

INTERNATIONAL MAIZE AND WHEAT IMPROVEMENT CENTER

Modeling Temperature Response in Wheat and Maize

Jeffrey W. White, Editor



Natural Resources Group

Geographic Information Systems Series 03-01



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Proceedings of a Workshop, CIMMYT, El Batán, Mexico, 23-25 April 2001

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Preface

This is the third international modeling workshop that CIMMYT's Natural Resource Group has hosted in Mexico. Workshop themes are moving from broad ("Directions in Modeling Wheat and Maize for Developing Countries," in 1998) to more specific ("Modeling Extremes of Wheat and Maize Crop Performance in the Tropics," in 1999) to even more specific, with this year's focus on modeling temperature responses.

The question of how best to describe a crop's response to temperature holds broad interest for CIMMYT's research activities. In order to serve our partners scattered throughout the developing world, CIMMYT deals with agroclimatic regions that vary from tropical lowlands, where high temperatures can limit growth and development, to highlands and temperate regions, where low temperatures and frosts are prevalent. While models frequently are adjusted to better represent specific local conditions, CIMMYT's needs are best served by models that show reliable and robust performance across environments, requiring a minimum of local calibration or adjustment.

CIMMYT further recognizes that temperature stresses often are a component of effects of water deficits, whether in rainfed or irrigated systems. To fully understand options for crop improvement and crop management where water is a limiting factor, crop responses to temperature is also a concern.

The prospect of global warming provides further arguments for the need to understand better how crops respond to temperature. Predictions of the Intergovernmental Panel on Climate Change that temperatures may rise 2° to 5°C by 2050 imply major shifts in cropping practices, cultivars and even crop species in coming years. Crop models can offer valuable insights into how agriculture will be affected by such changes, but for any predictions to have credibility, the underlying models must be based on sound physiological principles and be tested over a realistic range of conditions. The workshop topic thus is also timely given proposals for the CGIAR to develop a Challenge Program on Global Warming.

CIMMYT was especially pleased that most participants in the modeling workshop were able to stay an additional two days for the GCTE Tropical Cereals Network Inaugural Workshop, which saw the enthusiastic launch of this new GCTE network for maize, rice, sorghum and millets.

We thank David Poland, Marcelo Ortiz, Kristian Harrington-Colón, and others for their assistance in editing and laying out the final version for printing.

Larry Harrington Director Natural Resources Group CIMMYT

Introduction

The workshop "Modeling Temperature Response in Wheat and Maize," held from 23 to 25 April 2001 at CIMMYT's headquarters at El Batan, Mexico, examined various approaches for modeling responses of crops to temperature. Effects on both growth and development were considered.

One might expect that temperature responses have been examined so thoroughly that little novel or useful could emerge from such an undertaking. However, in the second modeling workshop, "Modeling Extremes of Wheat and Maize Crop Performance in the Tropics," the papers highlighted possible deficiencies in the responses of the CERES Maize and Wheat models, with attempts to improve temperature responses of the models during the working sessions. One suggestion was that these deficiencies reflected the under-representation of tropical and subtropical conditions among the model development and testing datasets.

Further incentives for the workshop topic derived from two growing and somewhat inter-connected fields of model application. Concerns over global change have lead to numerous studies on potential impacts of global temperature and CO_2 increases as well as on the potential for reducing atmospheric CO_2 through "carbon sequestering" in agricultural soils. The second topic is integration of crop models with geographic information systems. For land areas larger than a single village or a large farm, spatial variation in temperature is usually a primary determinant of differences in growth, yield and environmental impacts.

The first day of the workshop opened with short oral presentations on aspects of modeling temperature response in wheat and maize. The following two days were dedicated to informal working groups that examined specific topics in detail. In most cases, this involved running test data sets and modifying model code.

Immediately following the workshop, a meeting was held to inaugurate the Global Change and Terrestrial Ecosystem (GCTE) Tropical Cereals Network, to provide a home for modeling efforts in maize, sorghum and millet. (The GCTE Wheat Network was founded in 1992.)

Workshop Summary

During the workshop "Modeling Temperature Response in Wheat and Maize," held from 23 to 25 April 2001 at CIMMYT's headquarters at El Batan, Mexico, participants examined various approaches for modeling temperature effects in crops. Effects on both growth and development were considered.

A review of the FORTRAN code of the CERES models by Wilkens and Singh showed how temperature is thought to influence numerous processes, including carbohydrate production, growth, soil nitrogen dynamics, root growth and evapotranspiration. The effect of temperature on grain nitrogen filling rate showed an unexpected discontinuity, which merits further investigation. It was suggested that the software code be modified to allow greater flexibility in modifying temperature functions. This would facilitate testing of proposed model improvements.

White and Reynolds reviewed the expected temperature responses that crop models typically consider: development (including phenology and morphology), photosynthesis, respiration, partitioning, and to a lesser extent, nutrient uptake. Emphasis was given to the need to distinguish between immediate responses and acclimation effects, and to use realistic growing conditions.

In an experiment where wheat was subjected to different soil temperatures, McMaster and Hunt found that while increased soil temperature accelerated germination, soil temperature had no effect on subsequent development. The authors proposed that since meristematic regions in the shoot occur in various locations (i.e., apical meristem, internodes, and leaf sheath) and are subject to distinct thermal regimes, air temperature may have a greater effect on development than was previously expected.

CERES-Maize currently does not simulate tiller production as found at low populations. Du Toit and Prinsloo compared three approaches for modeling tiller production, including two that consider temperature and photoperiod effects.

During the working groups, wheat modelers focused on reviewing modeling response to planting dates for winter-sown spring wheats, using the data sets of S.S. Dhillon from Ludhiana, India for validation. The work was continued following the workshop and showed that both CERES-Wheat 3.5 and Sirius had difficulties simulating vernalization under the relatively warm conditions prevailing at Ludhiana.

To facilitate model validation and adaptation in the Highveld Ecoregion Project, two software packages were developed by Du Toit and Du Toit. The Model Statistical Package uses standard outputs of CERES-Maize 3.0 to calculate linear regression statistics (slope, intercept, and r²), D-index, and the systematic and unsystematic mean square errors. The Weather Analogue Program allows users to create mid-season projections of crop performance based on five sets of historical data showing the greatest similarity to the ongoing season. The Model Statistical Package was demonstrated during the working group and was found to be very promising for rapid assessment of model performance.

During the inaugural meeting of the Global Change and Terrestrial Ecosystem (GCTE) Tropical Cereals Network, participants reviewed models available for maize, sorghum and millet and identified possible sources of data for model evaluation. Plans for subsequent activities of the Network were outlined.

A Code-Level Analysis for Temperature Effects in the CERES Models

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Abstract

The developmental processes of a crop are inextricably linked to the production environment. CERES crop growth simulation models are driven by the accumulation of heat units, or thermal time, which in turn determine the duration and timing of phenological events. The existing CERES models have reliably predicted effects of temperature and photoperiod on crop development and yield. However, a critical examination of how and where thermal units are implemented in the structure of the models is warranted. Functional models often encapsulate photo-thermal effects within structures in the model itself. It is a useful (and necessary) exercise to examine where temperature variables and derivatives are implemented and the effective maxima and minima for these functions. This critical analysis is important when the models are utilized in environments not considered during model and/ or function development. The software code of CERES is reviewed for functions utilizing thermal inputs. Emphasis is given to the wheat version of the model, but most processes are modeled in a similar way for all cereals.

Introduction

Simulation models of crop and soil processes integrate existing scientific knowledge in a way that can elucidate current understanding of plant processes. Perhaps no other factor has a greater influence on crop growth and development than daily temperature minima and maxima. Indeed, temperature functions (and derivatives) in the CERES models directly influence phasic development, growth, soil temperature, soil water balance, and nitrogen transformations. The functions used in the CERES-Wheat model are based on our current understanding of these processes. As expected, some simplifications have been made and calibration and validation of a model are therefore essential steps.

Crop development, growth, and soil processes are in general affected by instantaneous temperature and (in some instances) the maxima or the minima temperature. Thus, temperature inputs at hourly (or more frequent) intervals would assist in simulating many of the processes. However, the accessibility of good quality weather data is an important limitation, particularly in the developing world. To increase the applicability and usefulness of the model, the CERES models use weather data in the form of daily maximum and minimum temperatures. To capture the instantaneous nature of many soil and plant processes and the bias of day versus night temperatures, the CERES models use empirical and weighting functions to provide "relevant" temperature input to the process-level equations. However, some of these functions may not perform as well with extreme temperatures or growth stages. This paper reviews temperature-related functions and plant and soil processes affected by temperature in CERES as distributed with the DSSAT V3.5 (Hoogenboom et al. 1999), with emphasis on the version for wheat. Key variables are defined in the main text, but all variables referenced in the example source code are listed in Appendix A to facilitate reading.

Crop Development

The phasic development (or phenology) of cereal crops is an ordered sequence of processes including sowing, emergence, floral initiation, anthesis, and maturity. Crop development is delineated into two processes, phasic and morphological development. Several researchers have studied the effect of temperature on the rate of development (e.g., Tollenaar et al. 1979; Swan et al. 1987; Ritchie and NeSmith 1991).

Thermal Time

In the CERES models, the accumulation of thermal time per day (DTT) drives crop development, where thermal time is defined as

$$T_d = \sum_{i=1}^{n} (T_a - T_b)$$
, where $T_a = Daily$ mean temperature
 $i=1$ $T_b = Base$ temperature
 $n = Number \text{ of } days$
 $T_d = Thermal time (°Cd)$

The CERES routines PHASEI and PHENOL use accumulated thermal time to define plant age and to advance the ontogeny of developmental events, with the base and optimum temperature varying by crop (Table 1). In addition, soil temperature rather than air temperature may be used for early development. In CERES-Maize, soil temperature is used to the tenth leaf stage or tassel initiation, when the growing point is near the ground (Singh 1985).

Growth/ Development Stages

Growth and development are ordered processes in CERES. Key developmental events that define end points of developmental phases include sowing, germination, emergence, end of the juvenile phase,

Table 1. B	ase and opti	imum temper	atures and	thermal time	emergence
requireme	nts (P9) for	various crops	s in the CEF	RES model.	-

Сгор	Base Temperature (°C)	Optimum Temperature (°C)	Thermal Time Requirement for Emergence (P9)
Maize	8	34	45 + 6.0 * Sowing Depth
Wheat	0	15	70 + 10.2 * Sowing Depth
Sorghum	8	34	50 + 6.0 * Sowing Depth
Millet	10	36	45 + 6.0 * Sowing Depth
Barley	0	15	80 + 10.4 * Sowing Depth

onset of panicle initiation, end of leaf growth, end of panicle growth, onset of grain filling, and physiological maturity.

The duration of the juvenile phase, the leaf-tip appearance rate, the duration of floral initiation to anthesis, and the grain filling duration all depend on thermal time in CERES. The vernalization requirements in the wheat and barley models are also temperature driven. In some of the models both photoperiod and thermal time influence the photosensitive phase (the end of the juvenile stage through floral initiation). The cultivar-specific differences in growth stages are accommodated by cultivar-specific genetic coefficients (Tables 2 and 3).

Table 2. Genetic coefficients in the CERES-Maize model.

Coeffic	ient Definition
P1	Thermal time from seedling emergence to the end of the juvenile phase (expressed in degree days above a base temperature of 8°C) during which the plant is not responsive to changes in photoperiod
P2	Extent to which development (expressed in days) is delayed. This increases for each hour increase in photoperiod above the longest photoperiod at which development proceeds at a maximum rate (considered to be 12.5 hours)
Р5	Thermal time from silking to physiological maturity (expressed in degree days above a base temperature of 8°C)
G2	Maximum possible number of kernels per plant
G3	Kernel filling rate during the linear grain filling stage under optimum conditions (mg/day)
PHINT	Phylochron interval; the interval in thermal time (degree days) between successive leaf tip appearances

Table 3. Genetic coefficients in the CERES-Wheat model.

Coefficient Definition

PIV	Relative amount that development is slowed for each day of unfulfilled vernalization, assuming that 50 days of vernalization is sufficient for all cultivars
PID	Relative amount that development is slowed when plants are grown in a photoperiod 1 hour shorter than the optimum (considered to be 20 hours)
P5	Relative grain filling duration based on thermal time (degree days above a base temperature of 1°C), where each unit increase above zero adds 20 degree days to an initial value of 430 degree days
G1	Kernel number per unit weight of stem (less leaf blades and sheaths) plus spike at anthesis (g ⁻¹)
G2	Kernel filling rate under optimum conditions (mg/day)
G3	Non-stressed dry weight of a single stem (excluding leaf blades and sheaths) and spike when elongation ceases (a)
PHINT	Phyllochron interval; the interval in thermal time (degree days) between successive leaf tip appearances

Sowing and germination

When the automatic planting option is chosen, a set of user-specified temperature limits set up the planting window. Temperature has no apparent effect on germination in CERES except for CERES-Rice. In general, the soil moisture content is the key driver for seed germination.

Emergence

The emergence of a germinated seedling is dependent on a management factor (depth of sowing) and thermal time accumulation (Table 1).

End of juvenile phase to floral initiation

The juvenile (basic vegetative) phase in maize, sorghum, and millet is primarily influenced by a thermal time-dependent genetic coefficient (Tables 2 and 3). In wheat and barley, the juvenile phase is not only controlled by thermal time but is also largely dictated by the vernalization requirement and/or photoperiod. The phase from the end of the juvenile phase to floral initiation in millet and sorghum is affected by a photothermal regime; in maize, it is affected by photoperiod alone. Wheat and barley often require an exposure to relatively cold temperatures before spikelet formation can begin, a process known as vernalization. The genetic coefficient that describes this temperature function is P1V (Table 3). It is described as the relative amount that development is slowed for each day of unfulfilled vernalization, assuming that 50 days of vernalization is sufficient for all cultivars. In CERES-Wheat, the relative development rate is calculated as a function of temperature and P1V. Temperatures of 0° to 8°C are most effective in satisfying the vernalization requirement. In wheat and barley the phase for beginning of ear development is also affected by thermal time.

End of leaf growth (anthesis)

In the CERES models, thermal time and leaf numbers affect the phase from floral initiation to anthesis. Leaf numbers are influenced by temperature and photoperiod.

Grain filling duration

For all crops in CERES, the grain filling duration is under cultivar-specific thermal time control (P5 in Tables 2 and 3). However, poor grain growth due to water, temperature, and/or N stresses can reduce grain filling duration.

Leaf appearance rate

The leaf appearance rate in the CERES models is also primarily temperature-driven. With the exception of the period of formation for the first two to three leaves, CERES assumes a constant thermal requirement for a single leaf to appear. The thermal time for a single leaf-tip to appear, the phyllochron interval (PHINT), is a cultivar-specific coefficient (Tables 2 and 3).

Tillering

The potential tiller growth rate and tiller number are affected by thermal time accumulation as well as the daily rate of accumulation (Figure 1). During the stage marked by the end of the vegetative stage and the beginning of ear growth in wheat (stage 2), the single tiller growth rate for any given temperature is also dependent on the phenological age of the crop (that is, the cumulative thermal time). As the wheat crop reaches the end of leaf growth to anthesis stage, the tiller growth rate is no longer dependent on the age of the plant. Unlike other development processes such as phase changes and leaf numbers, tiller growth and numbers are sensitive to water and nutrient stresses.



Figure 1. Wheat tiller growth as affected by thermal time during end of vegetative to beginning of ear growth (stage 2) and anthesis (stage 3). During stage 2 development age (SUMDTT) also influences tiller growth rate.

