldom available for wheat breeding nurseries.

The objectives of this paper are to test whether vernalization requirement, photoperiod response and earliness per se partially explain cultivar differences in GPC and to examine whether including effects of the three traits are useful in analyzing G × E interactions for GPC. Two contrasting sets of data were considered, one from a widely distributed set of international cultivar trials and one from a single location that involved detailed characterizations of cultivar responses.

The research was anticipated to require consideration of processes that interact strongly along causal paths. Path analysis can be used to test schematic models that specify causal relations among multiple variables. The procedure determines how well a proposed model successfully accounts for the actual relationships observed in the sample data (Hatcher 1994). For agronomic purposes, path analysis is often used to assist identifying selectable traits (Duarte and Adams 1972; Kang et al. 1983). To use path analysis for investigation of causal relations among traits influencing wheat phenology and GPC, a theoretical model must be specified first. Causal relations can be based on experimental results or on a priori grounds. Figure 1 presents a simple model of a possible cause and effect relationship between phenological traits and GPC. The single-headed straight arrows represent direct effects between endogenous variables (variables where the variability is predicted to be causally affected by other variables in the model) and

Fig. 1 The initial theoretical model (cause and effect relationship) among phenological traits and grain protein content

ᵃ Days from planting
E Error term
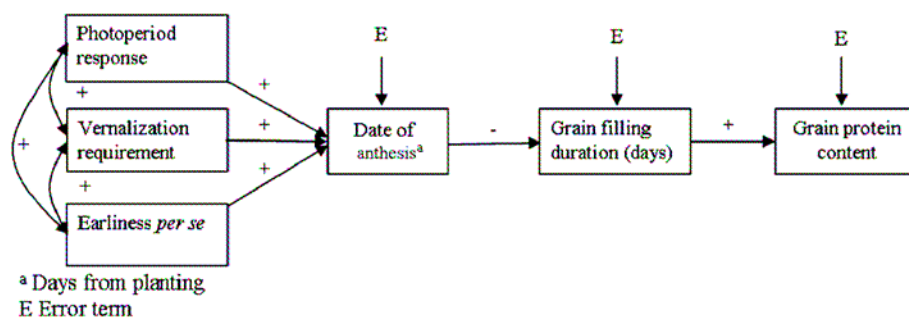
exogenous variables (constructs that are influenced only by variables that are outside the model). The double-headed curved arrows indicate correlations among exogenous variables.

Materials and methods

IWWPN trials

Data for GPC evaluated for a range of sites, years, and cultivars were obtained from digitized reports of the International Winter Wheat Performance Nurseries (IWWPN) stored at CIMMYT (IWIS; Payne et al. 2002). These series of trials were organized by the Nebraska Agricultural Experiment Station and the Agricultural Research Service, U.S. Department of Agriculture, under a contract with the Agency for International Development. The nurseries were distributed in over 40 countries. Altogether 168 wheat cultivars and breeding lines were tested from 1969 to 1981, the vast majority being winter types. Nurseries contained 30 entries per year and at each site, were arranged in four randomized complete blocks. Agronomic practices varied with site but most often were representative of nearby commercial production. Precipitation ranged from a high of 1,804 mm at Morioka, Japan in 1981 to a low of 22 mm at Toluca, Mexico in 1973. Supplemental irrigation was applied in a few nurseries (4–11 nurseries, depending on the year). Nitrogen fertilizer was applied to most nurseries, with rates ranging from 5 to 224 kg N ha^{-1}. GPC was determined at a single laboratory in Nebraska.

Twenty-four winter wheat and five spring wheat cultivars were selected based on available data for GPC (Table 1). The cultivars had been tested at 55 sites in 32 countries over 13 years (Table 2).

To simplify the interpretation of G × E variance components, locations were classified in seven regions according to the classification of Peterson and Pfeiffer

(1989) (Table 2). Locations associated with Region 1 tend to have low potential grain yield and due to the continental climate influence, winter stress affects cultivar adaptation. Region 2 locations have later heading and ripening dates, associated with higher grain yield potential, and they predominantly include locations from Western and Central Europe with a maritime climate. Regions 3 and 4 tend towards earlier heading and ripening dates and are centered in the Middle East and Eastern Europe, respectively. Region 5 has later heading and ripening dates. Region 6 includes three sites form South America, and Region 7, two sites from South Africa. These latter two regions have mild winters and are mainly considered as spring and facultative wheat regions.

Field experiments at Ihinger Hof

During the growing seasons of 2004–2005 and 2005–2006, field experiments with 12 winter wheat cultivars were conducted at Ihinger Hof, Germany (48°44′ N; 8°56′ E; 450 m elevation, 693 mm average annual precipitation, 8.1°C mean annual temperature) to provide data on crop growth and development. According to WRB-classification (FAO 1998), the soil type is a Haplic Luvisol. The texture ranges between silty clay and clayey silt. Seed was planted at October 23, 2004 and October 12, 2005 at a rate of 350 kernel m^{-2} in plots consisting of 12 rows, 14 cm apart and 6 m long. Nitrogen was applied as ammonium sulphate at the rate of 50 kg N ha^{-1} at the beginning of vegetative growth and as calcium ammonium nitrate at the rate of 25 kg N ha^{-1} at Zadoks stage 30 in 2004. In 2005, nitrogen was applied using the same fertilizer and stages at rates of 35 and 20 kg N ha^{-1}, respectively. Together with mineralized nitrogen (assessed before the first nitrogen application), the plants received approximately 100 kg N ha^{-1} in each trial. The experiment was arranged as a split plot

Table 1 Cultivar parameters P1V (days at optimum vernalizing temperature required to compete vernalization), P1D (percentage reduction in development rate in a photoperiod 10 h shorter than the optimum relative to the rate at the optimum) and calibrated sum of the component phase durations (P_{123}) of cultivars calibrated over 2 years at the research station Ihinger Hof, Germany and IWWPN cultivars calibrated over 55 sites and 13 years (Table 2)

Cultivar	Origin[a]	Habit	Cultivar parameters		
			P1V (days)	P1D (%)	P_{123} (°C days)
Aurora	USSR	WW	68	24	810
Balkan	Yugoslavia	WW	69	25	760
Bastion	Netherlands	SW	59	46	760
Bezostaya 1	USSR	WW	60	31	760
Biserka	Yugoslavia	WW	54	29	750
Bounty	England	WW	58	45	800
Bussard[b]	Germany	WW	55	61	740
Capppell Desprez	France	WW	68	38	810
Contra[b]	Germany	WW	56	55	760
Dream[b]	Germany	WW	48	63	760
Drifter[b]	Germany	WW	59	58	760
Dwarf Bezostaya	USSR	WW	68	25	780
Enorm[b]	Germany	WW	39	52	750
Excellent[b]	Germany	WW	45	58	740
Hybnos 2b[b]	Germany	WW	50	59	735
INIA 66	Mexico	SW	17	30	760
Irnerio	Italy	SW	47	32	780
Jugoslavija	Yugoslavia	WW	58	34	765
Lerma Rojo 64	Mexico	SW	31	39	740
Mandub[b]	Germany	WW	47	61	760
Maris Huntsman	England	WW	64	47	760
Maris Mardler	England	WW	57	43	800
Maris Nimrod	England	WW	71	37	805
Maris Templar	England	WW	77	37	790
Mironovskaya 808	USSR	WW	69	34	755
Moslavka	Yugoslavia	WW	55	20	775
Odesskaya 51	USSR	WW	61	19	790
Opus[b]	Germany	WW	59	59	740
Partizanka	Yugoslavia	WW	64	15	760
Phoenix	Australia	WW	52	16	810
Renan[b]	France	WW	44	54	740
San Pastore	Italy	WW	47	18	745
Sanja	Yugoslavia	WW	57	32	760
Sava	Yugoslavia	WW	39	40	755
Super X	Mexico	SW	49	33	765
Talent	France	WW	58	29	770
Terrier[b]	Germany	WW	61	59	750

Table 1 continued

Cultivar	Origin[a]	Habit	Cultivar parameters		
			P1V (days)	P1D (%)	P_{123} (°C days)
Tiger[b]	Germany	WW	51	57	740
Vakka	Finland	WW	55	43	780
Zlatna dolina	Yugoslavia	WW	62	24	770
Zlatoklasa	Yugoslavia	WW	56	24	770

Habit is as reported with SW = spring and WW = winter

[a] Origin of the non-German cultivars as reported in the International Winter Wheat Performance Nursery (e.g. Kuhr et al. 1984)

[b] Cultivars evaluated in the study conducted at the research station Ihinger Hof 2004/2005 and 2005/2006

design with three replicates, with cultivars as the main plots.

Developmental stages were assessed visually, based on when 50% of plants reached a given stage. At maturity, 1 m^2 from each plot was harvested to provide seed for the GPC analyses. Nitrogen content of grain was determined by the micro-Kjeldahl method (Bradstreet 1965). From this, GPC was calculated by the conversion factor 5.7 for winter wheat (bread) (Sosulski and Imafidon 1990). Durations from planting until date of anthesis and until physiological maturity were calculated from daily mean temperatures as growing degree days (°C days) assuming a base temperature of 0°C.