Crop Growth

Photosynthesis

Potential production of carbohydrate through photosynthesis is modeled on a daily basis as a function of temperature, CO₂, and stress factors, and is represented in the code as:

```
Υ1
      = 1.5-0.768*((ROWSPC*0.01)**2*
         PLTPOP)**0.1
PCARB = 2.1*SRAD/PLTPOP*(1.0-EXP(-Y1*LAI))
!Calculate Photosynthetic Response to CO2
     = TABEX (CO2Y, CO2X, CO2, 10)
PCO2
PCARB = PCARB*PCO2
PRFT
      = 1.0 - 0.0025 * ((0.25 * TMIN + 0.75 * TMAX))
         -26.0)**2
PRFT
     = AMAX1(PRFT, 0.0)
CARBO = PCARB*AMIN1(PRFT, SWFAC, NSTRES)
      = AMAX1(DTT,0.0)
DTT
```

The carbohydrate production for any given day (CARBO) may be reduced from the potential rate (PCARB) by sub-optimal temperature (PRFT), water stress (SWFAC), and N stress (NSTRES). Note that only the most restrictive factor (the one with the smallest value) is considered due to the use of the AMIN function of Fortran.

The temperature stress is obtained through a function that uses a weighted mean of the daily maximum and minimum temperatures (Figure 2).

As mentioned, the inputs to the CERES model are the daily maximum and minimum temperature. Hence,



Figure 2. Effect of mean daytime temperature on daily carbohydrate accumulation in wheat.

the temperature modifier for photosynthesis will be biased by the weighted maximum and minimum temperature estimation and the difference between the maximum and minimum temperature. The model shows that optimum temperature response is obtained at maximum temperature of $\geq 20^{\circ}$ C and as the minimum temperature decreases (Figure 3). The response also shows the optimum is spread over a wider range than is evident in Figure 2.

Growth

Root

The depth of root development in the soil (rooting depth) in CERES is directly influenced by thermal time (DTT), a soil hospitality factor (SHF), and water stress (SWFAC, SWDF) as shown:

RTDEP = RTDEP + DTT*0.1*SQRT(SHF(L)*AMIN1 (SWFAC*2.0,SWDF))

The root growth and the root length density (distribution) are affected by daily photosynthesis, growth stage, partitioning rules, and root depth.

LAI/leaf growth

The effect of temperature on leaf area index and leaf growth comes through leaf appearance rate, leaf number, growth stage (partitioning rules), and daily carbohydrate accumulation rate.

Grain filling

Grain number, grain filling rate, and grain filling duration are the main yield-determinants in the CERES models. Grain filling duration, as discussed previously,



Figure 3. Effect of maximum and minimum temperature on daily carbohydrate accumulation in wheat.

primarily varies with thermal time. Grain filling rate is also very sensitive to temperature (Figure 4). In general, the wheat grain filling rate decreases as the mean temperature falls below 25°C. The model seems to indicate better grain filling rate when the temperature difference between maximum and minimum is minimized. The sensitivity range for these differences needs to be evaluated against the expectation that higher grain filling should occur when there is a large difference between maximum and minimum temperature due to reduced night respiration.

The effect of temperature on the nitrogen grain filling rate shows a similar trend–as the mean temperature increases, the grain N fill rate increases linearly (Figure 5). The differences in maximum and minimum temperature did not have as much effect as with the grain filling rate. Here, however, as the temperature difference increases, the N accumulation per kernel also increases. The figure also shows a discontinuity in the grain-N-filling rate at 10°C, which appears to represent an error in coding of the physiological concepts. Figure 5 has been simplified by assuming the daily thermal time for any given day is the same as the mean temperature where base temperature for wheat is taken as 0°C.

Water Balance

The soil water balance model in CERES is a onedimensional model that computes the daily flux in soil water content by soil layer due to infiltration of rainfall and irrigation, drainage, unsaturated flow, soil evaporation, and root water uptake. The soil input file has parameters that describe its surface conditions and layer-by-layer soil water holding and conductivity characteristics. Thermal inputs into the model are used to calculate soil temperature and evapotranspiration, as shown in the code below:

SUBROUTINE PETPT(SALB,SRAD,TMAX,TMIN, XHLAI,EO)

```
IMPLICIT NONE
```

REALALBEDO, EEQ, EO, SALB, SLANG, SRAD, TD, TMAX, TMIN, XHLAI

TD = 0.60*TMAX+0.40*TMIN

IF (XHLAI.LE.0.0) THEN ALBEDO=SALB ELSE ALBEDO=0.23-(0.23-SALB)*EXP(-0.75*XHLAI) ENDIF

```
SLANG=SRAD*23.923
EEQ=SLANG*(2.04E-4-1.83E 4*ALBEDO)*(TD+29.0)
EO=EEQ*1.1
IF(TMAX .GT. 35.0)THEN
EO=EEQ*((TMAX-35.0)*0.05+1.1)
ELSE IF (TMAX .LT. 5.0) THEN
EO=EEQ*0.01*EXP(0.18*(TMAX+20.0))
ENDIF
EO=MAX(EO,0.0)
```



Figure 4. Effect of mean temperature and temperature difference (max-min) on wheat grain-filling rate.



Figure 5. Effect of mean temperature, temperature difference (max-min) and daily thermal time (temperature assumption in this figure as base temp = 0).

Nitrogen

All soil nitrogen transformation processes are affected by changes in soil temperature. Soil temperature in the CERES models is simulated using daily air temperature data, soil moisture status and available water content (water balance simulation), albedo, solar radiation, and day of the year. The CERES models use a simple soil temperature relationship to modify soil N rates (Figure 6). As the soil temperature increases, the rate of the processes continues to increase linearly.



Figure 6. Effect of soil temperature in a given layer on nitrogen transformation processes.

Conclusions

Temperature and temperature derivatives are linked to nearly every process in the CERES model. Temperature-based functions can obfuscate true physiological responses in some cases and need to be critically evaluated as we continue model development. Increased flexibility in modifying temperature functions may be needed to improve the CERES models.

To help address these concerns, the DSSAT crop models have been re-designed and programmed to facilitate more efficient incorporation of advances in understanding of the underlying science. The basis for the new DSSAT Cropping System Model (CSM) design is a modular structure in which components are structured to allow easy replacement or addition of modules (Jones et al. 2003). This modular approach makes it easier to isolate temperature effects from one process (module) to another, in order to avoid spurious or auto-correlated temperature-related effects.

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Appendix As permittens of fundatios forefred to in the example source touc for threat forsion or so	Append	lix A.	Definitions o	f variable	es referred	to in t	he examp	le source co	ode fo	or CERES-W	heat vers	sion 3.5.
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Variable	Definition
ALBEDO	Albedo of crop plus exposed soil
PIV	Relative amount that development is slowed for each day of unfulfilled vernalization, assuming that 50 days of vernalization is sufficient for all cultivars
PID	Relative amount that development is slowed when plants are grown in a photoperiod 1 hour shorter than the optimum (considered to be 20 hours)
Р5	Relative grain filling duration based on thermal time (degree days above a base temperature of 1 °C), where each unit increase above zero adds 20 dearee days to an initial value of 430 dearee days
G1	Kernel number per unit weight of stem (less leaf blades and sheaths) plus spike at anthesis (per a)
G2	Kernel filling rate under optimum conditions (mg/day)
G3	Non-stressed dry weight of a single stem (excluding leaf blades and sheaths) and spike when elongation ceases (g).
PHINT	Phylochron interval, the interval in thermal time (degree days) between successive leaf tip appearances
SUMDTT	Cumulative growing degree days (sum of DTT over time)
DTT	Increment in thermal time each day
CARBO	Realized production of carbohydrate per day after accounting for potential effects of temperature and stress factors
CO2	Ambient concentration of CO ₂
C02X	Reference concentration of $ ilde{C0}_2$ associated with a given effect of C0 $_2$ on photosynthesis
C02Y	Effect of CO ₂ concentration on photosynthesis for a given level of CO_2
EEQ	Equilibrium evaporation rate
EO	Potential evapotranspiration (mm/day)
LAI	Leaf area index
NSTRES	Index of nitrogen stress (0 to 1 scalar)
PCARB	Potential production of carbohydrate per day as limited only by solar radiation and light interception
PCO2	Effect of CO $_2$ on photosynthesis at reported concentration of CO $_2$ (scalar)
PLTPOP	Population of plants in field, usually assumed equal to sowing rate (plants/m²)
PRFT	Effect of temperature on carbohydrate accumulation
ROWSPC	Distancing between rows of plants in field (row spacing, in cm)
RTDEP	Depth of root development (cm)
SALB	Albedo of bare soil
SHF(L)	Soil hospitality factor at depth L (0 to 1 scalar)
SLANG	Solar radiation
SRAD	Solar radiation as reported in file of daily weather (MJm ⁻² day ⁻¹)
SWDF	(0 to 1 scalar)
SWFAC	(0 to 1 scalar)
TD	Average daily temperature
TMIN	Minimum temperature as reported in tile of daily weather (°C)
IMAX	Maximum temperature as reported in tile of daily weather ("C)
XHLAI	Leat area index

A Physiological Perspective on Modeling Temperature Response in Wheat and Maize Crops

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Abstract

In process-based models of wheat and maize crops, temperature typically influences both growth and development as well as having indirect influences through water and nutrient balances. Modeling crop response to temperature would thus seem to be a straightforward enterprise, as temperatures are readily measured and controlled through familiar procedures. Although there is a large and valuable literature on physiological responses to temperature, we are far from having a comprehensive understanding of how crops respond to temperatures, especially as models move towards quantitative accuracy. This paper reviews the physiology of temperature effects on development, photosynthesis and respiration, with emphasis on maize and wheat. The paper also suggests ways to make research more relevant for application in efforts to model and predict crop response to the elevated temperatures expected under climate change scenarios. These include accounting for possible effects of acclimation, ensuring that temperature treatments are relevant to field conditions, using a wide enough range of temperatures to fully characterize responses, and characterizing the genetic makeup of the plants under study.

Introduction

At first glance, modeling the response of a crop to temperature would seem straightforward. Temperature is measured more readily than other environmental variables, and differences in temperature regimes are readily obtained under field conditions by varying planting dates or using sites that differ in elevation or latitude. In controlled environments, temperature is easily modified through thermostatically controlled heating and cooling systems. Introductory biology courses teach that reaction rates of many metabolic processes increase exponentially with temperature, approximately doubling with each increase of 10°C. The widespread and highly repeatable occurrence of heat shock protein (HSP) responses (Waters et al. 1996; Nakamoto and Hiyama 1999) would seem to provide a direct window into the molecular biology of crop response to temperature.

In practice, however, quantifying the temperature response of crops has proven remarkably difficult. Different parts of a plant experience different temperature regimes (Monteith and Unsworth 1990; McMaster and Hunt, p. 18, this volume). Responses vary according to conditions a plant has grown under, reflecting the important ability of crops to acclimatize. Finally, attempts to improve adaptation through selection for specific stress responses, such as the one to heat shock, have met with limited success.

Notwithstanding these potential complexities, concerns over global warming-thought to be on the order of 1.4° to 5.8°C from 1990 to 2100 (IPCC 2001)– are driving widespread interest in estimating the impacts of increased temperature on crops (e.g., Amir and Sinclair 1991; Goudriaan 1996; Rosenzweig and Tubiello 1996). Process-based crop models are often used in assessing impacts of global warming, so there is justification for reviewing the physiological processes represented in such models. This paper reviews basic physiological concepts related to the effect of temperature on crop growth and development with emphasis on wheat (*Triticum aestivum*) and maize (*Zea mays*) crops. The expectation is that such a review can help identify areas where crop models can readily be strengthened or, alternately, suggest areas where more research is needed.

Developmental Responses

Phenology

Phenological development is usually analyzed in terms of progress toward stages such as germination, seedling emergence, initiation of floral primordia, flowering, and physiological maturity. Progress is estimated by integrating a developmental rate over the interval from one stage to the next. The rate usually is a function of temperature and photoperiod but also may vary with nitrogen or water deficits, depending on the developmental stage and crop species. If the daily mean air or crown temperature is used, then the integration is numerically equivalent to a summation. If lower or upper temperature limits are imposed and the effect of temperature on development rate is assumed constant, the approach is equivalent to the widely used "growing degree day" (GDD) or "thermal time" concept. In this concept the lower limit is termed the base temperature (T_{base}) and the upper limit is termed the optimal temperature (T_{opt}).

From this core simplicity among approaches, however, numerous variants arise. Mean temperature may be replaced by a diurnal curve, often interpolated from daily minimum and maximum temperatures. While conventional GDD models assume that above T_{opt} the rate continues at its maximum value, many simulation models assume a decline in developmental rate at very high (supra-optimal) temperatures (Hunt et al., p. 23, this volume).

In wheat, vernalization represents a mechanism independent of the basic temperature effect on development in which seeds or plants require exposure to low temperatures in order to initiate floral primordia. Spring wheats have a low vernalization requirement, while winter wheats may require 30 to 40 days of vernalization (Flood and Halloran 1986). The process is generally assumed to occur at temperatures of 0° to 10°C and is unusual in that cooler temperatures speed up the process, down to temperatures near 0°C. Models that include vernalization usually represent the process through a rate of progress or "vernalization day" accumulator.

Besides direct effects of temperature on development, increased temperatures are sometimes associated with greater photoperiod sensitivity (e.g., Wallace et al. 1991; White et al. 1996). This effect has been noted for time to tassel initiation in maize (Ellis et al. 1992) and appears to involve a decrease in the critical daylength at higher temperatures (Edmeades and Bolaños 2001). Cao and Moss (1989) found a temperature x photoperiod effect in wheat and barley. Slafer and Rawson (1995) interpreted similar results as evidence for an effect of photoperiod on the basic temperature response of wheat; mechanistically, however, it seems easier to conceive of low temperatures slowing synthesis of an inhibitor that is produced under less inductive photoperiods (Hoogenboom and White 2003).

In contrast to processes such as photosynthesis and respiration, there has been little effort devoted to integrating research on the biochemistry of phenology with quantitative models. Recent advances in understanding the control of flowering in Arabidopsis, where approximately 60 genes are now known to affect floral development (Koornneef et al. 1998), may offer a road for merging biochemistry and modeling. For example, the FLF gene of Arabidopsis affects vernalizationdependent flowering by encoding a protein that represses the transition to flowering (Sheldon et al. 1999). Activity of FLF is greater in vegetative rosette leaves of Arabidopsis than in reproductive tissue and is sustained at a uniform level at least until time of bolting. Such information should allow developmental stages to be defined more accurately and assist in determining which tissues are the most relevant in temperature or photoperiod responses.

The effect of temperatures in reducing the length of the growth cycle, especially the grainfilling phase, is usually identified as the single most important factor in explaining reduced yields at higher temperatures. Wiegand and Cuellar (1981) found a 3.1 day shortening of grain filling per °C temperature increase, vs. 2.8 days per °C in seven previous studies they reviewed. The effect on yield was mainly through decreased grain weights.

Morphology

Temperature affects morphology through differential effects on cell division and expansion. Higher temperatures are associated with larger specific leaf

area (e.g., Midmore et al. 1984). In their classic study of temperature responses among 22 races of maize, Duncan and Hesketh (1968) found that highland races had greater relative leaf area growth rates than lowland races at temperatures up to 30°C (Figure 1). In contrast, the effect of warmer temperatures on increasing final leaf number was similar across races. Of course, due to the dominant effect of temperature on development, crops grown at higher temperatures often have a lower Leaf Area Index (LAI) and canopy size simply because of the shorter growth duration.

Growth Processes

Growth is usually defined as an irreversible increase in size, with "size" quantified as height, volume, or fresh or dry weight. We focus our discussion on changes in dry weight through an increase in biomass due to photosynthesis, with the increase balanced against losses through respiration and senescence.

Photosynthesis

Species differ markedly in how temperature affects leaf net photosynthetic rates (A_n), and these differences play a major role in adaptation (Björkman et al. 1980). Stomatal limitations do not appear to be a major factor. Several studies have shown that stomatal conductance increases at higher temperatures and vapor pressure deficits (VPDs) (Idso et al. 1984; Cornish et al. 1991; Amani et al. 1996).



Figure 1. Effect of temperature on relative leaf growth rate for means of four highland and four lowland races of maize grown in controlled temperature glasshouses (Duncan and Hesketh 1968).

The quantum efficiency of photosynthesis in C_3 species decreases almost linearly with temperature, due mainly to increased photorespiration. In contrast, C_4 species show remarkably little variation over a broad range of temperatures (Ehleringer and Pearcy 1983).

The stability of lipids in the thylakoid membranes is also thought to influence temperature response of photosynthesis (Raison et al. 1980; Carpentier 1999). Membranes undergo phase transitions at critical low and high temperatures. The values of the critical temperatures are related to the degree of saturation of membrane lipids and possibly the types of carotenoids present (Carpentier 1999). The composition of membranes varies with growth temperature, and such variation is presumed to be a major part of acclimation mechanisms.

Studies of the short-term response of leaf net photosynthetic rate in wheat suggest that sensitivity to high temperature is very dependent on acclimation. Both Blum (1986) and Sayed et al. (1989) showed that the carbon exchange rate was relatively stable when measured in the 23-33°C range if plants were acclimated to daytime temperatures in the region of 30°C. However, plants grown with cooler day temperatures (13-20°C) showed a marked decline in A_n at temperatures above 25°C. The relative stability of leaf A_n for wheat acclimated to warm conditions was confirmed in field studies of 16 genotypes, where A_n was stable when leaf temperatures varied naturally (with time of day) between approximately 29° and 34°C (Reynolds et al. 2000). Nonetheless, genetic variation for leaf A_n among cultivars at high temperatures has been shown by both Sayed et al. (1989) in controlled environments and by Reynolds et al. (2000) in the field. Furthermore, longer-term exposure to high temperature reduces A_n. Al-Khatib and Paulsen (1990) described an accelerated development rate at 32°/27°C versus 22°/17°C (day/ night) temperature regimes, resulting in decreased duration of photosynthetic activity and lower kernel weights, especially in sensitive cultivars. Prolonged exposure to high temperatures in controlled environments also resulted in premature loss of chlorophyll (Al-Khatib and Paulsen 1984). In warm field environments, a large proportion of variation in photosynthetic rate among cultivars during grainfilling was explained by differential chlorophyll loss after anthesis, which explains 30-35% of the variation in final grain yield (Reynolds et al. 2000).

Interestingly, other photosynthetic tissues in wheat respond quite differently. Blum (1986) found that glume photosynthesis declined drastically above 25°C whether plants were acclimated or not, while carbon fixation by awns increased with higher temperature irrespective of acclimation. Awns may intercept an appreciable proportion of incident radiation (e.g., >20% in genotypes with long awns, such as many durum wheat cultivars). They are hence likely to contribute significantly to total canopy photosynthesis during grainfilling, especially in warm environments.

While photosynthesis may be relatively heat stable in acclimated plants, studies of how starch synthesis responds to temperature suggest that grainfilling may be affected more by the inhibition of conversion of sucrose to starch at temperatures above 30°C (Bhullar and Jenner 1986); soluble starch synthase appears to be especially sensitive (Keeling et al. 1993).

Duncan and Hesketh (1968) found that highland and lowland maize races showed similar responses of A_n to growth temperature, but lowland races had higher rates above 18° C (Figure 2).

Respiration

Respiration rates usually increase exponentially with temperature up to an inflection point, where various effects can slow metabolism (Loomis and Connor 1992; Smith et al. 1999). Such responses are mainly



Figure 2. Effect of growth temperature on leaf photosynthetic rate for highland and lowland races of maize grown in controlled temperature glass houses. The temperature is the daytime maximum and corresponds to the measurement temperature. Based on data from Duncan and Hesketh (1968).

attributed to the maintenance (instead of growth) component of respiration (Loomis and Connor 1992). Differences in temperature response of respiration are often associated with differences in adaptation, leading Smith et al. (1999) to suggest that these responses may be better indicators of adaptation than those found for photosynthesis.

In a study of 16 wheat cultivars grown under warm field conditions, dark respiration rates measured in two experiments with different sowing dates were substantially higher in the warmer environment. Taken with the fact that final biomass, but not leaf photosynthetic rate, was reduced in the warmer environment, this finding supports the idea that respiration had a higher metabolic cost under warmer conditions (Reynolds et al. 2000). Nonetheless, temperature was clearly not the only factor influencing respiration. Respiration rates in both environments were relatively stable until anthesis but declined by approximately 35% during grainfilling, more or less mirroring loss in total leaf chlorophyll. Despite these clear main effects for respiration, the trait was not well correlated with any of the performance traits when comparing cultivars.

Stress Responses

Relatively little is known about how metabolic responses to temperature interact to mediate adaptation of crops to stressful environments with respect to performance. Theoretically, the functional genomics approach to understanding stress response would make it possible to reveal the biochemical and genetic basis of any given phenotypic response to the environment. However, adaptation to stress at the whole plant level involves the interaction of many genes which are expressed at multiple levels (i.e., tissue, phenological stage, time of day, etc.). Considerable investment will be needed before such applications become routine. Moreover, much of the research at the molecular level considers survival mechanisms rather than productivity, which depends more on stress avoidance than tolerance. Notwithstanding these possible complexities, transformation of wheat has been attempted based on known metabolic responses to stress. For example, lateembryogenesis-abundant (LEA) proteins appear when drying initiates in developing seeds and disappear after imbibition (Roberts et al. 1993). The genes are similar to those expressed in drought stressed vegetative tissue of

wheat (Curry et al. 1991), and ABA can induce expression of these proteins. Sugar synthesis also seems to play a role in drought stress, providing compatible solutes for osmotic adjustment (Bohnert et al. 1995) or through various protective roles, including protection of membranes (Crowe et al. 1992). Antioxidants such as superoxide dismutase and ascorbate peroxidase increase in response to drought stress (Mittler and Zilinskas 1994) and probably play a role in tolerance, since the excess radiation and increased photorespiration associated with stress can result in accumulation of active oxygen species. Other relatively simple biochemical processes involved in drought stress may also lend themselves to genetic transformation. These include osmotic adjustment, repair and degradation of proteins, and structural adjustment-for example, of the cell wall (Ingram and Bartels 1996).

Cold Stress

Fowler et al. (1999) reviewed physiological and molecular research on cold tolerance in wheat and used this synthesis to guide modification of the CERES Wheat model. Their approach included cumulative effects of hardening, acclimation, and de-hardening, all as functions of the daily mean crown temperature.

For maize cultivars in Canada, Ying et al. (2000) found that recently released hybrids showed less reduction in photosynthesis after exposure to low night temperatures. This effect was also reflected in changes in chlorophyll fluorescence, suggesting a stress effect on photosystem II; however, subsequent work indicated that the effect is not through photoinhibition (Ying et al. 2002).

Freezing injury is associated with membrane damage and subsequent tissue dehydration (Thomashow 1999). Acclimation at the cell level appears to involve processes that either stabilize membranes or reduce the freezing point of the cytoplasm.

Nutrient Uptake

The main effects of temperature on plant nutrition are presumably indirect and derive from effects on overall plant growth, including root elongation. However, temperature also affects availability of nutrients in the soil solution and uptake at the root surface. At low temperatures, uptake and metabolism of ammonium is greater than that of nitrate. This difference can greatly alter the cation-anion balance and root-induced changes in rhizosphere pH (Marschner 1986). Similarly, low temperatures can increase problems of zinc deficiency, apparently due to decreased solubility of soil Zn (Lucas and Knezek 1972). For phosphorus, Mackay and Barber (1984) concluded that temperature effects on P movement in the soil and P uptake at the root surface were much less important than temperature effects on root growth per se.

Whole Plant or Community Responses

While the previous discussions have focused on separate processes affected by temperature, the ultimate question is how the various physiological processes interact to affect overall growth and yield. To examine aggregated responses physiologists rely on various analytic approaches, with growth analysis being perhaps the most widely used approach to analyze the behavior of a crop as a community of plants.

Growth Analysis

Although the life cycle of a wheat crop is accelerated and reduced in its duration at higher temperatures (Midmore et al. 1982), the reduction in cycle length only partially accounts for lower productivity. In field studies comparing performance of different genotypes in contrasting thermal environments, the grainfilling rate was on average over 10% lower at the warmer site. In addition, above ground biomass was 6% lower for the three most heat tolerant genotypes and 15% lower for the three most heat sensitive lines (Reynolds et al. 1998). One factor seems to be related to reduced light interception. In a parallel experiment, canopy establishment of a single heat tolerant cultivar was compared at two sowing dates contrasting in temperature. Plant dry weight at the 5-leaf stage was considerably lower at the warmer sowing date and was associated with lower ground cover and reduced early light interception (Badarrudin et al. 1999). In the comparison by Midmore et al. (1984) of wheat lines in contrasting thermal environments, green-area index measured shortly after flowering showed substantially lower values at the warmer sites. Several values fell under the critical LAI value of 3, an approximate lower limit for full interception of radiation. Finally, loss of chlorophyll during grainfilling has been associated with reduced field performance in warm environments

(Reynolds et al. 2000). Reduced stand establishment, lower final green-area index, and accelerated chlorophyll loss are all factors that reduce light interception under warm conditions, and are likely to have a negative impact on total canopy photosynthetic rate.

The impact of reduced source on yield is confirmed by numerous reports of reduced kernel weight in response to elevated temperature, with kernel weight affected typically by a 2-5% decrease per °C increase (Wardlaw and Wrigley 1994). In addition to the direct effect of temperature on source potential, other studies have shown that potential kernel number in wheat shows a negative association with temperature during the spikegrowth stage. Fischer (1985) calculated a kernel number reduction rate of 4% per °C in the range of 14°-22°C. In a study attempting to explain wheat species by year interactions in a relatively stable environment (northwest Mexico, irrigated), one of the factors best explaining why certain years favored bread wheat over durum yield was temperature during the spike growth stage (Reynolds et al. 2002). Durum wheat was found to be more sensitive to warmer temperatures during this period. A similar analysis was conducted for 16 wheat genotypes grown in 20 contrasting thermal environments (representing sites in various countries). These were a subset of the 40 environments (Reynolds et al. 1998) for which detailed temperature data were available. The analysis again revealed that temperature in the spike-growth stage was the most significant factor explaining G x E effects. Specifically, average minimum temperature during approximately 30 days before flowering ranged from 10.5° to 16°C, depending on environment (Vargas et al. 1998). The results would suggest that high night temperatures reduced grain number (and therefore yield) either because accelerated development resulted in a shorter spike growth stage or because high respiration costs reduced spike growth itself. It is also possibly due to a combination of both factors. Hardacre and Turnbull (1986) found that relative growth rate and net assimilation rate of maize increased with temperature in controlled environments from 16° to 28°C.

Radiation Use Efficiency

The amount of biomass accumulated per unit solar radiation intercepted, radiation use efficiency (RUE), is another widely used indicator of crop performance (Charles-Edwards 1982; Sinclair and Muchow 1999). In simplified terms, RUE integrates effects of canopy structure and light interception, photosynthesis within the canopy, and loss of assimilate through respiration and senescence. Implicit in this analytic approach are the assumptions that photosynthesis is proportional to weight loss through respiration and that the response of canopy photosynthesis to solar radiation is linear (Charles-Edwards 1982; Kiniry et al. 1989).

In a review of published values of RUE for maize and sorghum, Kiniry et al. (1989) concluded that there was no variation in RUE with temperature for a range of 19° to 27°C. Using a range of planting dates giving mean temperatures from 16° to 21°C, however, Andrade et al. (1993) found that maize RUE increased linearly from 2.2 to 3.2 g/MJ.

Harvest Index

Batts et al. (1998), studying winter-wheat grown at mean temperatures from 9° to 12°C in temperature gradient tunnels in the UK, found that harvest index (HI) of one cultivar was constant while it declined slightly at higher temperatures in the other. In the study of Midmore et al. (1984) on spring wheats in Mexico, the highest values of harvest index (0.34 to 0.39) were obtained at the site with intermediate temperatures. In an extensive experiment where 16 wheat cultivars were grown in over 40 environments internationally (Reynolds et al. 1998), harvest index was found to be sensitive to temperature. Averaged across genotypes, harvest index ranged from 0.4 in the cooler environments to 0.3 at some warmer sites.

Lafitte and Edmeades (1997), comparing performance of diverse maize types in Mexico, found that the response of harvest index differed with expected adaptation of cultivars. Two lowland cultivars showed a slight increase in harvest index (roughly from 0.3 to 0.4) for mean temperatures from 17° to 28°C, while highland cultivars decreased from values of 0.35 to almost 0.

Integrated Response

Studies looking directly at temperature effects on growth and yield at the field level generally use either multiple locations or sowing dates (e.g., Muchow et al. 1990; Midmore et al. 1982 and 1984; Lafitte and Edmeades 1997) or temperature treatments applied to either open top chambers or temperature gradient tunnels (e.g., Batts et al. 1998). Table 1 summarizes reported effects of temperature on yield, including both field studies and simulation exercises. In most studies, warmer temperatures reduced growth duration, which in turn limited total biomass accumulation and yield.

Maximum Temperature Temperature grain yield effect on grain (kg ha⁻¹) vield (kg ha⁻¹ °C⁻¹) Source Description range (°C) **Spring Wheat** Midmore et al. 1984 Diverse cultivars grown at various sites and sowing 5.900 450 dates in Mexico 14 - 25Amir & Sinclair 1991 Simulated for 10 year period in Israel 9,500 760 [8°C range] White et al. 2001 Simulated for cv. Seri M-82 with CERES-Wheat assuming 18 MJ m⁻²d⁻¹ solar radiation 10 - 3010,000 500 Winter Wheat Simulations with CERES-Wheat at four locations in the USA Rosenzweig & Tubiello 1996 (maximum yields and effects shown here correspond to the four sites) [4°C range] 3,000 300 2.000 190 1,800 110 1,600 280 Wheeler et al. 1996 Two seasons data for winter wheat cv. Hereward grown in an outdoor temperature gradient tunnel in the UK 14 - 21 9,000 1040 Batts et al. 1998 Mean of two winter wheat cultivars grown in an outdoor 9-12 1800 temperature gradient tunnel in the UK 8,500 <u>Maize</u> Muchow et al. 1990 Field trials at five locations in Australia and the USA with various cultivars 18 - 29 17,000 810 White et al. 2001 Simulated for cv. Suwan 8222 with CERES-Maize assuming 18 MJ m⁻²d⁻¹ solar radiation 15 - 30 14,000 530

Table 1. Reported effects of mean temperature on grain yield in wheat and maize. Effects were estimated as declines from maximum reported grain yields in each study.

The large variation in the magnitude of the response presumably reflects differences in management and solar radiation regimes. Based on this limited set of data, wheat appeared to be more sensitive than maize, which agrees with the expectation that C_4 crops are more heat tolerant than C_3 crops. The responses predicted by simulation models generally were smaller than those observed in the field, perhaps indicating the importance of the additional influences of water deficits, diseases and pests.

Methodological Issues

Temperature Measurement

Monteith and Unsworth (1990) illustrated the potential for large gradients of air temperature within a crop canopy, both for daytime and nighttime conditions. In wheat, mid-day canopy temperatures of well-watered crops are often 5° to 8°C lower than the air temperature (e.g., Amani et al. 1996). While air temperature is readily measured, Ehleringer (1991) emphasized that accurate measurement of different tissues within a plant requires careful attention to energy budgets of the tissue and the temperature probe. A recent study with a set of 16 wheat genotypes grown under different thermal regimes in the field involved measuring different organ temperatures. While there were significant main effects for leaf, stem and spike temperature, no interaction with genotype was found (Ayeneh et al. 2002), an important finding for extrapolating modeling approaches to different cultivars.