Cultivar parameters

Cultivar differences for the 12 cultivars used in the field study and the 29 cultivars selected from the IWWPN trials were characterized using the model parameters P1V for vernalization requirement, P1D for photoperiod response, and P1, P2 and P3 for earliness per se from CSM-Cropsim-CERES-Wheat model Version 4.0.2.0 (Jones et al. 2003; Hoogenboom et al. 2004). The three coefficients affecting earliness per se were summed to provide the factor P_{123} with units of °C days. P1V, P1D and P1 were estimated using the GenCalc2 software, which facilitates testing ranges of parameter values and estimating goodness of fit (Hunt et al. 1993). Calibrations for the IWWPN entries were done on the subset of nurseries used by White et al. (2008), representing approximately one third of the locations and data available for those cultivars. P2 and P3 were held constant during the calibration. The cardinal temperatures for

Table 2 Countries, site, latitude, number of cultivars, years and experiments, selected for the analysis of the impact of E, G, G × E and the influence of the cultivar parameters as a co-variable on grain protein content

Country	Site	Latitude	Number of cultivars	Number of years	Number of experiments
Region 1					
Finland	Jokioinen	60.49	21	7	34
Japan	Morioka Iwate	39.45	20	9	50
Norway	Vollebekk	60.00	11	6	19
South Korea	Suwon	36.19	22	10	49
Turkey	Ankara	40.00	19	9	55
Ukraine	Mironovski	50.15	6	3	11
	Odessa	46.00	22	6	40
United States	Akron	40.10	7	3	12
	Brookston	40.25	6	2	8
	Fort Collins	40.35	29	11	70
	Hutchinson	38.00	6	3	11
	Ithaca	42.30	29	11	63
	Lincoln	40.50	20	9	40
	Rowan Co.	35.42	29	13	70
	Stillwater	36.07	29	12	66
Region 2					
Austria	Vienna	48.12	29	11	68
Croatia	Zagreb	45.49	22	10	59
France	Orgerus	48.50	3	1	3
Germany	Langenstein	51.42	19	5	30
	Monsheim	49.35	29	12	72
	Weihenstephan	48.24	29	11	68
Netherlands	Wageningen	51.28	21	11	63
Poland	Przeclaw	50.18	15	5	27
	Warsaw	52.12	26	7	49
United States	Corvallis	44.30	24	6	42
United States	Pullman	46.42	27	10	90
Slovakia	Bratislava	48.29	26	7	46
Sweden	Svalof	55.35	22	11	92
Switzerland	Zurich	47.29	29	11	69
Region 3					
Iran	Karaj	50.35	21	10	58
Iraq	Sulaimaniya	36.30	19	8	50
Italy	Milano	45.13	29	11	72
	Rieti	42.24	29	11	63
Afghanistan	Heart	34.11	12	3	17
	Kabul	34.27	15	8	49
Argentina	Bordenave	−37.51	29	12	78
Bulgaria	Tolbukhin	43.40	20	9	54
Russia	Krasnodar	45.00	26	9	61
Syria	Aleppo	36.05	7	2	10
United States	Davis	38.32	29	9	53

Table 2 continued

Country	Site	Latitude	Number of cultivars	Number of years	Number of experiments
Region 4					
Hungary	Martonvasar	47.21	20	9	56
	Szeged	46.00	19	8	49
Romania	Fundulea	44.03	29	12	73
Spain	Madrid	40.31	14	2	15
Serbia Montenegro	Novi Sad	45.30	29	12	77
Region 5					
Czech Republic	Sedlec	50.14	26	8	51
Turkey	Erzurum	39.58	26	8	52
	Eskisehir	36.45	21	10	61
United States	Billings	45.00	19	6	34
Iran	Hamadan	34.47	18	7	42
Region 6					
Argentina	Balcarce	−37.45	20	7	41
Chile	Chillan	−36.31	15	4	24
	Temuco	−38.40	22	10	58
Region 7					
South Africa	Bethlehem	−28.10	24	7	67
Mexico	Toluca	19.16	26	8	59

Region classification was based on Peterson and Pfeiffer (1989)

vernalization were modified from values of −5, 0, 7, and 15°C (Hoogenboom et al. 2004) to −4, 0, 3, and 15°C as suggested by White et al. (2008).

Path analysis to test the relationship between phenological traits and grain protein content

Path analysis was performed to test the theoretical model (Fig. 1) with data obtained from the field experiments at Ihinger Hof. Goodness of fit was estimated using two parameters. The P-value associated with the model χ^2 test and the non-normed fit index (NNFI; Bentler and Bonnet 1980) that represents the percentage of observed-measure covariation explained by a given structural model as compared with an overall, null model. To indicate acceptable agreement between modeled and observed values, the P-value associated with the model χ^2 test should exceed 0.05, the NNFI index should be over 0.9, and all path coefficients should be significant at the $P = 0.05$ level.

Before using the iterative approach of Hatcher (1994) to assess the fit between model and data, the causal relationships were reviewed to see whether causal relations could be improved by modifying the parameter set. This iterative approach consisted of reviewing residual normalized residual matrix, χ^2 test,

NNFI and significance tests for path coefficients. If a path did not improve model and data fit, it was deleted. If an alternative path improved the model, that path was added, and the revised model was re-estimated.

Statistical analyses

Statistical analyses were conducted using procedures of the SAS program (SAS Institute 2000). The MIXED procedure was used to evaluate the relative impacts of E, G, G × E on GPC by the determination of variance components and to conduct a covariance analysis to test the influence of the model parameters on GPC with the IWWPN dataset. Path analyses were conducted using the CALIS procedure with the maximum likelihood method of parameter estimation. These analyses were performed on a variance-covariance matrix.

Results

Importance of genotype, environment and their interactions on grain protein content

The estimated variance components of GPC for the IWWPN dataset showed large effects of region ×

site × year and regions × site (Table 3). Cultivar differences explained 7% of the total variance for GPC as compared to 41% explained by region ×

Table 3 Estimated variance components for cultivar, region, site and year on grain protein content

Covariance parameter	Variance component	% of total variance	Standard error	P-value
Cultivar	0.31	7	0.10	0.001
Region	0.31	7	0.26	0.113
Region × cultivar	0.08	2	0.03	0.003
Region × site × cultivar	0.19	4	0.03	<0.001
Region × year × cultivar	0.05	1	0.02	0.006
Region × site	0.80	18	0.22	<0.001
Region × year	0.09	2	0.08	0.129
Region × site × year	1.85	41	0.16	<0.001
Residual	0.85	19	0.04	<0.001

Data were for a subset of IWWPN trials (e.g. Kuhr et al. 1984) and included 5 spring and 24 winter wheat cultivars, 7 regions, 55 sites and 13 years (Tables 1 and 2)

Table 4 Covariance analysis for effects of the cultivar parameters P1V (days at optimum vernalizing temperature required to compete vernalization), P1D (percentage reduction in

site × year and 18% by regions × site. The remaining variation of 34% was explained by region (7%), region × cultivar (2%), region × year (2%), region × site × cultivar (4%), and regions × year × cultivar (1%), leaving a residual variation of 19%.

The covariance analysis indicated that the effects of P1V, P1D and P_{123} on GPC differed with growth habit (Table 4). When spring and winter wheats were examined together, effects of P1V, P1D and P_{123} on GPC varied with region, site and year. When the analysis was restricted to the 24 winter wheats, the effects of region, site and year were still observed for P1V but not for P1D and P_{123}. Covariance analysis for the five spring wheats detected no effect of P1V, P1D and P_{123} on GPC.

To analyze location-specific responses of P1V, P1D and P_{123} on GPC, the effects were estimated within regions, and locations were arranged and displayed according to their latitude (Fig. 2). The effect of P1V on GPC declined at higher latitudes in Regions 2 and 4 (Fig. 2a). The effect of P1D on GPC decreased with latitude in Region 3 and 4 (Fig. 2b), and in Regions 2 and 4, the effect of P_{123} also decreased with latitude (Fig. 2c).

development rate in a photoperiod 10 h shorter than the optimum relative to that at the optimum) and calibrated sum of the component phase durations (P_{123}) on grain protein content

Effect	Habit								
	DF			F-value			P-value		
	SW	WW	SW + WW	SW	WW	SW + WW	SW	WW	SW + WW
P1V	1	1	1	0.00	0.03	3.66	0.999	0.872	0.571
P1V × region	6	6	6	0.00	0.19	1.38	1.000	0.979	0.222
P1V × region × site	46	48	48	0.39	14.01	47.28	0.968	<0.001	<0.001
P1V × region × year	77	77	77	0.00	0.14	16.72	1.000	1.000	<0.001
P1V × region × site × year	233	313	314	1.32	12.90	14.42	0.396	<0.001	<0.001
P1D	1	1	1	0.00	0.04	0.03	0.999	0.8362	0.869
P1D × region	6	6	6	0.00	0.50	0.50	1.000	0.8075	0.136
P1D × region × site	30	48	48	0.44	0.86	2.35	0.938	0.7269	<0.001
P1D × region × year	15	72	77	0.00	0.59	1.95	1.000	0.9926	<0.001
P1D × region × site × year	14	310	312	0.61	1.09	1.56	0.789	0.2944	<0.001
P_{123}	1	1	1	0.00	0.04	0.49	1.000	0.8472	0.483
P_{123} × region	5	6	6	0.00	1.41	1.47	1.000	0.2152	0.189
P_{123} × region × site	22	47	48	0.47	1.90	4.01	0.910	0.0026	<0.001
P_{123} × region × year	5	65	77	0.00	0.81	2.09	1.000	0.8269	<0.001
P_{123} × region × site × year	2	271	299	0.11	1.43	1.68	0.897	0.0116	<0.001

Data were for a subset of IWWPN trials (e.g. Kuhr et al. 1984) and included 5 spring (SW) and 24 winter wheat (WW) cultivars, 7 regions containing 55 sites, and 13 years of evaluations (Tables 1 and 2)
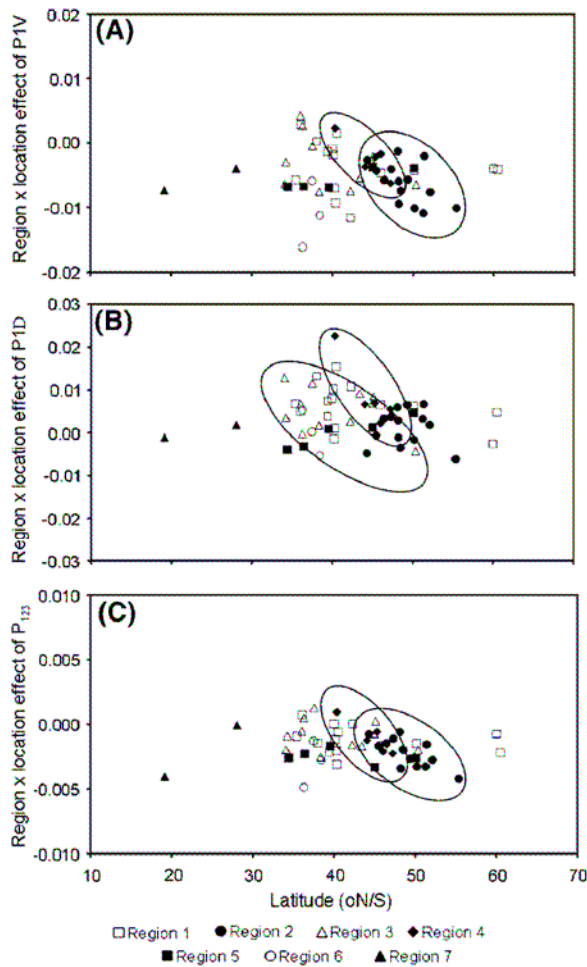
Fig. 2 Relations between location effect of model parameters P1V, P1D and P_{123} on GPC and absolute latitude of 5 spring and 24 winter wheat cultivars tested in the IWWPN dataset. (**a**) P1V, (**b**) P1D, and (**c**) P_{123}. The ellipses indicate specific regions showing strong relations between effects and latitude

Path analysis of the traits measured in Germany

Weather conditions during the two experiments in Germany were similar (Table 5). Seasonal patterns for air temperature during 2004–2006 were almost the same, and precipitation in both growing seasons was adequate to avoid water deficits. The high rainfall in August 2006 delayed maturity, but over all, the two seasons resulted in similar responses for phenology and GPC.

The initial path model using days to anthesis and maturity for 12 winter cultivars evaluated over two seasons showed poor agreement with observed data (Table 6), so the model was revised to use thermal time (Model 1; Table 7). This improved the goodness of fit, but the results were still judged unacceptable (Table 7). Thus, Model 1 was rejected, and an attempt was made to identify a better model by reviewing whether any of the paths in Model 1 should be deleted. The t values for the path between P1V and thermal time until anthesis and thermal time anthesis and grain filling duration were not significant ($P < 0.05$), so their paths were excluded. The resulting Model 2 was then re-estimated and found to provide a good fit to the data (Table 7), with all path coefficients significant at $P < 0.05$ (Fig. 3a).

To examine whether Model 2 was sensitive to year of evaluation, Model 2a was estimated using data only from the year 2005. Goodness of fit indices from Model 2 and Model 2a were comparable (Table 7).

In the path analyses with Model 2 (Fig. 3a), thermal time to anthesis had a negative direct effect (path coefficient $pc = -0.66$; $P < 0.001$), whereas grain filling

Table 5 Monthly mean temperature and precipitation during the growing seasons in 2004/2005 and 2005/2006 at the research station Ihinger Hof, Germany

Data	Growing season	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug
Mean temperature, °C	2004/2005	11	4	0	1	−2	4	9	13	18	18	15
	2005/2006	11	4	0	−3	0	2	8	13	17	22	14
	Mean for 1977–2004	9	3	1	−1	0	4	7	12	15	17	17
Precipitation, mm	2004/2005	88	28	40	34	42	60	58	73	44	85	80
	2005/2006	32	26	29	11	26	60	63	69	33	57	138
	Mean for 1977–2004	60	51	54	44	40	47	50	82	78	73	64

Table 6 Relationships between pairs of variables for 2005 data (above the diagonal) and for combined 2005 and 2006 data (below the diagonal) of 12 winter wheat cultivars tested at the research station Ihinger Hof, Germany

	Time to anthesis (days)	Thermal time till anthesis (°C days)	Grain filling duration (days)	Grain filling duration (°C days)	P1V	P1D	P_{123}	GPC
Time to anthesis (days)	–	0.99***	−0.09	−0.17	0.31	0.88***	0.48	−0.58*
Thermal time till anthesis (°C days)	0.42*	–	−0.09	−0.17	0.30	0.88***	0.49	−0.58*
Grain filling duration (days)	−0.52**	−0.03	–	0.99***	−0.42	−0.03	−0.14	0.15
Grain filling duration (°C days)	0.69***	0.29	0.22	–	−0.45	−0.12	−0.15	0.21
P1V	0.08	0.32	−0.15	−0.07	–	0.38	0.12	−0.48
P1D	0.18	0.72***	0.24	0.28	0.38	–	0.12	−0.56
P_{123}	0.13	0.53**	−0.01	0.08	0.12	0.12	–	−0.14
GPC	0.02	−0.59**	−0.09	0.05	−0.44*	−0.41*	−0.31	–

*, **, *** Significant at $P < 0.05$, <0.01 and <0.001, respectively

Table 7 Goodness of fit indices for the path models

Model	χ^2	DF	P-value	Non-normed fit index
Initial model	15.773	7	0.03	−0.401
Model 1[a]	15.413	7	0.03	0.503
Model 2[b]	0.504	3	0.92	1.243
Model 2a[c]	0.579	3	0.90	1.347

[a] Identical to the initial model (Fig. 1), except using thermal time for the duration from planting till anthesis and anthesis to physiological maturity

[b] Identical to the Model 1, the path between P1V and thermal time till anthesis and the path between thermal time till anthesis and grain filling duration were deleted

[c] Identical to the Model 2, but using only data from the year 2005

duration showed a positive direct effect ($pc = 0.25$; $P < 0.05$) on GPC. Direct effects on thermal time until anthesis were −0.67 for P1D ($P < 0.001$) and 0.45 for EPS ($P < 0.001$). Results for 2005 were comparable with results obtained using both years (Fig. 3b). Path coefficients of second-order variables on GPC were obtained by calculating the product of the intermediate path coefficients within the path to GPC (Table 8). The path coefficients for P1D and P_{123} on GPC were −0.44 and −0.30, respectively.

Discussion

The IWWPN provided data for a widely distributed and diverse set of germplasm and environments,

including differences in altitude, latitude, climate and management. Peterson and Pfeiffer (1989) proposed that long-term performance nursery data allow more precise definition of site relationships because the multiple years of observation minimize the effect of
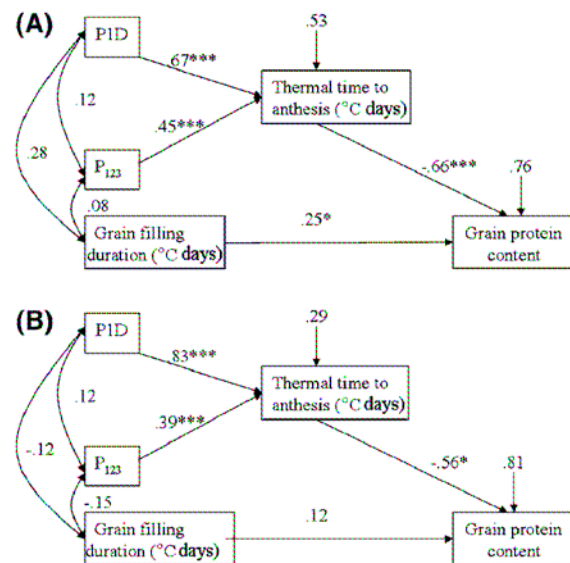

Fig. 3 Path diagram for 12 cultivars tested at Ihinger Hof, Germany. Standardized path coefficients appear on single-headed straight arrows, and correlations appear on double-headed curved arrows. **(a)** Model 2 (identical to the initial model, except that the path between P1V and thermal time until anthesis and the path between thermal time until anthesis and grain filling duration were deleted) applied to data from 2005 and 2006. **(b)** Model 2a. Path diagram as in **(a)** except restricted to 2005. *, **, *** Significant at $P < 0.05$, <0.01 and <0.001, respectively

Table 8 Path coefficients of phenological traits on grain protein content and traits along its path to grain protein content

Exogenous variable	Path coefficients	
	Thermal time till anthesis (°C days)	Grain protein content
Grain filling duration (°C days)		0.25
Thermal time till anthesis (°C days)		−0.66
P1D	0.67	−0.44
P$_{123}$	0.45	−0.30

Data are for 12 winter wheat cultivars tested at the research station Ihinger Hof, Germany in 2005 and 2006

unusual or short term weather patterns. The variance components estimated for the impact of genotype, environment and their interactions on GPC confirmed that, as expected, environment had a major influence on GPC, but differences among genotypes were still readily detectable (Table 3). The covariance analyses showed that the cultivar parameters P1V, P1D and P$_{123}$ partially explained cultivar variation in GPC (Table 4), but further indicated that the effects varied with site and year within region. When only winter wheats were considered, the effect of P1V was similar to the combined analysis but not for P1D and P$_{123}$.

The analysis of location effects of P1V versus latitude (Fig. 2) emphasized that relationships between GPC and the three phenological traits varied with environment. For regions where strong relations with latitude were found (e.g. Region 4 for all three traits), the effects decreased with latitude. This agrees with the expectation that at high latitudes, temperatures are cool enough to ensure full vernalization and photoperiods are long enough to minimize effects of photoperiod. We note, however, that the impact of these traits on GPC requires detailed analysis for each region. Ideally, this would include use of datasets where soil nitrogen status is characterized in order to allow application of simulation models.