Temperature Treatments

Due to the effects of the total energy budget, imposing meaningful temperature treatments is also problematic. Growth chambers seldom provide radiation regimes similar to natural environments. Photosynthetically active radiation is usually lower than in natural sunlight, and net radiation will never match conditions in the field. Similarly, while varying elevation, latitude, or planting date will result in readily measured changes in air and soil temperature, these treatments are usually associated with changes in the radiation regime, photoperiod, or soil conditions. In their review of phenology in wheat, Slafer and Rawson (1995) noted that use of sowing date studies to characterize temperature sensitivity of phases prior to anthesis is problematic. Developmental stages just prior to flowering are usually exposed to a narrower and more favorable range of conditions than earlier stages.

A further concern is that standard approaches for imposing temperature treatments seldom allow use of true replication. Replication within a chamber, glasshouse or sowing date plot is statistically equivalent to sub-sampling.

Analytical Approaches

Physiological processes vary remarkably in their response to temperature. While maintenance respiration increases exponentially with temperature (up to a point), development and photosynthesis seem better described with other types of curves.

The widespread use of "broken-stick" models that use straight lines to represent temperature responses seems to be viewed with embarrassment by researchers who favor models rooted in physical processes. There clearly is a problem in assuming a linear response if the temperature response is dictated by kinetic energies showing a Boltzmann distribution at the molecular level, which thus should show an exponential response (e.g., Nobel 1991). Not surprisingly, various researchers have attempted to explain the robustness of linear models as essentially simplifications of inherently curvilinear responses. For example, Sinclair (1994) argued that a linear approximation works well because responses "are usually obtained in a relatively narrow temperature range, say 288° to 303°K."

Our growing understanding of genetics and biochemistry of development, however, indicates that many processes involve complex biochemical networks, in many cases with surprising levels of redundancy or alternate pathways (von Dassow et al. 2000). Some regulatory processes may involve only one or two molecules per cell binding to a single DNA molecule (Anonymous 1999), suggesting that models based on probability distributions of kinetic energy will often be inappropriate. Similarly, in cases where membranes are involved, responses may reflect phase changes or abrupt shifts in binding of proteins to membranes. Note that approximately 20% of proteins show trans-membrane segments (Boyd et al. 1998; Wallin and von Heijne 1998).

Conclusions

While our qualitative understanding of temperature effects appears quite detailed, we are still far from

being able to convert such knowledge into the quantitative predictions of adaptation sought by breeders, agronomists and modelers. These predictions are also implicit in attempts to assess the impact of global warming on agriculture. Processbased models offer an attractive vehicle for integrating knowledge of effects of temperature in a quantitative framework, with the dual goals of providing "best bets" on the effects of temperature based on current knowledge and of guiding further research.

In attempting to improve our understanding of the effects of temperature, we suggest various points that researchers and modelers should keep in mind:

- Assess effects of conditioning or acclimation.
- Use a large enough number and broad enough range of temperature treatments to permit different shapes of response curves to be distinguished.
- As far as possible, grow plants under field conditions or demonstrate how results from controlled environments relate to field conditions.
- Monitor air, soil, leaf, or crown temperatures as appropriate to ensure that the physiologically relevant temperature is quantified.
- Use materials that are genetically well characterized for major genes that may influence responses (e.g., for photoperiod and vernalization).
- Distinguish clearly among models that are proposed as pragmatic solutions for a well defined geographic domain and those that represent analytical tools for understanding physiological processes.

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Re-examining Current Questions of Wheat Leaf Appearance and Temperature

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Abstract

The rate of leaf appearance, or the phyllochron, is critical in simulating canopy development, structure, and dynamics. Many factors can influence the phyllochron of wheat (Triticum aestivum L.), but the most important factor is temperature. This paper explores some current questions about the complicated relationship between wheat leaf appearance and temperature. Specifically, the questions of whether the phyllochron is linearly related to temperature and where the site of temperature perception is located are addressed. While the temperature response across the entire temperature range is clearly non-linear, the existence of a linear region has caused some confusion. Another confounding factor is that both during and across days, temperatures when leaves are produced are normally within the linear region, but often can fluctuate beyond the linear phase. In addition, cultivars can vary slightly in their temperature response, and temperature can interact with other factors. While measuring the phyllochron response to temperature may be largely a physics problem, it is complicated by the question of where to measure the temperature since the meristematic region covers a significant distance and temperatures in other parts of the plant will affect secondary factors that influence the phyllochron.

Introduction

Many factors influence the rate of wheat leaf appearance, or phyllochron, including light (quality, quantity, and photoperiod), water, nutrient availability, salinity, and CO_2 (McMaster 1997 and Wilhelm and McMaster 1995 provide reviews). However, temperature is always cited as the primary factor controlling the phyllochron. Unfortunately, all these factors interact in a very complex manner (especially light, water, and salinity), and it is difficult to isolate temperature response from other factors.

A great deal of work has examined the relationship between temperature and the phyllochron, particularly in the last four decades. Some work raises new questions, and other times questions arise because earlier work has been "forgotten" while some of us pursue the "new" questions. Queries such as, " Is the response to temperature linear?" and, "Where should we measure temperature (e.g., air temperature above the canopy vs. soil temperature at crown depth)?" are examples of questions receiving much attention and generating confusion in the last decade.

Leaf appearance is a critical process involved in canopy development, structure, and dynamics (Wilhelm and McMaster 1995). This paper explores some aspects of the complicated relationship between wheat leaf appearance and temperature.

Background

Although different definitions of plastochron and phyllochron have been used across time (Wilhelm and McMaster 1995), we define these terms as normally used today. The plastochron is the interval of time between appearance of successive leaf primordia on a shoot apex; the phyllochron is the interval of time between appearance of successive leaves through the whorl of the subtending leaf on a shoot. The inverse of the phyllochron is also referred to as the leaf emergence or appearance rate. The phyllochron is therefore the result of the rate of leaf primordia initiation (i.e., the plastochron) and subsequent development and growth of the leaf primordium. One consideration of the phyllochron is that each leaf must grow through successively greater sheath lengths before emerging.

The plastochron is primarily composed of the normal growth process during which cells first divide at the meristem (in this case the shoot apex) and then enlarge to form the leaf primordium. The growth process of the leaf primordium then proceeds by further cell division and expansion (Dale 1988). The region where this occurs is commonly referred to as the leaf extension zone (Skinner and Nelson 1995) and certainly can be considered a meristem. Although there is some debate whether the leaf extension zone is a separate meristem from the shoot apex, for purposes of this paper it is important to recognize only that cell division and expansion are occurring across a certain distance within the shoot. The plastochron is therefore the result of one meristem (the shoot apex) covering a limited distance, whereas the phyllochron is the result of two meristems (the shoot apex and the leaf extension zone) covering a much greater distance.

There are significantly more cells in the mature leaf (blade plus sheath) than in the leaf primordium. Therefore, we suggest some reasons that the plastochron so often seems to be even more influenced by temperature than the phyllochron:

- The cell life cycle is very much controlled by temperature (Arkebauer and Norman 1995)
- Cell expansion rates are not only influenced by temperature, but are also dependent on resources such as water for turgor pressure, and nutrients and carbohydrates for building the cell
- Given that there are so many more cells forming the mature leaf, considerably more resources are needed for cell expansion, allowing other factors to interact with temperature effects

Resources needed for cell division and expansion (water, nutrients, and carbohydrates) originate in areas outside of the shoot apex. Uptake or production of these resources in the root and canopy systems are influenced by temperature, but the temperature varies throughout these systems and may differ substantially from the shoot apex temperature.

Is the Temperature Relationship Linear?

The question, "Is the temperature relationship linear?" became important in the last few decades once researchers started quantifying the phyllochron using thermal units to represent time rather than days. Based solely on the many temperature response studies in growth chambers, there is no debate—the temperature response is not linear across the entire temperature range within which wheat can grow. Two studies strongly illustrate this.

In a classic study, Friend et al. (1962) studied the main stems of a spring wheat (cv. Marquis) under controlled environments. Constant day/night temperatures of 10°, 15°, 20°, 25°, and 30°C were used in combination with varying light intensities and duration. Some of the important results were that:

- Temperature interacted with photoperiod and light intensity
- Within constant conditions, the phyllochron within the main stem was linear, so that age or position of leaf does not matter (negating the ontogenetic decline hypothesis postulated by some)
- The phyllochron was "linear" from 10° to 25°C, and decreased slightly at 30°C (Figure 1)

Twenty-seven years later, Cao and Moss (1989) revisited this question for eight winter wheat and barley varieties. In controlled environments of constant day/night temperatures of 7.5° , 10° , 12.5° , 15° , 17.5° , 20° , 22.5° , and



Figure 1. Leaf emergence rates adapted from two studies. Note: Actual values are approximations from graphs.

25°C with varying photoperiods, the appearance rate of the first four leaves on main stems were measured. The important results to note for this paper were that there were slight variations among cultivars in response, that temperature and photoperiod interacted, and that the phyllochron was "linear" from about 10° to 17.5°C, either reaching an asymptote or decreasing slightly after about 22.5°C (Figure 1).

The third result in both studies is critical because it clearly shows that the response is not linear across the entire temperature range, just a certain portion of it. Furthermore, we should expect slight variation in temperature responses among cultivars but the pattern of response is generally the same for most, if not all, cultivars.

Why is there still a debate on whether the relationship between the phyllochron and temperature is linear? We previously alluded to part of the reason-how we represent temperature as thermal time. The most common form of calculating daily growing degree-days (GDD) (McMaster and Wilhelm 1997), is adding the daily maximum and minimum temperature and dividing by two to get the daily average temperature. The base temperature, below which the process does not occur, is typically set to 0°C (McMaster and Smika 1988; McMaster 1997) and is subtracted from the daily average temperature. Certainly, if the base temperature is set higher, then non-linearity at lower temperatures will tend to be negated. If an upper temperature threshold is used, then, mathematically, this would tend to mimic a slight depression found at higher temperatures.

Another reason is that when temperatures are considered either diurnally or across days, the temperatures are often in the "linear" portion of the temperature response or "equally" above and below these temperatures when leaves are being produced. We have calculated long-term monthly maximum, minimum, and average daily air temperatures for a number of wheat production locations throughout the world, and generally the results are the same. In Figure 2, Fort Collins, Colorado is used to illustrate the results of expected temperatures during leaf appearance. September (Sep), October (Oct), April (Apr), and May are the months when most leaves appear. The monthly maximum, minimum, and average temperatures for those months are as follow:

- Sep: 23.9° (max), 7.2° (min), and 15.5° (avg) C
- Oct: 17.9° (max), 1.2° (min), and 9.5° (avg) C
- Apr: 15.6° (max), 0.4° (min), and 8.0° (avg) C
- May: 20.4° (max), 5.6° (min), and 13.0° (avg) C

These temperatures fall within (or are close) to the linear region of temperature response reported by Friend et al. (1962) and Cao and Moss (1989).

Measurement interval can also affect the perceived influence of temperature. The longer the interval for measuring the phyllochron, the greater the chance that temperatures will primarily be in the linear region and the influence of temperatures in the non-linear region will be reduced. Unless either the temperatures are in the non-linear region for a significant percent of the measuring interval or are extreme, or both, the diurnal and daily fluctuations in temperature will result in the phyllochron appearing linear in field conditions.

What are the implications for modeling the phyllochron response to temperature? First, for most field conditions the simple GDD model of assuming a linear response to temperature works surprisingly well in predicting a complex process. This is not because it is theoretically correct, but because of some of the reasons listed above. One caveat is that if the cultivar being simulated is unusual in its temperature response pattern (e.g., shorter linear phase, linear phase not correlated with field temperatures, response to high temperatures differs, etc.), the accuracy will then be reduced. If greater accuracy is desired, non-linear approaches for calculating the GDD look promising (e.g., Yan and Hunt 1999).

Where to Measure Temperature?

When the issue of whether the phyllochron was linear

around 25 years ago, temperature was measured using

with temperature as measured using GDD surfaced



Figure 2. Expected temperatures during leaf appearance, Fort Collins, Colorado (N 40:34, W 105:05, elev. 236 m).

air temperature above the canopy. Yet we know from a long history of controlled environments and field root/ shoot temperature studies that soil temperature might be a better approximation of shoot apex temperature than air temperature, at least when the shoot apex is below the soil surface. As situations began to arise where the linear GDD model using air temperatures did not predict the phyllochron as well as desired, attention focused on shifting measurements to soil temperature at crown depth. Unfortunately, as with all good paradigms, troubling anomalies began to surface when using soil, rather than air, temperature. Let us mention a couple of these anomalies and then propose some adjustments to our paradigm.

The first anomaly was reported in 1998 (McMaster and Wilhelm). Although this examined phenology rather than the phyllochron, the results are applicable because again it is the shoot apex where many of the events occur. Examining 23 site-years across seven locations in the Central Great Plains with varying management practices and cultivars, it was found that using soil temperature provided no, or negligible, improvement over using air temperature in predicting phenological growth stages. Similar results were found, but not reported, by Betty Klepper and Ron Rickman in Pendleton, Oregon. One of the main reasons for this is that mean soil temperatures at 3 cm were very similar to mean air temperatures above the canopy (although the amplitude did vary slightly), and clearly the relationship between air and soil temperature was the same.

The other anomaly was found in an unpublished experiment completed in 2000. This experiment was an outgrowth of the GCTE Wheat Network Meeting in Maricopa, Arizona in May 1997. At that time, a number of modelers (John Porter, Wally Wilhelm, Pete Jamieson, Joe Ritchie, and Michael Kirby, among others) designed an experiment conducted in the field at Fort Collins, Colorado. A spring wheat (cv. Nordic) was planted at three planting dates (mid-March, mid-April, and mid-May) for two years. A complete randomized block design with four replications was used for two treatments. One treatment was ambient soil temperature; the second treatment raised the soil temperature at 2 cm depth (presumably crown depth) 3°C above the ambient soil temperature. This was done by means of heat tape located 3 cm below the seed, which was planted at 2 cm. As expected, raising the soil temperature resulted in earlier seedling emergence by as much as a week; however, the rate of leaf appearance was not affected by increasing the soil

temperature as expected (Fig. 3). This was true for all planting dates in both years. The phenology experiment anomaly was largely explained because of the similarity of soil and air temperature, but this could not be the explanation in this experiment because there was a significant difference in soil temperatures that should have been reflected in differences in the phyllochron. How can this anomaly be explained and our paradigm saved?

Two explanations may play an important role. The first is that if a non-linear beta response function is used to calculate GDD (Yan and Hunt 1999; Hunt et al., p. 23, this volume), then differences in the phyllochron prediction between the two soil temperature treatments are largely accounted for. The second explanation returns to the issue of the site of temperature perception and some aspects of wheat anatomy and development discussed previously.



Figure 3. Main stem Haun values (Haun 1973) for three planting dates in two years. The two treatments were heating the soil at 2cm depth to $+3^{\circ}$ C (+3) over ambient soil temperature (+0).

Two meristems result in the phyllochron: the shoot apex producing the leaf primordium and the leaf extension zone where the leaf primordium develops and grows the mature leaf. Until the growth stage of single ridge, the length of the shoot apex is roughly 1 cm, with a primordium length of about 1.5 mm reported for tall fescue (Festuca arundinacea Schreber) (Skinner and Nelson 1995). A further complication is the need to know the depth at which the crown is located. Cultivars vary in their crown depth, and within a cultivar the crown depth can vary considerably according to many factors. A temperature gradient normally exists with respect to depth from the surface. Therefore, the first problem is knowing at which "point" or depth to measure soil temperature.

Another complication in deciding the appropriate depth at which to measure soil temperature is the importance of the leaf extension zone. Skinner and Nelson (1995) delineate the leaf extension zone into different sections, such as cell division, cell expansion, secondary cell wall growth, carbohydrate and N deposition, etc. for tall fescue. These sections overlap to varying degrees, and the total distance can be as much as 70 mm. Because expansion of the cells pushes the older leaf tissue up through the whorl of subtending leaves, we presume that much of this zone occurs more or less vertically from the leaf primordium. Depending on the depth of the crown/ shoot apex and length of the leaf extension zone, some of the leaf growth could be occurring above the soil surface, and certainly across a temperature gradient in the soil. Again, what point is to be used to measure soil temperature? The final confounding factor recognizes that the water, carbohydrates, and nutrients required for cell division and growth are coming from other parts of the plant, and that these parts are experiencing different temperatures than the shoot apex/leaf extension zone.

Conclusions

Simulating the complicated relationship between the phyllochron and temperature of wheat can be aided by understanding the location of meristematic tissue producing leaves, the temperature response pattern (non-linear across the entire range, but linear within certain temperatures), temperatures during leaf production and whether the temperature is in the linear region or not, factors that interact with temperature to influence the phyllochron, and certain limitations of the GDD characterization of the effect of temperature. The simple linear GDD approach that uses air temperature above the canopy works well in most situations. If improvements are desired, the use of non-linear responses shows promise.

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Simulating Response to Temperature

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Abstract

Temperature is one of the most important factors determining plant growth, development, and yield. Accurate summarization of plant temperature response is thus a prerequisite to successful modeling of crop systems and application of models to management. This paper reviews various equations that have been used to describe temperature response for a number of crop plants. The beta function, as used in some recent analyses, has been shown to summarize data dealing with the overall growth and development of maize and wheat in a realistic manner. However, consideration of research dealing with photosynthesis indicates that the function may not be appropriate for all processes, especially processes (such as photosynthesis) that involve many sub-processes, each with its own response characteristics. Further, different parameters may be necessary for different genotypes, different times during a plant's life cycle or different regions or over contrasting climate change scenarios. An approach involving interpolation between data points describing specific temperature responses, rather than a mathematical function, may well have the widest utility. Such an interpolation should be non-linear.

Introduction

Temperature is arguably the most important environmental factor that affects plant development, growth, and yield. All biological processes respond to temperature, and all responses can be summarized in terms of three cardinal temperatures: a base or minimum (T_{min}), an optimum (T_{opt}), and a maximum (T_{max}) . However, the nature of the response to temperature between these cardinal points, which is important for calculating the phenology, adaptation, and yield of various crops (Wang 1960; Cross and Zuber 1972; Undersander and Christiansen 1988; Shaykewich 1995), is not summarized as easily. There have been, however, numerous attempts to develop functions describing response to temperature, some with more general application than others. Some of these attempts are summarized and illustrated here.

Temperature Response Functions

Within a limited range of temperature, the rate of plant development or growth is often found to be a linear function of the temperature. In this range, the time required to develop to a certain stage is related to the sum of daily temperatures above a specified base or minimum temperature. Such a linear model is convenient and effective when the temperature does not approach or exceed the optimum, Topt (Summerfield and Roberts 1987). However, temperatures frequently approach and exceed the T_{opt} in natural conditions. To accommodate this situation, many researchers have adopted a bilinear approach (e.g., Olsen, McMahon and Hammer 1993) in which two different linear equations (Equation 1) are used to describe the responses to sub-optimum and supraoptimum temperatures. This approach has been successfully applied to several crops (Omanga et al. 1995 and 1996 for pigeonpea; Craufurd et al. 1998 for sorghum, among others).

$$\begin{cases} r = a_1 + b_1 T & (T < T_{opt}) \\ r = a_2 + b_2 T & (T > T_{opt}) \end{cases}$$
 Eq. 1

There are four parameters in the bilinear approach, a_1 , b_1 , a_2 , and b_2 , from which the three cardinal temperatures can be derived. However, the derivations may not always be meaningful. As Craufurd et al. (1998) point out, "The estimation of T_{min} usually

requires considerable extrapolation and the standard error (SE) of this T_{min} is large in comparison with the SE of T_{opt} ." The same can be said for the estimation of T_{max} . In the work of Craufurd et al. (1998), estimates of T_{max} ranged from 36.8° to 58.9°C for leaf appearance rate; for leaf tip appearance rate a value of 198°C was obtained for one genotype, obviously an overestimation. Further, the maximum rate of any process at T_{opt} is also likely to be over-estimated since it is obtained from two linear equations, while the real response curve is generally curvilinear.

A multilinear model can be constructed from three or more linear components (e.g., Coelho and Dale 1980) making it less rigid than the bilinear model. Some crop system simulation packages (e.g., CROPSIM, Hunt and Pararajasingham 1995 and later versions) have adopted this approach, even though five or more parameters are required to describe the temperature response of a process. Although closer to reality than linear or bilinear models, the greater number of parameters renders this approach subject to calibration errors. Moreover, the parameters are usually high empirical.

Rather than rigid combinations of linear equations, some researchers have argued that it is preferable to use an approach in which a smooth curve describes the temperature response of a given process (e.g., Cross and Zuber 1972, Shaykewich 1995). Exponential, logistic, and polynomial equations give smooth curves. Of these, an exponential equation is usually effective in describing the responses at low to intermediate temperatures. It does not describe the response to high temperatures, however, because it does not allow for a reduced rate of development at high temperatures (e.g., the curve in Tollenaar et al. 1979).

By contrast, a three parameter logistic equation allows for very slow activity at high temperatures, and has been used by Shakewich (1994) to summarize leaf appearance rate data obtained by Tollenaar et al. (1979) for maize:

$$LAR = LAR_{max}/(1 + e^{a+bT})$$
 Eq. 2

where
$$LAR = Leaf$$
 appearance rate
 $LAR_{max} = Leaf$ appearance rate, maximum
(0.61 leaves/d)
 $a = 5.84$
 $b = 0.30$

This equation gave an $r^2 = 0.94$ and an inflection point at 19°C.

A three-parameter quadratic equation (Yan and Wallace 1996, 1998) goes one step further than the logistic by allowing for a reduced rate of development at high temperatures:

$$r = R_{max} - b(T - T_{opt})^2$$
 Eq. 3

This form of expression has been used in the heat unit system (Brown 1975) for maize (*Zea mays* L.) with a T_{min} of 10° and a T_{opt} of 30°C for the daytime part. Because the true temperature response is rarely a symmetric parabola, however, estimation of T_{min} and T_{max} can be difficult. Applications of the quadratic model at low or very high temperatures can be inaccurate as a result. Higher order polynomials can produce a more realistic temperature response curve (Tollenaar et al. 1979) and improve prediction of crop development (Stewart et al. 1998). In addition to requiring more parameters, however, higher order polynomials also have parameters that are difficult to interpret in biological terms.

The standard "beta-distribution," described in many handbooks of mathematics and characterized by a unimodal curvilinear response to an independent variable x in the range of [0,1], also has been used to describe temperature response in plants (Yin et al. 1995):

$$\mathbf{r} = \mathbf{R}_{max} \left[\left(\frac{T - T_{acum}}{T_{opt} - T_{min}} \right) \left(\frac{T_{max} - T}{T_{max} - T_{opt}} \right)^{\frac{T_{max} - T_{opt}}{T_{opt} - T_{min}}} \right]^{C} \qquad \text{Eq. 4}$$

Equation 4 fits experimental data to five parameters: the three cardinal temperatures, the maximum rate R_{max} at T_{opt} , and *c*, a parameter that determines the shape of curve. Yin and colleagues (Yin and Kropf 1996; Yin et al. 1996) reported successful simulation of rice development using this equation.

Compared with previous models, the expression by Yin and colleagues has the advantage of producing smooth, and for some processes, realistic curves. All parameters except *c* are biologically meaningful. Yan and Hunt (1999) simplified the equation by eliminating *c* and placing T_{min} equal to zero, and reported on the effectiveness of this simplified equation in summarizing published temperature response data for the growth and development of a number of species. The simplified expression, however, essentially replaces the 'shape' parameter of the basic beta function (i.e., *c*) with the maximum temperature. This replacement may produce realistic curves in some circumstances, but certainly not for all processes and situations.

Examples of Temperature Functions

A multilinear function fitted to data from various maize experiments is shown in Figure 1. This function, which had four segments and five parameters (6°, 21°, 28°, 32°, and 44°C), could be used to compute the effectiveness of any given day for the growth and development of maize. However, the sharp 'shoulders' may limit the value of the approach particularly for the first 'leg' of the response curve. This section of the curve is part of a generalized logistic type, with activity increasing slowly with temperatures at values just above the base and accelerating until an apparently linear phase is reached.



Figure 1. Growth rate of corn at indicated temperatures divided by that at 28-32°C. Figure reworked from Coelho and Dale (1980).

Lines drawn from the following relationships:						
GR(N) = 0.027T - 0.16	6°C ≤ T <21°C					
GR(N) = 0.086T - 1.41	21°C ≤ T <28°C					
GR(N) = 1.0	28°C ≤ T <32°C					
GR(N) = -0.083T + 3.67	32°C ≤ T <44°C					
GR(N) = 0.0	6℃ ≥ T < 44℃ (14)					

10-cm-depth soil temperature used from planting to the date on which the growing point emerged from the soil, and air temperature thereafter. Note: Actual values are approximations from graphs. The problem of effectively describing the initial phase was overcome by Tollenaar et al. (1979) by making use of a polynomial (Figure 2). Such an approach was also found useful by Stewart et al. (1998) for summarizing the development of field grown maize during the planting to silking period (Figure 3).



Figure 2. Relationship between rate of leaf appearance and temperature for corn. After Tollenaar et al. (1979).

Curve A: polynomial equation of best fit to data $Y = 0.2834 - 0.0639T + 0.0491T^2 - 0.0000823T^3$ Curve B: alternate polynomial $Y = 0.0097 - 0.0360T + 0.00362T^2 - 0.0000639T^3$ Crosses indicate mean rate of leaf appearance at five constant temperatures (standard deviation = 0.043 leaves/day).



Figure 3. Thermal time calculated from field data for four maize hybrid groups over the planting to silking period. After Stewart et al. (1998). There were no significant differences in the optimum temperature between groups, which had growing degree day ratings from 1100 to 1400°Cd.

However, it proved less useful from silking to maturity (Figure 4).

Angus et al. (1981) found that an exponential function (Figure 5) without an initial 'leg' best summarized data from wheat experiments over a range of widely contrasting sites. This example emphasizes the need for a general function that can accommodate situations where 'legs' of different durations are clearly present, together with those in which there is no apparent 'leg' or only a very limited phase of rapidly increasing rate.



Figure 4. Thermal time calculated from field data for four maize hybrid groups over the silking to maturity period. After Stewart et al. (1998).



Figure 5. Exponential functions used to summarize development of wheat cultivar UQ189 at a number of widely separated locations.

The temperature factor calculated from the following expression: $R_{max} [1-e^{-3} (^{T-tmin})]$ where R_{max} is the maximum rate of development, and 3 and T_{mim} are parameters. Values for 3 were 0.15 and 0.077°C⁻¹ for emergence to anthesis and anthesis to maturity phases respectively, and for T_{min} 3.5 AND 8.9°C for the same periods. After Angus et al. (1981). The simplified 'beta' function of Yan and Hunt (1999) well summarized maize data (Figure 6), though the upper temperature serves as a 'shape' parameter in this simplified form (Figure 7). The more general function of Yin et al. (1998) seems in turn likely to have more general application. However, even for the general function, the 'shape' parameter affects both the ascending and descending legs of the curve; it thus may not allow for effective description of the impact of high temperatures, something essential for application of models to climate change scenarios involving an increase in temperature.



Figure 6. Measured relative rates of development or growth of maize, together with predicted relative rates based on a single modified beta function with $T_{max} = 41$ and $T_{out} 31^{\circ}$ C. From Yan and Hunt (1999).



Figure 7. Comparison of different temperature functions to illustrate the effect of changes. T_{max} on the slope of the low tempeature response arm of the modified beta curve of Yan and Hunt (1999).

---- Simplified beta function (T_{max} = 45.3, T_{min} = 21.8) for leaf appearance (Yan and Hunt, 1999) — Simplified beta function (T_{max} = 33.4, T_{min} = 20.6) for reproductive development (Yan and Hunt, 1999)

Discussion and Conclusions

Temperature is among the most important single factors determining plant growth and development (and hence agricultural production), and a model that allows for summarization (and hence simulation) of the temperature response of plant growth and development is necessary for several applications. Knowledge of the optimum and maximum temperatures for the growth and development of a genotype, and the nature of the response surface, is vitally important to the successful prediction of its maturity, adaptation, and yield in a particular environment. A beta function appears to be useful for summarizing the response surface for a number of processes, but may not have utility for all of them. This is especially true for those processes that may have a wide optimum temperature range, as may be found when the overall process is the resultant of a number of sub-processes. Photosynthesis is one such example. Early work (e.g., Murata and Iyama 1963; Figure 8) showed a wide optimum temperature range for the process; however, more recent work has shown that the nature of the response surface depends on the conditions under which measurements were made (e.g., Acock 1991; Figure 9) and that it may be possible

to describe overall temperature response surface by using simple functions for various sub-processes (Boote and Pickering 1994; Bernacci et al. 2001). The use of an approach in which an interpolation (possibly non-linear) between specified points is used instead of a specific mathematical formulation may thus have the most widespread application. Such an approach, which has been used widely in simulation modeling, can result in good simulation when the specified points or cardinal temperatures are realistic (Figure 10). Even with such an approach, however, the selection of the cardinal points for use with a particular process is not a simple matter. Many aspects must be considered, including the following:

- The nature of the response surface (i.e., the presence of a 'leg' or the width of the optimum band)
- Change through the life cycle
- Ecotype differences
- Acclimation possibilities (i.e., changes induced by the conditions experienced during growth)

The problem of effectively defining plant temperature, as contrasted to air or soil temperature, and the impact that this may have on any apparent temperature response (see Jamieson et al. 1995) must also be kept in mind.



Figure 8. Photosynthesis - temperature response curves for wheat and maize as reported by Murata and Iyama (1963).



Figure 9. Leaf net photosynthetic rates measured at various temperatures and two light flux densities. After Acock (1991).

Tomato Plants grown at 20°C and 380 μmol photon $m^{-2}s^{-1}$ with a 16-h photoperiod, and rates measured with 300 uL L^{-1} CO $_2$. Points are measured data and curves are predicted using a simple model.



Figure 10. Simulated and measured leaf numbers for wheat cultivar 'Nordic' planted on two dates in the field at Fort Collins, Colorado. Simulations were made with different temperature responses, as specified with cardinal temperature values (°C). Too low an optimum resulted in slow simulated leaf appearance; too high an optimum resulted in the opposite.

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Evaluation and Calibration of CERES3-Maize: Tiller Number Simulation

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Abstract

The purpose of this study was to adapt CERES3 to simulate differences in tillering potential among maize cultivars without increasing the number of genetic coefficients, as well as to simulate effects of management and environmental conditions on tiller number. The simulation of tiller numbers is of limited interest in maize production areas where the crop is produced at plant populations greater than 3.0 plants/m², but the contribution of tillers to yield can be significant at lower populations. Cultivars show great variation in tiller potential, and this potential varies with the planting date. Such variability is confirmed by field data from South Africa showing that the standard deviation of the measured values of tiller numbers was greater than the mean. An algorithm for the simulation of tiller numbers was developed using an average photoperiod and a minimum temperature for the time period from emergence to the end of the juvenile stage. The results indicated that tiller numbers could be simulated with some degree of success, but there is need for further investigation. The period of plant development in which tiller numbers are affected by environmental conditions is of particular interest. Although the influence of tiller numbers on kernel numbers is simulated, the impact of tillering on leaf development is not incorporated into the modified CERES. This topic also merits further investigation.