Path analyses for Ihinger Hof confirmed that GPC increases with a shorter pre-anthesis phase (e.g. Mou et al. 1994; Le Gouis et al. 2000; Talbert et al. 2001). A direct effect from time to anthesis on grain filling duration was not detected, but grain filling duration affected GPC, as observed by Knott and Gebeyehou

(1987) for durum wheat. In the Ihinger Hof dataset, P1D and P$_{123}$ had negative effects on GPC (Table 8). For P1V, the relation obtained in the co-variance analysis was not confirmed by the path analyses. The absence of an effect of P1V at this location likely was due to all cultivars being completely vernalized.

The foremost implication of this work is that even for traits such as GPC that appear to be relatively remote from pre-anthesis development, vernalization requirement, photoperiod sensitivity and EPS may still have important influences. For GPC, research should identify combinations of these traits that are best suited for their target population of environments. The genetic control of the traits is relatively well understood (e.g. Laurie et al. 2004; White et al. 2008), and recent progress in sequencing the *Vrn* and *Ppd* loci gives promise that genetic information may become readily available for many cultivars (e.g. Sherman et al. 2004; Beales et al. 2007). This would further facilitate targeting of germplasm to environments, as proposed by Kato et al. (2001) for additive effects of *Vrn-1* loci.

Direct simulation of effects of cultivar traits on GPC is another promising option (Martre et al. 2006), but requires greater attention to characterization of soil conditions and crop management. Models integrate specific hypotheses about interacting processes and thus beyond their use as predictive tools, have utility in guiding additional research.

Conclusions

Analyses at contrasting geographic scales confirmed that cultivar differences in GPC can be influenced by vernalization requirement, photoperiod response and earliness per se. An immediate practical application of these findings is that attempts to analyze cultivar differences in grain nitrogen should consider the influence of simply inherited traits that help determine the duration of vegetative growth. The work also provides a foundation for more explicit consideration of how altering crop phenology in response to climate risk or global change would affect environmentally sensitive traits such as GPC.

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6 General Discussion

The general discussion of the present dissertation is arranged in three sections: Firstly, findings across chapters are displayed and classified according to the goal of the dissertation (6.1). Secondly, the results and conclusions of the chapters are discussed together to highlight their consequences for practical applications (6.2 and 6.3). The last section presents how findings can contribute to adapt cropping systems to climate change trends in China (6.4) and to ensure a sustainable resource use in the North China Plain (6.5). Perspectives for future development of the approaches conclude the discussion.

6.1 Aims and Findings of the Dissertation

Phenology is an important factor in conditioning adaptation of plants in environments because it determines how well the plant life-cycle matches resources of the environment. Understanding wheat phenology is crucial for farmers, plant breeders as well as for agronomists. Depending on the scope and the environmental constraints, there are many aspects where knowledge about factors influencing wheat phenology and their interactions with environment is helpful. Studies presented in the dissertation are used to quantify and test the impact of factors influencing wheat phenology on grain yield and grain protein content by the use of the crop simulation model CSM-Cropsim-CERES-Wheat and underlying genetic information.

Cultivar differences in wheat phenology before anthesis are mainly determined by vernalization requirement, photoperiod response and earliness *per se.* Photoperiod and vernalization response are often characterized by comparing time to heading or anthesis of plants grown under different vernalization and photoperiod conditions in controlled environments (e.g. Davidson et al., 1985). The use of growth chambers or glasshouses to quantify the responses often reduces the applicability of results, especially when they should be used to predict field performance. Quantitative characterizations of these factors were determined by the use of pre-planting vernalization treatments and two planting dates that provided different photoperiod regimes. In a further step, the results were compared with corresponding model input parameters estimated for the CSM-Cropsim-CERES-Wheat model Version 4.0.2.0 (Chapter 2). Results showed that different planting dates combined with vernalization pre-treatments allowed accurate characterization of genotypes, so field evaluations can be a substitute of controlled environment studies to characterize vernalization requirement, photoperiod response and earliness *per se*

among wheat cultivars. Furthermore, the results confirmed that model parameters representing vernalization requirement (P1V) and photoperiod response (P1D) allowed a prediction of phenology and were consistent with corresponding data on cultivar differences in genetic makeup. Given the observed variability in earliness *per se*, the model parameters P1V and P1D were re-estimated for each cultivar, allowing P1 and P3 to vary according to data on final leaf number and observed earliness *per se.* The cultivar specific adaptation of earliness *per se* improved the estimates of the effect of P1V and P1D and coefficients showed much stronger association with field-based results. As shown in the study, to get reliable results for the calibration of these genotypic model parameters, complex field trials were necessary and required, experiments over multiple cropping seasons for evaluation. The rely of the calibration on phenotypic data can produce an over-calibration of location effects that may reduce the reliability of model-based predictions. To overcome this problem, one possibility can be to link the genotypic model parameters with gene information as shown in the next study (Chapter 3).

Genotypic variation in phenology till anthesis is largely determined by groups of loci that affect requirement for vernalization and sensitivity to photoperiod. Vernalization requirement depends mainly on three homologous *Vrn* loci whereas sensitivity to photoperiod is determined by three *Ppd* loci (e.g. Laurie et al., 2004). Approaches used in GeneGro (White and Hoogenboom, 1996) suggested that relations which express effects of genes on genotypic model parameters can be programmed external to the model code. The use of gene information to estimate genotypic model parameters for vernalization requirement and photoperiod response was developed and applied with CSM-Cropsim-CERES-Wheat model Version 4.0.2.0 (Chapter 3). Firstly, genotypic model parameters were estimated conventionally and than estimated using regression for *Vrn* and *Ppd* loci. Results indicated that both, the gene-based and conventionally estimated coefficients, explained large portions of the variation in days to flowering whereas the gene-based estimates predicted about the same variation than the conventionally estimated coefficients. As examined in the previous studies, genetic variability in phenology can be reproduced by genotypic model parameters. To assist genetic improvement, one possibility could be to use analysis with genotypic model parameters for breeding purposes which was implemented in the next study (Chapter 4).

Numerous studies showed how crop models and their genotypic parameters can be used to select varieties suiting for a specific environment (Chapman et al., 2000; Boote et al., 2003; Messina et al., 2006a). Modeled responses to environmental parameters vary according to

genotypic parameters, so it is of interest to ascertain how cultivar parameters affect the performance of hypothetical varieties under different management and environmental scenarios. The impact of selected agronomic traits (represented by model parameters) on grain yield was examined by a sensitivity analysis of the parameters under different scenarios in the North China Plain (Chapter 4). Beside model parameters affecting wheat phenology such as P1V, P1D and grain filling duration also parameters which affected yield directly such as stress tolerance, kernel number per spike and kernel weight were considered in the analysis. By combining genotypic model parameters with corresponding phenotypic traits, the use for plant breeding was shown by designing ideotypes for the specific environmental conditions. Results showed that kernel number per spike followed by kernel weight had the highest impact on grain yield over all scenarios. P1V and P1D affected yield considerable under dry conditions because lower responses caused earliness, allowing crops to avoid late-season water deficits. Since the CSM-Cropsim-CERES-Wheat model is able to characterize cultivars by the use of genotypic model parameters such model-based characterizations can help to explain genotype x environment interactions for other agronomic traits such as grain protein content.

Martre et al. (2007) showed in a simulation analysis how physiological traits, represented by model parameters, can improve the simulation of nitrogen use efficiency and grain protein concentration in wheat. Used as inputs to a process-based model, such parameters can reliably predict field performance. However, the investigation of the impact of genotype model parameters on quantitative traits such as grain protein content in simulation models often shows unrealistic responses (Asseng et al., 2000). To accomplish this problem one solution could be to combine model-based characterizations of traits which can be reproduced successfully in the model with statistical analyses. The impact of P1V, P1D, and earliness *per se* (represented by genotypic model parameter P_{123}) on grain protein content was statistically examined in Chapter 5. First, the relative impact of environment, genotype and genotype x environment in a set of diverse environments over different altitudes, latitudes, climates and years was evaluated by estimating variance components. In a second analysis, the influence of the genotypic model parameters on grain protein content was examined by covariance analysis using REML analysis. To examine relations for a single environment in more detail, path coefficient analysis was used to test the influence of vernalization requirement, photoperiod response and earliness *per se* for a two year field experiment in Germany. Results confirmed that cultivar differences in grain protein content are influenced by P1V, P1D and P_{123}, but their effects varied with region, site and year. Path

analyses confirmed that GPC increased with earlier anthesis, which was influenced by P1D and P_{123}.

6.2 Description of Cultivar Characteristics by the Use of a Crop Model

The traditional approach to evaluate genotypic adaptation is analyzing the variation in multi location x year trials using a phenotypic model as shown in equation [1]:

$$P = G + E + GE \qquad [1]$$

where P, G, E and GE refer to phenotypic, genotypic, environmental and genotype x environmental interaction effects, respectively (Shorter et al., 1991). Plant breeders as well as agronomists use various analytical methods to identify variation in genotypic response. The success of the method depends highly on which proportion of GE interactions can be explained by the analysis. Although numerous statistical methods have been developed such as linear factorial regression or biadditive factorial regression (van Eeuwijk, 1995; Brancourt-Hulmel et al., 1997), they cannot provide insight into the biological mechanisms underlying the GE interactions. Crop models based upon current understanding of GE interactions by estimating genotypic model parameters over different environments attempt to capture the character of physiological characteristics that determine response to environmental factors. Crop models are often tested in a broad range of environments (Mavromatis et al., 2001) and thus they should be capable to taking different conditions into account.

Many crop models have the ability to show genetic variability among cultivars by the use of genotype specific parameters. CERES and CROPGRO models (which are included into DSSAT; Jones et al., 2003) use genotype model parameters which are assumed to be constant among genotypes (species parameters) and those that vary with the genotype (cultivar parameters).

6.2.1 Characterization of Traits Affecting Wheat Phenology by Genotypic Model Parameters

Genotypic model parameters are assumed to be stable among environments and can therefore be used to describe the performance of a cultivar across environments. Mavromatis et al. (2002) showed that genotypic parameters affecting yield were not stable among sites, whereas

parameters affecting plant development such as photoperiod response were robust regardless of data origin. Genotypic differences in wheat phenology are usually modeled using parameters that modify sensitivity to photoperiod and vernalization regimes or determine minimum durations of specific developmental phases (e.g. Ritchie, 1991). As presented in Chapter 2, field-evaluated genotypic differences in vernalization requirement, photoperiod response and earliness *per se* can be successfully characterized using the corresponding genotypic model parameters in CSM-Cropsim-CERES-Wheat model Version 4.0.2.0.

The study further suggests that wheat germplasm can be characterized for traits that affect phenology by using the model parameters for the corresponding physiological traits instead of somewhat arbitrary durations (measured in calendar days or thermal time) from seedling emergence or transplanting to heading or anthesis compared under different vernalization or photoperiod regimes as used by e.g. Davidson et al. (1985). Model parameters should be more comparable across studies and facilitate studying more complex genotype x environment interactions such as possible interactions of temperature with photoperiod sensitivity. Furthermore, rigorous and reproducible characterizations are required to explain more complex genetic systems that may underlie earliness *per se*.

Although it is assumed that genotypic model parameters can describe the performance of a cultivar, there are two main constraints that could restrict the use of model parameters for description of traits (i) the estimation procedure of the genotypic model parameters (ii) the availability of field data to estimate the genotypic model parameters.

The best approach to estimate genotypic model parameters may appear to be the direct measurement. However, such measurements which may be costly, especially when they require controlled environment conditions or involve large numbers of cultivars (Reymond, 2001). For most genotypic parameters the estimation procedure consists of estimating parameters by minimizing the differences between measured and calculated values. Hunt et al. (1993) developed software that used this approach to estimate genotype parameters in the DSSAT models, but this method has one important disadvantage: The physiological significance of the parameter may be compromised because the variables, on which the optimization is based, are often slightly correlated with the estimated parameters. If several parameters are estimated simultaneously, this drawback will become more important. In CSM-Cropsim-CERES-Wheat model Version 4.0.2.0, no genotype coefficient calculator is implemented, and the estimation of model parameters is based on trial and error, fitting simulated output with field observation of phenology

(Hoogenboom, 2004a). An initial step in such calibrations is to select a suitable ecotype represented through the sum of the component phase durations from germination to the end of spike growth (P_{123}). In most cases, the duration for a specific cultivar is not available and thus in order to bypass the problem, a guess is made as to a suitable ecotype based on the example file provided with the model. As shown in Chapter 2, this can reduce the accuracy in determining the responses to vernalization and photoperiod and thus resulting in inaccurate estimation of final leaf number. Inaccurate leaf number, in turn, can reduce the reliability of model-based predictions of phenology and ultimately of biomass production and grain yield. A relatively simple approach to solve the problem is to estimate P1 in accordance with final leaf number, which is a trait that can be easily evaluated in field experiments. A more accurate method would be, of course, to estimate earliness *per se* with growth chamber studies or, as shown in Chapter 2, through appropriate field experiments.

Estimating P1V and P1D in CSM-Cropsim-CERES-Wheat Version 4.0.2.0 requires field observations of date of seedling emergence and date of anthesis, along with daily maximum and minimum temperature (Hoogenboom, 2004a). These data is readily obtained through field studies, but to use crop models as a decision support tool, genotypic model parameters must be available as soon as the cultivar is marketed (Mavromatis et al., 2001). Crop performance tests and nurseries run by breeders often involve large numbers of genotypes, but it is uncommon to record date of seedling emergence and anthesis. Thus, a contribution to facilitate model applications could be to record traits determining phenology in every crop performance test.

6.2.2 Characterization of Traits Affecting Wheat Phenology by Gene-based Estimates of Genotypic Model Parameters

Crop models often show unrealistic responses because of the inadequate description of cultivar differences. This discrepancy between model output and field-observed plant responses is mainly due to inaccuracy in adjusting genotypic model parameters (White and Hoogenboom, 2003). Advances in plant genetics, as well as better understanding of physiological processes, can facilitate the inclusion of genetic information in crop models (White, 2006). If genotypic model parameters are based on genomic data, this inaccuracy can be reduced.

There have been several efforts to integrate genomics with physiology in crop models. The most promising approach is to identify relations between gene combinations and crop model genetic coefficients through field research and then to use these relationships to estimate

coefficients in the crop model (Messina et al., 2006a). For common bean (*Phaseolus vulgaris* L.), data for seven loci predicted phenology, yield and grain size as well as the parent model using cultivar-specific parameters (White and Hoogenboom, 1996; White and Hoogenboom, 2003). For soybean, the same approach was used by Messina et al. (2006b). For modeling specific traits, use of data on quantitative trait loci (QTL) instead of Mendelian loci shows promise (e.g. Reymond et al., 2003; Nakagawa et al., 2005). Attempts to parameterize whole plant models using QTL appear less encouraging (Yin et al., 2000). For wheat, the availability of data on genotypes and field performance is still a potential limitation for combining gene information with model parameters. However, as suggested by White (2006), when integrating gene information into a crop model for wheat, several questions must be clarified: where to access genomic data, which trait to focus on and which statistical method to model associations between traits and genotypic model coefficients should be used (White and Hoogenboom, 2003). Although the genome of wheat is very large, for some traits the genetic makeup is more or less well described, e. g. traits affecting wheat phenology such as vernalization requirement (*Vrn* locis), and photoperiod response (*Ppd* locis). There are several databases (Martynov et al., 2006) and publications (Laurie et al., 2004; Law et al., 1976; Worland et al., 1987) where the information can be extracted. In addition to ease of data access, traits affecting phenology have the advantage that they have relatively simple inheritance and can be measured accurately. White and Hoogenboom (1996) and Messina (2006b) used linear models using regressions to estimate the genotypic model parameters. This approach used allelic information at given loci and demonstrated predictability across cultivars and seems thus suitable to estimate gene-based genotypic model parameters influencing phenology in wheat. Other approaches use molecular markers and mapping algorithms to predict the genotypic model parameters (Wang et al., 2003), which has the limitation that phenotypic markers are not always reliable predictors of the genotype (Messina et al., 2006a). In the study presented in Chapter 3, in case of a single gene with two alleles, the equation [2] was used:

$$P = a + bG \quad [2]$$

where P is the genotypic model parameter controlling the physiological process (here P1V and P1D) the variable G indicates which allele of the given loci is present (in the case of vernalization requirement *Vrn* loci and photoperiod response *Ppd* loci) whereas this variable can

take a value of 1 for dominant and 0 for recessive alleles. Variables a and b are estimated through linear regression.

Results presented in Chapter 3 showed that gene-based estimates of genotypic model parameters can describe a large percentage of variation in flowering. With gene-based estimates for P1V and P1D, one of the mentioned constraints of using these parameters for descriptions of wheat germplasm might be removed. If the linkage between genes and plant traits is well established, estimation would no longer require field trials (White, 1998). Baenziger et al. (2004) proposed that by using genomic data for estimation of genotypic model coefficients the need for "tweaking" the model should be reduced. The problem of data availability remains, because despite the efforts in characterizing loci determining photoperiod response and vernalization requirement, gene information cannot be made available for every cultivar breed immediately after releasing.

Integrating gene information into genotypic coefficients creates an improved accuracy in simulating physiological processes and cultivar differences. One consequence for modeling research can be the better understanding of metabolic pathways during different phases of plant development. The applied research may benefit from the improved explanation of G x E interactions that have impact on several model applications. For plant breeding applications, it means that breeder can concentrate more on selection work than on recording needed traits for the estimation of the parameters such as date of seedling emergence and date of anthesis. Phenology and hence parameters affecting wheat phenology are important in determining how well a cultivar is suited for a specific environment. Gene-based estimates of those parameters can explain G x E interactions more accurately and thus improve the quality of such analyses. Furthermore, gene-based estimates of model parameters improve the quality of analyses to find the best suited cultivar for a specific environment and to find the best management for a specific cultivar. Especially the timing of planting and harvesting would be affected because effects like temperature can be investigated more precisely.

6.3 Use of Crop Models in Plant Breeding Applications

Modern plant breeding involves not only developing improved cultivars adapted to target environments, but requires optimizing more and more constraints, where the plant breeder must draw from knowledge in multiple scientific disciplines. Crop models can support plant breeding by providing information about physiological and biochemical processes, the environment, agronomic practices and genetic information (Messina et al., 2006a). There are many studies in which crop models were used to assist genetic improvement. The use of crop models to characterize target populations of environments and their challenges was investigated by Chapman et al. (2002). Such characterizations can guide plant breeder in deciding which environments are best suited for field testing and in interpreting field results in the context of the type of environment sampled by a given experiment. Optimizing the combination of genotype and management for a target environment is a further application. Adapting crop management to a specific cultivar requires identifying the best management factors to exploit the potential of the cultivar. The approach is to optimize management factors for a cultivar with known genotype specific parameters for a specific environment. There are several studies that worked with this approach (e.g. Royce et al., 2001). To assist genetic improvement in plant breeding, models can be used to assess specific traits for designing improved plant types (ideotypes) as demonstrated in Chapter 4. Another application is to generate hypotheses and investigate causal relationships to help understand physiological causes of genetic improvement as presented in Chapter 5.