Introduction

Tiller formation is common in the gramineae (Verwey and Hammes 1989), and tillers often make important contributions to grain and forage yields. The tillering process is simulated in CERES3 routines for barley (Otter-Nacke et al. 1991), millet (Singh et al. 1991), sorghum (Alargarswamy and Ritchie 1991), and wheat (Godwin et al. 1989). However, maize is simulated as a single plant in CERES Maize v1.0 (Jones and Kinry 1986), CERES-Maize v2.1 (Ritchie et al. 1992), and CERES3 (Hoogenboom et al. 1994), in spite of the maize plant producing tillers in plant populations below 4.0 plant/m² (Tetio-Kagho and Gardner 1988).

Verwey et al. (1994a) determined that more tillering occurs at night temperatures of 5°C than at either 10°C or 18°C during the first 17 days after emergence. Results by Pretorius (1985) showed that tillering varies with cultivars, planting dates, and plant populations. Tetio-Kagho and Gardner (1988) reported differences in the amount of tillers over seasons, and Verwey et al. (1994b) found that tiller numbers differed between various sites within the same season. Du Toit (1996) showed that a contribution of 25% by tillers to total grain yield is not uncommon, with the number of ears per plant (main, secondary, and tiller) making a significant contribution to the simulation error of the standard CERES3 model.

The purpose of this study was to adapt CERES3 to simulate differences in tillering potential of maize cultivars without increasing the number of genetic coefficients, as well as to simulate tiller development for different management and environmental conditions.

Materials and Methods

Field Trials

Two trials were conducted for the development of the tiller algorithm. One trial involved different planting dates at Potchefstroom, South Africa (lat. 26.73°S, long.

27.08°E, elevation 1345 m) in 1990-91. The other pertained to the determination of genetic coefficients, and was conducted in 1992-93. These two trials were combined, providing 123 data points with 20 cultivars and 21 planting dates over two seasons.

Model Modifications

Three approaches were attempted to improve the simulation of tiller numbers:

- 1. Adapting the algorithm for tiller production used in CERES3-Sorghum. The logic used in this subroutine is described later in this paper.
- 2. Modifying the CERES3-Sorghum algorithm to include effects of environmental factors that might affect tiller production (also described later in this paper).
- 3. Estimating tiller number as a function of a maximum potential number that is subsequently reduced due to environmental and management effects. This approach is explained below.

The period from emergence to the end of the juvenile stage (ISTAGE 1) was used to estimate the number of tillers initiated. The maximum number of tillers (TILG2) per cultivar was calculated from the genetic coefficient G2 (maximum possible kernel number per plant) as indicated in Equation 1.

The basis for the functions is described later in this paper. In Equation 2, tiller number was calculated from the average minimum temperature (ATMIN) from emergence to the end of the juvenile stage:

Equation 3 calculates tiller number from the average photoperiod (APHOTO) for ISTAGE 1.

When TILMIN and TPHOTO are greater than or equal to one tiller per plant and Equation 2 is greater than or equal to the theoretical value of 81.55% of Equation 3, then the number of tillers per plant (TILN) is the maximum value of TPHOTO and TILMIN. However, if TPHOTO is greater than TILMIN, TILN is equal to TILG2. When TPHOTO and TILMIN are both less than one tiller per plant, and TILMIN is less than 81.55% of TPHOTO, TILN is the minimum of TILMIN, TPHOTO and TILG2 * TILMIN. However, if TILN is less than or equal to 0.24 tillers per plant TILN is calculated from Equation 4.

TILN = (-6.26 + 0.01 * G2 - 8.81E-6 * G2**2) + (3.61 + 6.75E + 22 * EXP(-4 * APHOTO)) Eq. 4

To simulate the influence of row width on the number of tillers, a function was developed using the data of Du Toit (1996). Inter-row spacing (TT) was used in Equation 5 to calculate tiller number where TT is the inter-row spacing in meters.

Tetio-Kagho and Gardner (1988) calculated tiller number from plant population. This function was included through Equation 6 in order to prevent the simulation of TILN for populations greater than 3.8 plants/ m^2 .

TILN = AMIN1(TILN, (2.9 - 0.76 * PLTPOP)) Eq. 6

Based on experimental data, kernel number for a tiller was assumed to be 60% of the kernel number of the second ear on the main stem.

Results and Discussion

Tiller Numbers

The results in Table 1 indicate greater tiller numbers for the first planting date than the second and third planting dates, which is consistent with results by Pretorius (1986) that early planting dates tend to have more tillers. This is possibly due to the effect of low minimum temperatures during the early part of plant development on tiller number (Verwey et al. 1994a). Lower average minimum temperatures were recorded for the first planting date than for the second and third planting dates, while the average minimum temperatures for the second planting date were lower than those of the third planting date.

Cultivar	Planting date							
	07 Sept 92	19 Oct 92	22 Nov 92	Average				
SENKUIL	0.30	0.00	0.08	0.13				
SR-52	0.63	0.00	0.10	0.24				
RS-5206	0.70	0.03	0.05	0.26				
PAN-6479	0.70	0.03	0.20	0.31				
PAN-6578	0.78	0.05	0.13	0.32				
A-210	0.98	0.25	0.15	0.46				
CRN-4526	1.13	0.10	0.15	0.46				
PAN-473	0.63	0.35	0.50	0.49				
PAN-6364	1.00	0.08	0.45	0.51				
PAN-6528	1.40	0.05	0.10	0.52				
PAN-6363	1.30	0.23	0.23	0.58				
A-1257	1.03	0.30	0.60	0.64				
SNK-2340	1.98	0.10	0.08	0.72				
SNK-2776	1.58	0.38	0.35	0.77				
A-1849W	2.03	0.03	0.38	0.81				
RO-410	1.75	0.20	0.53	0.83				
CRN-3414	1.90	0.18	0.43	0.83				
RO-411	2.38	0.15	0.38	0.97				
PAN-6552	1.83	1.08	1.65	1.52				
TX-24	2.25	0.95	1.58	1.59				
Average	1.31	0.23	0.40	0.65				

Table 1. Tiller number for 20 cultivars planted on three planting dates (Potchefstroom, South Africa) as reported by Du Toit (1996).

Sorghum Algorithm

The existing sorghum tiller algorithm in CERES3 was used as a first step in developing a tiller algorithm for maize in CERES3.

CERES3-Sorghum simulates tiller production from 120 heat units after emergence until the end of the juvenile stage. The influence of solar radiation (SOLRAD) and of daily heat units (DTT) on tiller number (TILN) is accumulated (SUMRTR) over this period as follows:

The average influence per day (RTR) is calculated by dividing SUMDTR by the duration of the period in days (TDUR):

$$RTR = SUMRTR / TDUR$$
 Eq. 8

If RTR is less than 27, then TILN equals unity. This rule was not applied to the maize model, so two temporary constants (TC1 and TC2) are calculated. TC1 is calculated from RTR, while TC2 is calculated from plant population (PLTPOP) and TILN as follow:

$TC1 = 1.0/25.0^{*}(RTR-27.0)$	Eq. 9
TC2 = 6.25E-5*(40.0-PLTPOP*TILN)**3	Eq. 10

TILN is accumulated over this period from the fraction of a leaf emerging day⁻¹ (TI), the smallest value (AMIN1) of TC1 and TC2, and the water stress factor (TURFAC):

However, if TILN multiplied by PLTPOP exceeds 40.0 plants/m² then:

$$TILN = 40.0/PLTPOP Eq. 12$$

The observed standard deviation (Stdev) was greater than the mean (Table 2) in the sorghum algorithm, an indication of the great variation in tiller numbers. R² and D-indexes indicated very low levels of accuracy. Root mean square error (RMSE) and root mean square error systematic (RMSEs) values similarly indicated that almost all the error could be explained by the bias of the tiller simulation. Thus, applying the CERES3-Sorghum tillering algorithm to maize showed little promise.

Environmental Factors

To simulate differences between cultivars, linear correlations were calculated between the genetic coefficients used to represent cultivar differences in

Table 2. Quantitative measures of the calculation of maize tiller numbers by the sorghum algorithm in CERES3 using 123 data points (Du Toit 1996), as compared to outputs from three routines for simulating tiller production in CERES-Maize.

		Modeling approach for tiller development					
Parameter ¹	Observed	CERES3- Sorghum	CERES3-Sorghum + environmental effects	Proposed method			
Minimum	0.01	0.01	0.0064	0.12			
Maximum	2.38	0.37	2.48	1.72			
Mean	0.49	0.134	0.67	0.45			
Std. Deviation	0.53	0.069	0.55	0.39			
Slope		-0.26	0.62	1.02			
Intercept		0.53	0.073	0.033			
MAE		0.40	0.39	0.25			
RMSE		0.64	0.49	0.36			
RMSEs		0.64	0.25	0.25			
RMSEu		0.07	0.42	0.26			
D-Index		0.40	0.78	0.83			
R ²		0.00	0.42	0.55			

¹ MAE = Mean Absolute Error; RMSE = Root Mean Square Error; RMSEs = Root Mean Square Error - systematic; RMSEu = Root Mean Square Error - unsystematic; D-Index = index of agreement, Willmott (1982). See also Du Toit et al. (2000) and Du Toit & Du Toit, p. 42, this volume.

CERES-Maize and tiller production by various cultivars (Table 3). P5 (growing degree days from silking to maturity) was excluded because tiller initiation occurs before the sixth leaf stage (Hanway 1966). The significant correlation of P1 with tiller number suggested that the initiation of tillers occurred during the juvenile stage. This was also noted in previous research where the tiller number was determined in the first 17 days after emergence (Verwey et al. 1994b).

The significant correlation between G2 and tiller number suggested that G2 could be used to calculate the genetic potential of a cultivar to produce tillers. Assuming that the resulting tiller number results from processes that reduce a potential or optimal number, Equation 2 was developed to estimate the optimal number for a given cultivar.

A second step was to identify environmental factors that might affect tiller numbers. Measured tiller numbers were subtracted from the calculated values to give the residuals of Equation 1. Using backward regression, the average photoperiod (AFOTO) during the juvenile stage appeared to be the environmental factor showing the strongest relation with the residuals. A cubic function with AFOTO as the dependant factor gave the greatest r^2 for the residuals. Tiller numbers were simulated by adding the values of the cubic function to the values of Equation 1, providing the results shown in Table 2. The root mean square error-unsystematic (RMSEu) was greater than the RMSEs but closer to the RMSE, indicating that the error is random. To improve accuracy, changes need to be made in the algorithm for tiller simulation.

Table 3. Linear correlation between tiller numbers and four genetic coefficients.

YV	/ariable	Correlation (r)	Slope (b)	Y Int. (a)	Р
P1:	Duration of juvenile phase	-0.18	-7.17	247	0.046 *
P2:	Effect of photoperiod on development rate	-0.07	-0.029	0.88	0.358 ns
G2:	Maximum possible number o kernels per plant	f +0.21	30.35	527	0.017 *
G3:	Kernel weight coefficient	-0.08	-0.06	6.55	0.358 ns

* P < 0.05

Model Modifications

The third approach was the one described in the section on model modifications above. Of the three approaches, the last approach showed the greatest level of accuracy (Table 2). Comparison of the RMSE, the RMSEu and the RMSEs for the latter two approaches indicated that the systematic errors of the two approaches were almost the same in areas where both the RMSE and the RMSEu decreased. The RMSEu showed the greatest decrease, possibly due to the use of both minimum temperature and photoperiod in the calculation of tiller numbers. The RMSEu and the RMSEs were similar, indicating that the error is both random and biased. This suggests that further factors need to be included in the calculation of tiller numbers.

Conclusions

The simulation of tiller number is of limited use in maize production areas where the crop is produced at plant populations greater than 3.0 plants/m². However, the contribution of tillers to yield in the western Highveld is significant (Du Toit 1996) and it is also important in many small-holder systems. Cultivars show great variation in tiller potential, which is also affected by planting date. This is confirmed by the observation in this study that the standard deviation of the measured values was greater than the mean.

An algorithm for the simulation of tiller numbers was developed using average photoperiod and minimum temperature from emergence to the end of the juvenile stage. The results indicate that tiller numbers could be simulated with some degree of success but merits further investigation. The period of plant development in which tiller numbers is affected by environmental conditions is of particular interest. The basis for the simulation of tiller number in maize was improved for CERES3, without an increase in the number of genetic coefficients. Although the influence of tiller number on kernel number is simulated, the impact of tillering on leaf development is not incorporated in the modified CERES and also merits further investigation.

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A Comparison of Approaches to Modeling Phenology as Applied to Genotype by Sowing Date Interactions in Wheat

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Abstract

Eliminating land preparation for wheat crops following rice allows the wheat to be sown much earlier in the ricewheat rotations prevalent in South Asia. The earlier sowing exposes the crop to warmer temperatures and longer photoperiods during crop establishment. To test how well wheat models can account for possible cultivar differences in response to early plantings, simulations from the CERES Wheat and Sirius models were compared to observed responses for two cultivars sown on multiple dates at Ludhiana, Punjab, India. Both models showed problems, especially in handling vernalization. The Ludhiana environment is on the edge of vernalization effectiveness, so any error in assumptions about the upper limiting temperature for vernalization response is likely to have a large effect.

Introduction

The rice-wheat system of South Asia is one of the most productive agricultural systems in the world. Through double cropping of rice and wheat, farmers make efficient use of the year-round growing season, matching rice to the warm, wet monsoon season and irrigated wheat to the cool, dry winter season (Fujisaka et al. 1994). Concerns over both the biophysical and socioeconomic sustainability of this system have fostered extensive research on strategies for protecting yield gains while improving factors usually thought to be associated with conserving the resource base. These include crop diversification, more efficient use of irrigation water, increased soil organic matter, and reduced use of external inputs. Various strategies for eliminating tillage between the rice and wheat crop have shown particular promise (Hobbs et al. 1997; Mehla et al. 2000; Timsina and Connor 2000). A key aspect is that wheat can be sown closer to the optimal date by eliminating the period of waiting for paddies to dry and be tilled. With the earlier, optimal sowing, the wheat crop matures under cooler, more favorable conditions, which is

reflected in higher yields. Estimates from the Punjab are that wheat grain yield declines 1 to 1.5% per day of delay in sowing (Dhillon and Ortiz-Monasterio 1993; Ortiz-Monasterio 1994). Further benefits include that the sowing date is less subject to adverse events such as untimely rains that can delay or prevent land preparation.

Given the prospect of more frequent early sowing, the question has arisen whether certain cultivars are especially suited for such practices (Mehla et al. 2000). Although characteristics such as the ability to emerge from a rough seedbed with surface residues are also desirable, an appropriate phenological response seems essential. So-called "green revolution" wheats that predominate in the region are relatively insensitive to photoperiod and have a low vernalization requirement, but it is possible that these low levels are still sufficient to influence development. Mehla et al. (2000) noted that two cultivars favored for timely (early) sowing, WH 542 and PBW 343, have a longer vegetative phase and shorter grain-filling phase than older varieties such as HD 2009 and HD 2329.

Simulation models are potentially valuable analytic tools for analyzing cultivar differences in the response of phenology to sowing date. Many wheat models allow for quantitative differences among cultivars in inherent earliness (earliness per se), vernalization requirement, and photoperiod sensitivity. These models would thus seem suited to analyzing the underlying processes of genotype by sowing date interactions. This paper compares simulations from two models, CERES-Wheat and Sirius, for contrasting genotypes described in the sowing date study reported by Dhillon and Ortiz-Monasterio (1993) and Ortiz-Monasterio et al. (1994). The two models have similar objectives but differ in their approach to simulating development.