6.3.1 Model-based Sensitivity Analyses to Design Ideotypes

Donald (1968) defined the term ideotype as a model for the entire appearance of a plant by integrating all physiological knowledge. Integrating physiological knowledge into an ideotype concept implies that the knowledge for a specific trait under varying conditions is available. Crop models have the potential to assess effects of traits on growth or yield by varying genotypic model coefficients within known genotypic ranges. By the use of sensitivity analyses or optimizations in the model, the combination of plant traits that maximize yield for a specific environment can be accomplished. Such sensitivity analyses have been conducted for many crops, including soybean, maize and rice (e.g. Boote and Tollenaar, 1994). Boote et al. (2003), and more detailed Messina et al. (2006a), conducted sensitivity analyses in which grain yield variations were recorded for variations in the genetic coefficients LFMAX (maximum leaf photosynthesis) and SLAVAR (specific leaf area). In a first scenario, these coefficients were varied independently, and in a

second step appropriate couplings between parameters were considered. In the absence of coupling, yield continued to increase with increasing leaf-specific leaf weight. In the presence of the coupling, the yield response to increasing SLAVAR via leaf-specific leaf weight rapidly reached an asymptote.

As shown in the model-based sensitivity analysis in Chapter 4 phenology plays an important role to avoid stress especially in target environments where drought during important periods of plant growth occurs. This analysis is analogous to the creation of genetic isolines since only one parameter is changed while the rest of the plant characteristics are kept constant. It could help breeders to understand the physiological background before selecting a specific trait, but normally breeders select for multiple traits to improve yield. Accounting several traits for designing ideotypes was used e.g. by Aggarwal et al. (1997) for rice. In this approach, different traits were considered to be stochastic and by the use of the Monte Carlo simulation the optimal combination of traits that maximize potential rice yield in irrigated tropical environments were generated. This technique allowed determining the extent of divergence required from the mean value of different traits and their consequence on yield potential. However, the success of every ideotyping approach depends upon the capability of the simulation model to accurately simulate the manner of action of traits and upon genetic linkages among various traits. Once these limitations are overcome, ideotyping approaches such as presented in Chapter 4 can provide useful information on traits required for higher yield potential.

6.3.2 Analyses of Causal Relationships in Plant Physiology

For quantitative traits such as grain protein content, genetic differences are often masked by environmental factors. To evaluate how traits interact with environment and to investigate causal relationships, plant breeders must conduct field experiments over a number of years and across different environments. As proposed by Oury et al. (2003), there are two possibilities to reduce environmental influences in comparison to genetic effects: firstly, by examining large genetic variations in a single environment or secondly by averaging out environmental effects by using mean values obtained from a network corresponding to a wide range of environments.

Since crop models integrate interacting effects of genotypic differences and management, it seems likely that model-based characterizations of cultivars can help explain G x E interactions. Improved understanding of the underlying physiological processes of past genetic improvement can increase the efficiency of plant breeding programs by helping define selection criteria and

breeding objectives (Messina et al., 2006a). This is true for simple traits such as traits affecting phenology, but for complex traits such as grain protein content, model performance often proofs problematic. As investigated in several studies, the CERES-Wheat model tends to overestimates grain protein at high protein concentrations and underestimates at low protein concentrations (Otter-Nacke et al., 1986; Asseng et al., 1998). Furthermore, although grain protein is well simulated in maritime climate, simulation results under extreme climatic conditions are less meaningful than expected (Asseng et al., 2000). If a model has problems testing interactions among simple traits and complex traits, how can this problem be overcome? As shown in Chapter 5, regression analysis with model parameters could be a solution. It was applied for the investigation of the coherences between traits affecting pre-anthesis phenology (represented by genotypic model parameters) and grain protein content.

In consideration of the arguments mentioned, an innovative contribution to examine causal relationships to define selection criterias could be to combine two approaches: (i) characterization of simple traits by genotypic model parameters (ii) regression analysis to investigate relationships between complex traits and their parameters. The advantage of such an approach is greatest when the availability of data for modeling is restricted, especially when data are based on breeding trials that are distributed over many locations and years. Due to the need for a full characterization of the initial soil conditions, it is seldom feasible to conduct such simulations with breeding trials such as the IWWPN used in Chapter 3 and 5. Furthermore, for most breeding trials, one would not have the data required to simulate N dynamics accurately.

The main drawback of this approach could be that by using regression analysis, the character of physiology that determines response to environmental factors can not be investigated. In addition, limitations of regression analyses such as the fact that the genotype mean is not independent of the marginal means of the environment (relevant for small numbers of genotypes) or that the assumed linear relationship between interaction and environment means reduces the effectiveness of the approach (Crossa, 1990).

6.4 Contribution to Adapt Cropping Systems to Climate Change Trends in China

During the last decades, the trend of global warming has been well documented in many areas around the world and this trend is projected to continue or even accelerate in the future (IPPC, 2001). In China, especially in the last two decades, the mean temperature has increased with the highest increase in the north and a smaller increase in the south (Tao et al., 2003). The most relevant trend observed over the last fifty years in China was the warming rate in winter of about 0.4°C/decade (Zhai et al., 1999). This spatial and temporal changes in temperature are presumed to provoke significant changes in crop development and thus in the composition and productivity of the cropping systems in China (Tao et al., 2004).

Wheat is a main component of many cropping systems across China and the adaptability of wheat (especially of phenology) to diverse climate conditions enables a crop rotation with miscellaneous arable crops (FAO, 1994). This adaptability of wheat is an advantage, but if the observed trends in global warming will continue, wheat cultivation and thus the cropping systems including wheat will have to adapt to the arising problems, too. Results of a study conducted from 1981 to 2001 indicated that with increasing maximum and minimum temperatures, wheat growth stages became earlier and yield decreased slightly at some locations in China (Tao, 2006).

In Chapter 2, 3 and 4, factors influencing wheat phenology were described and model-based recommendations regarding the influence of phenology, especially on yield, were put on a reliable basis. However, before using a crop model to adapt cropping systems in China to global warming trends, several factors that could contribute to the uncertainty of modeling impacts of climate change on agricultural systems must be considered (Parry et al., 1999). One uncertainty is the fact that yield estimates obtained in climate impact assessments vary from one model to another (Mearns et al., 1999). Another uncertainty can be the spatial resolution. Crop models simulate processes at fine scales, whereas climate change scenarios that drive crop models are typically produced by climate models operating at coarse scales (Easterling et al., 1998). Statistical downscaling techniques and nested, numerical, limited area models have shown large simulated yield discrepancies between coarse-resolution and fine-resolution (downscaled) climate change scenarios. Mearns et al. (1999) demonstrated for a site in the Great Plains that yields can change depending on the resolution of the climate change scenario.

Nevertheless, if these uncertainties are considered, model simulation analyses can show the impact of e.g. higher mean temperature on wheat phenology and therefore on the composition

and total yield of a cropping system. Chinese farmers would profit from the model-based prediction of phenology through a more accurate adaptation of cropping systems to future demands. The obtained information could help adjusting planting dates or demonstrate the effect on yield when using two crops in one year versus a single crop, as proposed by Binder et al. (2007). Summing up, to examine the relation between climate variation, crop phenology and crop production by conducting model simulation analysis could be an excellent possibility how genotypic model parameters determining wheat phenology can contribute to adapt cropping systems to climate change trends.

6.5 Contribution to a Sustainable Resource Use in the North China Plain

Wheat is a major crop in the NCP and is mainly cultivated together with summer maize in a double cropping system. During the wheat growing season, which lasts normally from October to June, rainfall provides only 25-40% of crop water requirement. To maintain and enhance yield, irrigation is required. Water resources for irrigation are mainly exploited from groundwater and have caused in addition to water table decline many other environmental problems within this region (Liu and Wei, 1989).

To attain optimal and high wheat yields, the application of mineral N-fertilizer is also important and has increased rapidly during the last decades in the NCP. Investigations in Shunyi and Tongzhou Counties showed that the average amount of N-fertilizer application was 309 kg N ha^{-1}yr^{-1} for winter wheat (Zhao, 1997) whereas in two high-yielding counties, Wenxian, Henan Province, and Huantai, Shandong Province, the N-fertilizer application rate reached even 587 kg N ha^{-1}yr^{-1} (Gao et al., 1999). Unqualified N-fertilization results in low nitrogen use efficiency and causes high losses to the environment.

To cope with the water shortage problems and the over N-fertilization of wheat in the NCP, it is essential to reduce agricultural water use by improving water use efficiency and on the other hand diminish nitrogen losses while maintaining high yield to meet the demand of the increasing population. There are several approaches to solve these problems, but the crucial point is to match the demand of the plant with the application of nitrogen and water. The understanding of phenology and of the factors influencing it is essential for this purpose. Cropping system models (CSMs) could be consulted as decision tool.

However, CSMs as e.g. CSM-CERES-Wheat, can only be used as a decision support tool at farm level when the gap between CSMs and the applications is closed (Jones et al., 2003). The

understanding how traits interact with the environment is an essential linkage. The investigations and results in Chapter 2 and 3 can facilitate the use of crop models as a decision tool for farmers by providing the needed connection. Model-based analyses of the impact of phenology on water use efficiency and nitrogen use efficiency can provide information that enables farmers to time N-fertilizers and irrigation more accurately which would contribute to a sustainable resource use while maintaining high yield.

For plant breeders, selecting traits based on the knowledge of a model-based sensitivity analysis can be an excellent addition to a plant breeding program when adjusting cultivars to constraints of target environments in the NCP. The resulting phenologically-adapted cultivars could use water and nitrogen more effectively because growth stages occur at the most appropriate times.

6.6 Future Perspectives

Duration of different development phases and variation in life cycle is arguably one of the most important genetic variations contributing to yield potential of different cultivars. Physiologists and plant breeders know that potential yield is coupled with life cycle differences that optimize the use of the growing season duration available at a given location. As proposed by Boote et al. (2003), there is much potential for collaboration of crop modelers, physiologists and plant breeders to study effects of genetic improvement in traits as simulated by crop models. The approach of estimating genetic effects using linear regressions appears readily applicable to other traits as well as to other models. This would on one hand require improved genetic characterization of wheat lines and on the other hand a crop where cultivar specific characterization of loci is available and the genome is not too complex. A good example could be maize. Furthermore, gene-based prediction of phenology could lead to a more accurate targeting of germplasm and analysis such as crop response to climate risks.

One of the questions asked of plant breeders in future is whether genetic improvement can keep pace (both adapt to climate change and increase yield potential) as the global climate changes. Designing phenological-adapted ideotypes based on model-based sensitivity analyses and projected climate scenarios could be an innovative contribution to assess genotypes for demands caused by climate change. Boote et al. (2003) proposed that certain traits show more response when investigated under good management or poor management. For phenology this

could mean that when planting or harvest date is earlier/later, management can influence phenology too. Therefore, a future approach designing a phenological-adapted ideotype by the use of model-based sensitivity analyses should also consider management and possible genotype x management interactions.

To use crop models for plant breeding purposes or the analyses of genetic improvement, crop models must continue to improve, and the complexity among cultivars should be considered. The results of Chapter 2 indicated the importance of considering cultivar variation in earliness *per se* when estimating vernalization requirement and photoperiod response. In Chapter 3 variation for earliness *per se* loci were not considered due to insufficient information on variation in earliness *per se* loci among cultivars.

Thus, future research should focus on testing and incorporating the effects of the *Eps* loci in the gene-based approach. This should both improve the overall performance of the model and allow more accurate characterization of effects of the *Vrn* and *Ppd* loci. Besides studies to clarify the inheritance of earliness *per se,* research is needed to determine whether measured earliness *per se* varies with temperature or other factors.

To ensure a further improvement of the sustainable resource use in the NCP, an interesting research approach could be to test the influence of wheat phenology on yield and improved resource use when planted under agroforestry or intercropping systems.

7 Summary

Predicting phenology of wheat is important for many aspects of wheat production as for example facilitating accurate timing of pesticides, fertilizers and irrigation, avoiding stress at critical growth stages, and adapting cultivar characteristics to specific environmental constraints or global changes in climate. The research of this dissertation was embedded in the context of the "International Research Training Group Sustainable Resource Use in North China" with the overall objective to analyse flows and systems and to assess resource detraction and changes in cropping systems at different levels. As a consequence of the importance of wheat in the North China Plain and the significance of predicting phenology, the comprehensive research idea of the dissertation was to focus on underlying determinants of variation in wheat phenology.

The aim of the dissertation was to characterize and test the impact of wheat phenology on agronomic traits through integrated use of crop models and information on the genetic makeup of cultivars. In order to achieve this goal, four studies were conducted that addressed the following objectives (i) to characterize vernalization and photoperiod responses of wheat cultivars using field-based assessments and compare these with model parameters (ii) to define relations between specific loci affecting phenology and genotypic model parameters based on field data (iii) to use genotypic model parameters for plant breeding by the implementation of an ideotype design (iv) to examine physiological coherences between genotypic model parameters and grain protein content.

The first main focus of this dissertation was to characterize traits affecting wheat phenology. In an initial study, cultivar differences in vernalization requirement, photoperiod response and earliness *per se* were distinguished by field-based indices and compared with corresponding model parameters in CSM-Cropsim-CERES-Wheat model Version 4.0.2.0. To determine whether field-based indices can provide accurate characterization of vernalization requirement, photoperiod response and earliness *per se*, 26 winter wheat cultivars were evaluated under field conditions at Ihinger Hof, Germany using two natural photoperiod regimes (from different transplanting dates) and vernalization pre-treatments. Field-based indices were quantified using rates of development calculated by reciprocal of thermal time to anthesis. To test whether these indices can accurately represent the cultivar variation, the accordance with genotypic model parameters estimated for CSM-Cropsim-CERES-Wheat was examined. Results indicated that combining planting dates with vernalization pre-treatments can permit reliable, quantitative characterization of vernalization requirement, photoperiod response and earliness *per*

se of wheat cultivars. Furthermore, genotypic model parameters appeared to be reliable estimates of cultivar differences in response to vernalization and photoperiod. In a second study, the model parameters for vernalization requirement (P1V) and photoperiod response (P1D) were estimated using gene information. To estimate these model parameters through integrating effects of *Vrn* and *Ppd* loci, flowering data obtained for 29 cultivars tested in the International Winter Wheat Performance Nursery (IWWPN) were used. This series of trials was distributed from 1968 to 1981 over 85 locations, which predominantly represented traditional winter wheat production areas but included also spring wheat areas. Using gene-based estimates of the parameters P1V and P1D in the model, 96% of variation in flowering was explained for the calibration dataset and 90% for the evaluation set, with root mean squared errors of 9 days and 10 days for the two datasets, respectively. Summarizing, results indicated that gene-based estimation of model coefficients was effective for prediction of phenology over a wide range of environments and appears feasible for studying wheat response to environment.

The second main focus of this dissertation was to highlight on the basis of two examples how model parameters affecting wheat phenology can be used for breeding purposes such as analyzing causal relationships between traits. To assist plant breeding with crop models a possibility could be to assess model parameters for designing improved plant types (ideotypes). CMS-Cropsim-CERES-Wheat was used to test model parameters concerning plant development and grain yield. In ideotyping sequences, the parameters were varied and the model was run in four different scenarios in the North China Plain. The scenarios consisted of two locations, Wuqiao and Quzhou in Heibei Province, and a dry and a wet growing season for each location. The parameter G1 (corresponding trait: kernel number per spike) showed the highest influence on yield over all scenarios followed by G2 (corresponding trait: kernel weight). Parameters affecting mainly wheat phenology such as P1V (corresponding trait: vernalization requirement) and P1D (corresponding trait: photoperiod response) also captured an important part in determining yield. Low vernalization requirement and low photoperiod response generated a higher yield compared to high responses for dry scenarios in both locations. Results obtained in this study could help breeders to select the relevant traits and integrate them in their breeding program for a specific population of environments. To investigate the coherences between pre-anthesis phenology and grain protein content the statistical analysis of causal relationships with genotypic model parameters was used. It was tested whether model-based characterizations of vernalization requirement, photoperiod response and earliness *per se* can help explain genotype x environment

interactions for grain protein content. Twenty four winter wheat and five spring wheat cultivars (International Winter Wheat Performance Nursery trials) and twelve winter wheat cultivars (of a two year field study at Ihinger Hof, Germany) were characterized using CSM-Cropsim-CERES-Wheat. In addition to the model parameter P1V and P1D, P_{123} for earliness *per se* was used. Covariance analyses of the International Winter Wheat Performance Nursery dataset indicated that about 7% of variation in grain protein content for the winter and spring wheat cultivars was explained by cultivar, with another 7% attributable to interactions of cultivar with region, site and year. Vernalization requirement, photoperiod response, and earliness *per se* all influenced grain protein content, but their effects varied with site and year within region. Path analyses using data from two seasons in Germany confirmed that grain protein content increased with a shorter pre-anthesis phase and indicated in accordance with the covariance analyses the environmental dependence of this trait. The results proposed that efforts to improve grain protein content should target levels of vernalization requirement, photoperiod sensitivity and earliness *per se* to specific populations of environments and seek to reduce the apparent large influence of environment on grain protein content.

The improved understanding of traits affecting phenology and the linkage with genotypic model parameters can be applied in China to solve arising and existing agricultural challenges. In China, model-based analyses can help adapting cropping systems to global warming. In the North China plain a more accurate timing of N-fertilizers and irrigation, as a result of modeling, can ensure a sustainable resource use while maintaining high yields.

Summarizing, the findings of this dissertation showed that traits affecting phenology in wheat can be successfully characterized by field-based indices, genotypic model parameters and gene-based estimates of genotypic model parameters. Furthermore, the research showed how genotypic model parameters can be used for breeding purposes, and to test causal relationships both at regional and local geographic scales.

8 Zusammenfassung

Die Prognose der Weizenphänologie ist für viele Aspekte der Weizenproduktion wichtig. Beispiele sind die termingerechte Anwendung von Pestiziden, Düngemitteln und Bewässerung, sowie die Vermeidung von Stress während kritischen Wachstumsstadien und die Anpassung von sortenspezifischen Eigenschaften an globale Änderungen des Klimas. Die Untersuchungen dieser Doktorarbeit waren Teil der "International Research Training Group Sustainable Resource Use in North China", welche das umfassende Ziel hat, Materialflüsse und Systeme, sowie Beeinträchtigungen von Resourcen und Veränderungen der Anbausysteme auf verschiedenen Ebenen zu analysieren. Auf Grund des Stellenwertes von Weizen in der Nordchinesischen Tiefebene und der Bedeutung der Prognose der Phänologie wurde als übergreifende Zielsetzung der Doktorarbeit die Erforschung von Einflussgrößen auf die Weizenphänologie definiert.