Materials and Methods

Field Data

Data for days to heading vs. sowing date for the spring wheat cultivars HD 2329 and PBW 34 were obtained from a series of genotype by sowing date experiments conducted from 1985 to 1992 at Punjab Agricultural University, Ludhiana, India (lat. 30.93°N, long. 75.87°E, elev. 247 m.), as reported by Dhillon and Ortiz-Monasterio (1993) and Ortiz-Monasterio et al. (1994). HD 2329 is reported to be dominant for all four *Vrn* loci, and thus has a very low vernalization requirement (J. van Beem, personal communication, 2001).

To calibrate HD 2329, seven sowing dates from 25 October to 25 December 1988 were used; for PBW 34, ten sowing dates from 25 October to 25 December 1985 were used. For validation, sowing dates for both cultivars were 15 October to 25 December 1989. In our analyses, days to anthesis was estimated to be seven days after heading, as reported in the original study. Trials were well irrigated and fertilized, so phenology data should show little effects of water or nutrient deficits. Figure 1 shows long term climatic conditions at Ludhiana, and Figure 2 shows variation in daily maximum temperature for three years to illustrate the year-to-year and within year variability in temperature.

Simulation Models

Both models use thermal time as their basis for predicting phenology and include effects of vernalization and photoperiod. However, the models use different approaches to account for these effects. CERES-Wheat uses a well-tested phasic development approach, where the thermal duration of phases between observable apical events is modified by factors related to photoperiod and the accumulation of vernalization. Variations on the approach are used in several wheat simulation models, such as AFRCWHEAT2 (Porter 1993), as well as various CERES derivatives, such as Cropsim-Wheat (Hunt and Pararajasingham 1995). The approach has proved robust in a variety of environments. Sirius attempts to move its empirical relationships down one level of organization to simulate the effect of photoperiod and vernalization on mainstem final leaf number (FLN) and, through it, on the thermal time to anthesis. This



Figure 1. Long term monthly values for mean maximum and minimum temperature and total precipitation at Ludhiana, India (FAO, 1998).



Figure 2. Variation in daily maximum temperature from October to April for three years at Ludhiana, India.

approach has also proved successful in a variety of environments. More detailed descriptions of both methods follow.

CERES-Wheat

Version 3.5 of CERES-Wheat was used as provided by P. Wilkens (IFDC). The most complete documentation is Ritchie and Godwin (N.d.) for version 2.0; additional information is found in Godwin et al. (1989) and Hoogenboom et al. (1996). Key developmental events in CERES-Wheat are germination, seedling emergence, and terminal spikelet initiation. The rate of development varies with temperature per se (thermal time or growing degree days), vernalization and photoperiod.

Vernalization is assumed to occur at temperatures between 0° to 15°C; temperatures above 7°C are assumed to have decreasing effectiveness. The relative vernalization effectiveness varies from 0 to 1 depending on the crown temperature. A cultivar-specific vernalization coefficient (P1V) conditions the cultivar sensitivity, with values of 1 or lower being representative of spring wheats. De-vernalization occurs if the number of vernalization days accumulated is less than 10 units and the maximum temperature is over 30°C.

Photoperiods shorter than 20 h (calculated based on civil twilight) delay development through a rate modifier (DF) that varies from 1 to 0 as photoperiods shorten. A cultivar-specific photoperiod sensitivity coefficient (P1D) conditions the cultivar sensitivity, with values of 0 to 3 being representative of day-neutral spring wheats.

Thermal development time (TDU) is accumulated up to 400 degree days, ending with terminal spikelet formation. Daily thermal time (DTT) is either reduced due to the influence of vernalization (VF) or photoperiod (DF), depending on which rate-reducing factor is smaller (and provides the greatest inhibition of development):

$$TDU = DTT * [minimum(VF, DF)]$$
 Eq. 1

There is still considerable discussion regarding the correct values for the cardinal temperatures of wheat, but a base temperature (Tbase) of 1°C and optimal temperature (Topt) of 25°C were found satisfactory in preliminary calibrations. The duration from terminal spikelet formation to anthesis is affected only by temperature and is assumed to take 5 phyllochrons (3 to end of leaf growth and 2 to more to anthesis).

Sirius

Sirius 2000 is the latest version of Sirius (Jamieson et al. 1998b). It is an advance on Sirius 99 (Jamieson and Semenov 2000), mostly differing in its description of soil water. The version used in this study has essentially the same phenological descriptions as the original, except that the temperature response of vernalization was modified based on the recent controlled environment work of Brooking and Jamieson (2001).

Whereas the phenological models in CERES-Wheat are based on phasic development-i.e., the (modified) thermal time intervals between observable apical events-in Sirius major variations in timing are associated with changes in final leaf number (FLN). Phases as such play a much less important role in Sirius (Jamieson et al. 1998a). The phenological events for which timing is described are emergence, flag leaf ligule appearance (FL, or full expansion of the flag leaf lamina), anthesis, and the beginning and ending of grain filling. The minimum FLN observed in the field is usually about seven or eight, but FLN can exceed 20. The thermal time intervals to emergence and between events after FL are assumed to be fixed in thermal time-e.g., FL to anthesis is three phyllochrons, and anthesis to beginning of grain filling is one phyllochron. The thermal duration of grain filling may vary with cultivar but is usually about 550°C days (0°C base). These aspects of the phenological model are similar in concept to CERES-Wheat. The major difference is that in Sirius the date of FL is calculated from FLN and the response of leaf appearance rate to temperature (Jamieson et al. 1995). FLN is itself calculated from responses to daylength (Brooking et al. 1995) and vernalization (Brooking 1996, Robertson et al. 1996). Thermal time for development is calculated using a base temperature of 0°C. No optimum developmental temperature is assumed, so the rate of leaf appearance increases along with temperature with no limit. Thermal time is not modified in any way by photoperiod or temperature (i.e., the concepts of photothermal or photo-vernal-thermal time are not used). Rather, the thermal time from emergence to FL (and therefore to later stages) depends on FLN.

To model the daylength (photoperiod) response, FLN is assumed to be fixed according to the daylength (DL) that occurs when there are FLN/2 leaves on the plant:

 $FLN = FLN_{min} + SLDL (16-DL)$ Eq. 2

FLN_{min} is the minimum number of leaves (usually about 8) produced in long days (i.e., exceeding 16 hours). The daylength response parameter SLDL is the number of extra leaves produced per hour of daylength below 16 hours. The procedure involves daily estimates of FLN based on current daylength, and a check to see whether the actual leaf number is half the estimated FLN. When this latter occurs, FLN is fixed and timing depends on how long it takes to produce the remaining leaves.

The vernalization model also predicts FLN as its main method of influencing time to flowering. It requires three parameters, which are:

- 1.- The maximum FLN (FLNmax). This is the number of leaves that would be produced on the mainstem in continuous exposure to warm long days.
- 2.- The vernalization rate at 0°C (VBEE). This is reciprocal of the time taken to saturate the vernalization requirement at 0°C.
- 3.- The temperature response of the vernalization rate (VAI), assumed to be the same for all cultivars.

Winter cultivars (i.e., those with a vernalization requirement) are assumed to have a large potential leaf number at germination (FLNmax). The number decreases as vernalization proceeds. Vernalization is completed when FLN is minimized, either because the number of leaf primordia (produced twice as fast as leaves appear) on the apex is equal to the potential FLN, or because the potential FLN has fallen to 8. The rate of vernalization increases with temperature from 0°C until 8°C (Brooking and Jamieson 2001) and then falls linearly to reach zero at 17°C. Vernalization does not proceed at temperatures outside the range 0° to 17°C.

Modeling Anthesis Date

Data were first assembled in DSSAT 3 format, a predecessor of the ICASA format for data interchange (Hunt et al. 2001). Each model was calibrated for the two cultivars using the data for 1985 (HD 2329) or 1988 (PBW 34) and then validated using the 1989 data. Standard parameters for goodness of fit were calculated to facilitate comparisons of model outputs.

Results

Overview of Field Response

The effect of sowing date on time to anthesis indicates the contrast between HD 2329 and PBW 34 (Figure 3).

For the 25 December planting, both cultivars behaved similarly. However, HD 2329 flowered much earlier than PBW 34 in earlier plantings. A simple qualitative explanation for this pattern is that flowering of PBW 34 was delayed in early sowings due to a vernalization response. Later flowering of HD 2329 with intermediate sowing dates could reflect either cooler temperatures or a sensitivity to short days.

Modeled Response

CERES Wheat

In calibration of CERES Wheat for HD 2329, the best fit between observed and simulated data was obtained by assuming that there was no vernalization response (P1V = 0) and a slight sensitivity to photoperiod (P1D = 2.0). Allowing for even a small vernalization requirement resulted in excessive delay in time to anthesis at early dates. In contrast, the best fit for PBW 34 required a moderate vernalization (P1V = 1.8). Determining the correct photoperiod response for PBW 34 proved problematic because CERES uses the minimum value of the two rate modifiers (i.e., for vernalization and photoperiod, Eq. 1). There was no effect for values of P1D from 0 to 2, but a value of 2.5 resulted in a slight improvement if combined with a shorter phyllochron interval (PHINT = 92).

The summary statistics for model performance of CERES Wheat suggest considerable room for improvement (Table 1). Figure 4 shows partial results of a sensitivity analysis where P1V was given values of 0, 1.0, 1.5 and 2.0, and P1D was varied from 0 to 3.0 in steps of 0.5. With no vernalization effect (P1V),



Figure 3. Effect of sowing date on days to anthesis in 1989 for cvs. PBW 34 and HD 2329. Based on data of Dhillon and Ortiz-Monasterio 1993.

increasing photoperiod sensitivity delays anthesis by 20 to 25 days (Figure 4A). Adding a vernalization effect overrides the possible effect of low photoperiod sensitivity (e.g., Figure 4B, C and D). This reflects the use of a minimization function in Eq. 2, in which only the stronger of the two processes affects development. Our understanding of the physiology of flowering indicates that vernalization and photoperiod are two separate processes that affect reproductive development. It is difficult to envisage a physiological justification for the minimization function.

An additional concern is that the photothermal time from emergence to terminal spikelet formation is fixed at 400 growing degree days. This implies that there is no difference in inherent earliness (earliness per se) of wheat cultivars, which is also not supported by data for wheat given vernalization treatments and grown under warm temperatures and long photoperiods (e.g., Midmore et al. 1982). Reducing the phyllochron interval (PHINT) will reduce time to anthesis but leads to unrealistic leaf numbers.

Table 1. Results of simulations of the duration sowing to anthesis for HD 2329 and PBW 34 for the calibration and validation runs of CERES-Wheat and Sirius.

	CER	ES	Sirius		
	HD 2329	PBW 34	HD 2329	PBW 34	
Model coefficients					
Vernalization	0	1.8	0	0.22	
Photoperiod sensitivity	2.0	2.5	0.2	0.25	
Phyllochron	95	92	100	100	
Calibration					
r ²	0.69	0.92	0.81	0.48	
Slope	1.58	1.55	0.62	0.71	
Intercept	-58.8	-30.6	34.9	30.6	
MAD	4.7	4.2	4.7	6.9	
RMSE	6.4	4.9	5.3	9.0	
No. observations	7	10	7	10	
Validation					
r ²	0.94	0.74	0.95	0.40	
Slope	1.28	1.44	0.86	0.44	
Intercept	-32.0	-39.8	11.9	58.6	
MAD	6.4	4.3	1.9	5.0	
RMSE	6.8	5.2	2.1	7.1	
No. observations	8	8	8	8	

Note: The meaning of the calibrated model coefficients vary between the two models, and the coefficients are not quantitatively comparable across models. The calibration and validation parameters are: $r^2 =$ proportion of variance in Y (observed) that is explained by X (simulated); MAD = mean absolute difference; RMSE = root mean square error.



Figure 4. Sensitivity analysis for days to anthesis with CERES-Wheat using varying sensitivity to vernalization (P1V) and photoperiod (P1D). Simulations are for 1989-1990 weather data at Ludhiana.

Sirius

Calibration of HD 2329 assumed no vernalization response. In the absence of other information, the phyllochron was chosen at a midrange value of 100 °C days. The experiment site is at latitude 30.9°N, and daylength variation over the range of sowing dates used was small (10.0 to 12.7 h). This rules out daylength variation as a major cause of variation in the duration sowing to flag leaf emergence. With no daylength response (i.e., a fixed FLN of 8), anthesis was systematically predicted early. Setting the daylength response parameter SLDL at 0.2 leaves/hr resulted in the addition of nearly one further leaf and gave a close match between simulated and observed anthesis date (Table 1). Variation in predicted FLN over the range of sowing dates in either the calibration or validation datasets was only about 0.2 leaves, equivalent to about 20°C days or about one day. The predictions provided a very close match to observed anthesis dates in the validation dataset.

The situation with PBW 34 was quite different. In contrast to HD 2329, the variation in the interval sowing-anthesis implied substantial variation in FLN. Because of the small variation in daylength, this could only be associated with a vernalization response. Use of vernalization parameters typical of European wheats resulted in systematic, very late prediction of anthesis. The phyllochron, as with HD 2329, was set at 100 °C days. SLDL was chosen so that FLN would be about nine, with vernalization saturated by emergence. Insufficient vernalization would then add further leaves to increase the duration. The best value for VBEE (0.22/day) provided a good fit for the later sowings, but the errors in anthesis prediction for the early sowings were large and both early and late. The performance of the model in this situation was substantially inferior to the less mechanistic but more conservative approach used by CERES-Wheat. This bears further investigation.

Sirius simulations were run for the 1989 dataset with FLN adjusted so that the simulated anthesis date matched the observed anthesis date for each run. This FLN was then designated as "observed." If the actual phyllochron had been larger or smaller than assumed, these values of FLN woul have been systematically high or low, but the pattern of change would have been preserved. These values were then compared with FLN predictions using the parameter values from the calibration (Figure 5). In this set, there were five very close matches of simulated FLN observed, as well as one substantial overestimate and two substantial underestimates. These corresponded with the large errors in estimated anthesis date. Note that the pattern of variation was systematic, with the overestimate of FLN derive from an early sowing and the underestimates from later sowings. Both observed and predicted FLNs for the late sowings were close to nine leaves, and indicated that the vernalization requirement was satisfied very early–probably by emergence.

The errors in the predictions of FLN led to some odd behavior in the simulations. The predicted anthesis date for the second sowing was substantially later than those predicted for the next two later sowings.

It is clear that, as far as simulation is concerned, the Ludhiana environment is on the edge of vernalization effectiveness. Any error in assumptions about the upper limiting temperature for vernalization response is likely to have a large effect. In Sirius this temperature is set at 17°C, but the maximum daily temperature during the wheat growing season was always greater. Vernalization then relied on the fact that minimum temperatures were less than 17°C for a portion of the season. Coupled with the small vernalization requirement of the cultivar, this meant that the slight differences in temperature regime associated with different sowing dates can lead to significant differences between simulation results and what is observed in nature. The environment is a severe test of vernalization models, and the dataset is extremely valuable for that reason alone.



Figure 5. Comparison of Sirius simulated final leaf numbers with those observed for PBW 34 in 1989.