Das Ziel der Doktorarbeit war, die Phänologie von Weizen zu charakterisieren und ihren Einfluss auf landwirtschaftliche Merkmale unter der Verwendung des Pflanzenwachstumsmodells CSM-Cropsim-CERES-Wheat 4.0.2.0 und sortenspezifischen genetischen Informationen zu prüfen. Dazu wurden vier Studien durchgeführt, die folgende Zielsetzungen verfolgten (i) die Reaktion von Weizensorten auf Photoperiode und Vernalisation mit Hilfe einer feld-gestützten Bewertung zu testen und deren Reaktion mit sortenspezifischen Modelkoeffizienten zu vergleichen (ii) basierend auf Felddaten Zusammenhänge zwischen spezifischen Loci, welche die Phänologie beeinflussen, und sortenspezifischen Modelkoeffizienten zu definieren (iii) die Verwendung von sortenspezifischen Modellkoeffizienten für die Pflanzenzüchtung durch die praktische Anwendung in einem Ideotyp-Konzept zu testen (iv) die physiologischen Zusammenhänge zwischen sortenspezifischen Modellkoeffizienten und Proteingehalt im Weizen zu erforschen.

Der erste Schwerpunkt der Dissertation war, Merkmale zu charakterisieren, welche die Phänologie von Weizen beeinflussen. In einer Ausgangsstudie wurden sortenspezifische Unterschiede in Vernalisationsbedarf, photoperiodischer Sensitivität und Frühzeitigkeit durch feld-gestützte Indizes differenziert und mit entsprechenden sortenspezifischen Modellkoeffizienten im Pflanzenwachstumsmodell CSM-Cropsim-CERES-Wheat verglichen. Um feststellen zu können, ob die Indizes eine genaue Charakterisierung des Bedarfes an Vernalisation, Photoperiode und Frühzeitigkeit liefern können, wurden 26 Winterweizensorten mit zwei natürlichen photoperiodischen Regimes (zwei unterschiedliche Pflanzzeitpunkte) und vorvernalisierten Varianten am Ihinger Hof, Deutschland, geprüft. Die feld-basierenden Indizes

wurden anhand der Entwicklungsrate errechnet, welche aus dem Kehrwert von Gradtagen bis Blüte errechnet wurden. Um feststellen zu können, ob diese Indizes die sortenspezifische Variation genau abbilden, wurden sie mit sortenspezifischen Koeffizienten aus CSM-Cropsim-CERES-Wheat verglichen. Die Resultate zeigten, dass die Kombination von Auspflanzzeitpunkten mit vorvernalisierten Behandlungen eine quantitative Charakterisierung des sortenspezifischen Bedarfs an Vernalisation, photoperiodischer Sensitivität und Frühzeitigkeit erlaubt. Darüber hinaus scheinen die sortenspezifischen Modellkoeffizienten eine vertrauenswürdige Schätzung von Sortenunterschieden bezüglich Vernalisation und Photoperiode zu sein. In einer zweiten Studie wurden die sortenspezifischen Modellkoeffizienten für Vernalisationsbedarf (P1V) und photoperiodischer Sensitivität (P1D) mit Hilfe von genetischer Information abgeschätzt. Um diese Modellkoeffizienten durch die Eingliederung von *Ppd* und *Vrn* loci schätzen zu können, wurden Blühdaten von 29 Sorten aus einer Internationalen Winterweizen-Leistungsprüfung herangezogen. Diese Serie von Versuchen wurde von 1968 bis 1981 in über 85 Orten durchgeführt. Es handelte sich dabei hauptsächlich um Winterweizenstandorte und einige Sommerweizenstandorte. Die Verwendung von gen-gestützten Schätzungen von P1V und P1D im Modell konnte 96% der Variation beim Zeitpunkt Blüte für einen Kalibrationsdatensatz erklären und 90% für einen Evaluierungsdatensatz, mit einem mittleren Abweichungsfehler von 9 bzw. 10 Tagen für die beiden Datensätze. Zusammenfassend zeigten die Resultate, dass die gen-gestützten Modellkoeffizienten bei der Prognostizierung von Phänologie über eine weite Spanne von Umwelten effektiv waren und es möglich erscheint, damit die Reaktion von Weizen hinsichtlich Umwelt zu untersuchen.

Der zweite Schwerpunkt der Dissertation war, anhand von zwei Beispielen aufzuzeigen, wie sortenspezifische Modellkoeffizienten welche die Weizenphänologie beeinflussen, für Züchtungszwecke wie zum Beispiel die Analyse von kausalen Zusammenhängen zwischen Merkmalen genutzt werden können. Die Anpassung der Modellkoeffizienten und die sich daraus ergebenden verbesserten Pflanzentypen (Ideotypen) kann eine Methode zur Unterstützung der Pflanzenzüchtung sein. Um die sortenspezifischen Modellkoeffizienten hinsichtlich Pflanzenentwicklung und Kornertrag testen zu können, wurde wieder CSM-Cropsim-CERES-Wheat verwendet. In so genannten Ideotyping-Sequenzen wurden die Koeffizienten in vier verschiedenen Szenarien in der Nordchinesischen Tiefebene variiert und mit dem Model simuliert. Die Szenarien ergaben sich aus zwei Standorten, Wuqiao und Quzhou in der Heibei Provinz, und einer trockenen und einer feuchten Wachstumsperiode. Den größten Einfluss auf den Kornertrag

über alle Szenarien hinweg hatten die Koeffizienten G1 (entsprechendes Merkmal: Kornanzahl pro Ähre) gefolgt von G2 (entsprechendes Merkmal: Kornmasse). Koeffizienten die hauptsächlich die Phänologie beeinflussen wie zum Beispiel P1V (entsprechende Merkmal: Vernalisationsbedarf) und P1D (entsprechendes Merkmal: photoperiodische Sensitivität) spielten eine ebenso wichtige Rolle bei der Bestimmung des Kornertrages. An beiden Standorten generierten bei trockenen Bedingungen ein geringerer Vernalisationsbedarf und photoperiodische Sensitivität einen höheren Kornertrag verglichen mit Erträgen bei höheren Ansprüchen. Resultate aus dieser Studie könnten Pflanzenzüchtern helfen, die relevanten Merkmale zu selektieren und sie in ihr Zuchtprogramm für spezifische Umwelten zu integrieren. Zur Untersuchung der Beziehung zwischen Vorblüte-Phänologie und Proteingehalt des Kornes wurde eine statistische Analyse von kausalen Zusammenhängen mit Hilfe der Modellkoeffizienten angewandt. Es wurde getestet, ob eine Charakterisierung von Vernalisationsbedarf, photoperiodischer Sensitivität und Frühzeitigkeit durch das Modell bei der Erklärung der Interaktionen von Genotyp und Umwelt behilflich sein kann. 24 Winterweizen und 5 Sommerweizensorten (aus der Internationalen Winterweizen-Leistungsprüfung) und 12 Winterweizensorten (aus einem Feldversuch am Ihinger Hof, Deutschland) wurden mit CSM-Cropsim-CERES-Wheat charakterisiert. Zusätzlich zu den Koeffizienten P1V und P1D wurde P_{123} als Maß für die Frühzeitigkeit verwendet. Die Kovarianzanalyse der Daten der Internationalen Winterweizen- Leistungsprüfung zeigte, dass ungefähr 7% der Variation des Proteingehaltes im Korn durch die Sorte und weitere 7% durch Interaktionen von Sorte mit Region und Ort erklärt werden konnte. Vernalisationsbedarf, photoperiodische Sensitivität und Frühzeitigkeit beeinflussten den Proteingehalt im Korn, die Effekte variierten aber mit Ort und Jahr innerhalb einer Region. Die Pfadanalysen eines Datensatzes aus zwei Versuchsjahren am Ihinger Hof bestätigten, dass der Proteingehalt im Korn mit kürzerer Vorblüte-Phase steigt. In Übereinstimmung mit der Kovarianzanalyse wurde die Abhängigkeit des Merkmals von der Umwelt sichtbar. Die Resultate implizieren, dass Anstrengungen zur Erhöhung des Proteingehaltes darauf abzielen sollten, umweltspezifische Niveaus von Vernalisationsbedarf, photoperiodischer Sensitivität und Frühzeitigkeit zu bestimmen und den offenkundigen Einfluss der Umwelt zu reduzieren.

Das optimierte Verständnis von Merkmalen, welche die Phänologie beeinflussen, und die Verknüpfung mit sortenspezifischen Modellkoeffizienten, kann in China zur Lösung von aufkommenden Problemen und aktuellen agronomischen Herausforderungen beitragen. Modell-gestützte Analysen können in China die Anpassung von Anbausystemen an die Klimaerwärmung

erleichtern. In der Nordchinesischen Tiefebene kann mit Hilfe der Modellierung eine termingerechte Anwendung von N-Düngung und Bewässerung erfolgen und so eine nachhaltige Landwirtschaft mit hohen Erträgen sichergestellt werden.

Zusammenfassend zeigen die Erkenntnisse dieser Doktorarbeit, dass Merkmale, welche die Phänologie beeinflussen erfolgreich mit feld-gestützten Indizes, sortenspezifischen Modellkoeffizienten und gen-gestützten Modellkoeffizienten charakterisiert werden können. Darüber hinaus zeigen die Untersuchungen, wie sortenspezifische Modellkoeffizienten für Züchtungszwecke und für die Analyse von kausalen Zusammenhängen in der Pflanzenphysiologie sowohl auf regionaler als auch auf lokaler Ebene verwendet werden können.

9 Overall List of References

The additional labelling with letters for references with identical first author and co-authors of the same publishing year applies only for citations in the introduction and the general discussion. For publications, the labelling was done separately in the respective chapter.

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