Conclusions

The simulation exercises highlight the potential impact of vernalization and photoperiod sensitivity with early plantings in rice-wheat systems of South Asia. They suggest that once-popular cultivars such as HD 2329 and PBW 34 would differ markedly in their response to early sowing due to simple genetic differences for vernalization and photoperiod genes. The data set of Dhillon and Ortiz-Monasterio contains data for 32 cultivars in series of experiments involving seven to ten plating dates over seven years with varying numbers of cultivars each year. This information represents a valuable source of data for unraveling this problem further. Furthermore, if the data set can be linked to more complete information on crop management (e.g., probable times of irrigation), the set could serve as a foundation for relating the genetic effects to grain yield.

The results also indicate that the development routines in CERES-Wheat and Sirius require revision. In CERES, the use of a minimization function for determining effects of vernalization and photoperiod appears unrealistic and makes calibration difficult. Furthermore, in order to predict leaf number accurately and reflect cultivar differences with respect to inherent earliness, the total photothermal time from emergence to double ridge formation should be a variable rather than a constant value of 400 GDD, as is currently assumed.

Prediction of anthesis dates for spring wheat cultivars with Sirius is satisfactory. However, a problem exists simulating vernalization effects for wheat cultivars in certain environments. These environments are those where temperatures are in the upper range of vernalization effectiveness and, for at least some of the time during early development, daily temperature ranges either span the upper limit or are entirely outside it. Solving this problem will require, at least, a sensitivity analysis of anthesis date prediction to variation in the upper temperature limit and the shape of the temperature response.

Both approaches had problems dealing with vernalization in this environment. We again emphasize that data from such environments are an extremely valuable resource because they provide a severe test of the assumptions assembled in simulation models. Only through exposure to such testing situations will advances in our understanding be made.

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Short Description of the Model Statistical Package and Weather Analogue Program

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Abstract

To facilitate model validation and adaptation in the Highveld Ecoregion Project, two software packages were developed. The Model Statistical Package (MSP) uses standard outputs of CERES-Maize 3.0 to calculate indicators of model accuracy, including the linear regression statistics (slope, intercept, and r²), D-index, and the systematic and unsystematic mean square errors. The Weather Analogue Program (WAP) allows users to create mid-season projections of crop performance based on the five sets of historical weather that show the greatest similarity to the ongoing season.

Introduction

The Highveld ecoregion of southern Africa is an important producer of rainfed maize but its highly variable rainfall patterns present a major challenge to producers. Simulation models offer various possibilities for guiding farmers on managing production risk. Two objectives of the Highveld Ecoregion Project¹ are "to validate existing ICASA models and adapt them to be applicable for agricultural systems in the Highveld Ecoregion." To facilitate model testing and application of models in the Highveld region, two software tools were developed to analyze outputs from the DSSAT group of models. These two tools were the Model Statistical Package (MSP) and the Weather Analogue Program (WAP). This paper describes these two tools, using CERES-Maize v3.0 as part of DSSAT models (Hoogenboom et al. 1994) to illustrate the software features. Such tools would also be of great use in evaluating proposed improvements in the temperature response of crop models.

The CERES Model

CERES models for maize, sorghum, wheat, millet, and barley have been combined, resulting in a generic

multi-crop CERES3. This version runs from a single executable fileset of code, incorporating the development and growth sections for each individual model into a single module with a single soil component (Tsuji et al. 1994). According to Ritchie (1991), generic models should allow users to follow more uniform procedures for validating models and for linking them with components not included in the generic model. The generic CERES3 (Hoogenboom et al. 1994) was used for the simulations, with modifications as reported by Du Toit (1996).

Model Statistical Package

In order to verify and calibrate a model, well-defined criteria are needed to evaluate model performance. It is generally accepted that the ultimate test of a simulation model is the accuracy with which it describes or mimics the actual system, usually involving comparisons between simulated and observed data (Willmott 1982; Jones and Kiniry 1986; Oreskes et al. 1994). A number of statistical methods for analysing model performance are available. These include linear regressions techniques as proposed by Jones and Kiniry (1986) and Flavella (1992) and Dindex, systematic and unsystematic mean square errors as proposed by Willmott (1982).

¹ Funded by the Ecoregion Fund Managed by ISNAR

Jones and Kiniry (1986) used linear regression techniques of the form y = a + bx with simulated results as the independent variable. Good model performance was obtained when the intercept (*b*) approached zero and the slope of the regression approached unity, indicating a near perfect relationship between observed and simulated values. Complementary to this regression, the Pearson correlation coefficient (R) can also be calculated, indicating the similarity or inverse similarity of a response in *y* for a response in *x*. The coefficient of determination (r²) is readily calculated from R, signifying the percentage of variation that is accounted for by the model.

The deficiencies of the latter statistical parameters were pointed out by Willmott (1982) and Harrison (1990). They indicated that the observed and simulated data might occur in a narrow band, whereas this is usually not the case with the coefficients. Secondly, although significance levels can be calculated, it is difficult to identify the point when a model is valid or not valid. Savage (1993) further warned against the use of a correlation coefficient if the data are not randomly distributed.

The D-index (index of agreement), RMSEs (root mean square error systematic), RMSEu (root mean square error unsystematic) and RMSE (root mean square error) are four indicators that Willmott (1982) recommended for model evaluation. Due to limitations in the use of correlation coefficients as an agreement index, Savage (1993) stated that the statistics as defined by Willmott (1982) should be used instead.

According to Wilmott (1982), the D-index of a "good" model should approach unity and the RMSEs approach zero, whereas the RMSEu should approach the RMSE. The mean absolute error (MAE) and RMSE are among the best overall measures of model performance, as they summarise the mean difference in the units of observed and predicted (Willmott 1982):

$$MAE = N^{-1} \sum_{i=1}^{N} |Pi-Oi|$$
 Eq. 1

RMSE =
$$\left[N^{-1}\sum_{i=1}^{n} (Pi-Oi)^{2}\right]^{0.5}$$
 Eq. 2

N is the number of observed values and Oi and Pi are observed and predicted values for the *i*-th data pair. The systemic and unsystemic RMSE require

calculating the intercept (a) and slope (b) of the least-squares regression, $^{P} = a + b0$ Pi (Willmott 1982),

RMSEs =
$$\left[N^{-1}\sum_{i=1}^{n} \left(\hat{P}i - Oi\right)^{2}\right]^{0.5}$$
 Eq. 3

$$RMSEu = \left[N^{-1}\sum_{i=1}^{n} \left(Pi - \hat{P}i\right)^{2}\right]^{0.5} Eq. 4$$

where Pi is regarded as the best estimate of the predicted quantity (Savage 1993). The advantage of RMSEs is that it indicates the bias (deviation of the actual slope value from the 1:1 line) in a particular model, instead of the random variation (RMSEu) that may occur (Savage 1993). Willmott (1982) proposed an "index of agreement" (D) of the form:

$$D = 1 - \left[\sum_{i=1}^{n} (Pi - Oi)^{2/2} \sum_{i=1}^{n} \left(P'i + O'i \right)^{2} \right]$$
 Eq. 5

where P'i = Pi - O (average of the observed) and O'i = Oi - O. The index (D) is intended to be a descriptive measure. It is also both a relative and bounded measure, which can be widely applied in order to make cross-comparisons between models (Willmott 1982)

Observed vs. simulated graphs, also known as 1:1 graphs, are widely used in simulation evaluations (Willmott 1982; Jones and Kiniry 1986). Harrison (1990) recommended that it is appropriate to combine whatever statistical method is used with a 1:1 graph since it may be particularly helpful in identifying the pattern of differences between the predicted and observed values.

The MSP software reports all of the above-mentioned statistical parameters using the "MAIN GROWTH AND DEVELOPMENT VARIABLES" provided in the file Overview.out by comparing the predicted with the measured values as indicated in Table 1. The measured values are then subtracted from the predicted values; the difference is the error or residual. A correlation matrix is calculated between the error and each of the 50 predicted environmental and stress factors as indicated in Table 2. The correlation matrix is presented as a regression matrix table by MSP as indicated in Figure 1.

Table 1. Main growth and development variables in the Overview.out file as output from a model run with CERES3.

0	VARIABLE	PREDICTED	MEASURED	
	FLOWERING DATE (dap)	81	-99	
	PHYSIOL. MATURITY (dap)	160	-99	
	GRAIN YIELD (kg/ha)	5882	5853	
	WT. PER GRAIN (g)	0.4016		
	GRAIN NUMBER (GRAIN/m2)	1237		
	GRAINS/EAR	824.99		
	MAXIMUM LAI (m2/m2)	1.20		
	BIOMASS (kg/ha) AT ANTHESIS	2441	-99	
	BIOMASS N (kg N/ha) AT ANTHESI	0	-99	
	BIOMASS (kg/ha) AT HARVEST MAT.	8244		

Table 2. ENVIRONMENTAL AND STRESS FACTORS in the Overview.out file as output from a single run with CERES3.

ENVIRONMENT-		-STRESS-		-		-			
-DEVELOPMENT PHASE	-TI	IME-		WEATHER-		- WA1	ER-	- NIT	ROGEN-
	DURA TION days	TEMP MAX OC	TEMP MIN oC	SOLAR RAD MJ/m2	PHOTOP [day] hr	PHOTO SYNTH	LEAF EXPAN.	PHOTO SYNTH	LEAF EXPAN.
Emergence-End Juvenile	15	28.27	11.67	20.86	13.47	0.000	0.000	0.000	0.000
End Juvenil-Floral Init	7	25.90	12.90	22.23	13.64	0.000	0.000	0.000	0.000
Floral Init-End Lf Grow	49	22.62	13.10	22.68	13.72	0.000	0.000	0.000	0.000
End Lf Grth-Beg Grn Fil	16	25.45	12.31	20.63	13.37	0.000	0.000	0.000	0.000
Grain Filling Phase	62	23.05	13.60	21.18	12.38	0.000	0.000	0.000	0.000

🛢. Statistic	al Evalua	tion								
File Crop	View Text File	e Readme								
					G	RAIN YIELD	(kg/ha)			-
					<u>г</u>		Observed	Simulated	Clic	k Here To
					N	4inimum -	781	5	55 Vie	ew Graph
					N	/laximum	4399	56	56	Graph
					N	/lean	3540.2	413	1.2	Graph
					9	Std Dev	1379.60	2287.	20	
					0	V	38.97	55.	36	
					9	olope		1.	38	
					- I	ntercept		-757.	11	
					N	4AE		91	7.4	
					F	RMSE		1013.	84	
					F	RMSEs		7	97	
					F	RMSEu		626.	63	
					0)-Index		0.	91	
					r	2		0.	91	
				Regres	sion					
		Enviro	nment			St	ress			
	Time		We	ather		{ \/	Vater		Nitrog	en
Phase	Days	Temp max	Temp min	Solor Rad	Photo	p Photo S	iynth Gro	wth Ph	oto Synth	Growth
End juvenile	0.0195	0.2331	0.0195	0.1884	1	0.000	01 0.9	305 ().0001	0.0001
Floral Init	0.5139	0.0391	0.8345	0.4896	0.836	7 0.000	0.0	001 (0.0001	0.0001
L Growth	0.9982	0.829	0.0314	0.433	0.844	2 0.552	28 0.5	994 ().0001	0.0001
Grn Fil	0.7298	0.0412	0.0002	0.028	0.884	1 0.939	92 0.9	547 (0.0001	0.0001
Filling phase	0.7198	0.6626	0.6807	0.8619	0.999	9 0.759	94 0.8	011 (0.0001	0.0001

Figure 1. Output of the MSP to indicate the statistical parameters and relationship between the environmental and stress factors and the difference between the observed and the simulated.

Weather Analogue Program

The Weather Analogue Program (WAP) was developed to assist seasonal predictions modeled for a given site. WAP uses an analogue methodology whereby the most current weather conditions of the present season are compared to the five best fitting historical seasons in the database. The information is then presented in the form of a graph and a table. The search algorithm uses the "index of agreement" (D) as represented in Eq. 5 (Willmott 1982) but compares daily weather data instead of observed or simulated crop performance. Each season is presented as the simulation output of a model with the current season as the observed values. Figure 2 shows the graph indicating the two closest years. Although they are presented as cumulative values, the search algorithm uses non-cumulative data.

The data are indicated as cumulative on the graph to help with interpretation. WAP finds the five models that best fit the weather data of the current season as indicated in Figure 3.

This program has a user-friendly spreadsheet interface for data input and stores data in standard DSSAT v3 and 3.5 ASCII format. The most recent data of the current season are appended to the historical weather datasets as indicated in Figure 4.

The program also exports five files, consisting of the most recent weather data from the current season combined with daily data for the five analogue years that are used to complete the season. The program can be run via the keyboard or from an ASCII file used within a GIS framework.

CERES runs from a control file that describes the experimental simulation trial. For South Africa, such a trial consisted of six plantings at two-week intervals in combination with super short, short, medium and long growing season cultivars. All of these were in combination with a low, medium, and high plant population. Each of these treatments was then run for all five of the analogue weather files exported by WAP (Figure 5).



Figure 2. The current season in comparison with the two closest analogue years.

1 63 68.81892 2 76 66.31044 3 96 65.9582 4 87 65.11074 5 60 61.09431
2 76 65.31044 3 96 65.9582 4 87 65.11074 5 60 61.09431
4 87 65.11074 5 60 61.09431
5 60 61.09431
Avg 750,4878
Stand Dev 116.7275
Highest 75 1156.202
Lowest 68 455.9016

Figure 3. The five closest analogue years and weather statistics.

<u>F</u> ile							
Data Ar	nalogue <u>G</u> raph	Grid					
[<u>Y</u> ear: 1	Season C 1 Ju C 1 Jar	start at Manuary	save	Aria -	Add Sjiv H 00-01	•
Day	Year/Day	SRAD	TMAX	TMIN	RAIN	DEWP	W
Jul 1	00183	016.4	018.8	002.5	000.0		
Jul 2	00184	011.2	018.5	-01.0	000.0	1	
Jul 3	00185	008.9	019.0	-01.8	000.0		
Jul 4	00186	009.7	019.3	-01.5	000.0	Į.	
Jul 5	00187	012.2	017.0	-01.5	000.0		
Jul 6	00188	012.6	019.5	-02.5	000.0	1	
Jul 7	00189	012.5	018.8	001.5	000.0		
Jul 8	00190	013.1	018.0	-01.5	000.0	<u></u>	
Jul 9	00191	013.0	017.7	-01.4	000.0		
Jul 10	00192	015.4	018.9	-00.6	000.0	1	
Jul 11	00193	013.9	017.7	-01.6	000.0	<u>[</u>	
Jul 12	00194	013.6	019.5	-01.6	000.0		

Figure 4. Spreadsheet type interface for data input, indicating both calendar date and Julian date.

Both programs have been included as tools for DSSAT4 and will be distributed with the DSSAT4 software. For DSSAT3+ users the two programs can be obtained via D.L. du Toit.



Figure 5. Flow diagram for the WAP crop growth simulation framework.

Conclusions

Both programs are distributed in 18 countries worldwide and over 100 requests for the programs have been received. WAP has been installed on a number of farmers' and consultants' computers in South Africa. It was also included in the yield estimate methodology of ARC-GCI. MSP and WAP have been included and released as utility software for DSSAT 4. Both programs are available from either author and are distributed free of charge. Please send an email to either Deon@igg2.agric.za or ADToit@mail.ifas.ufl.edu for more information.

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Report of the GCTE Tropical Cereals Network Inaugural Workshop¹

A.S. Du Toit, John Ingram, and Jeffrey W. White

Background

The inaugural workshop of the GCTE Tropical Cereal Network was held at CIMMYT Headquarters, Mexico on Thursday 26–Friday 27 April 2001. It was convened in association with the CIMMYT workshop Modeling Temperature Response in Wheat and Maize held 23-25 April 2001.

The objectives of the GCTE Tropical Cereals Network are:

- To refine and adapt current crop production models for tropical cereals for use in global change studies in a wide variety of conditions.
- To design and undertake experiments to provide improved mechanistic understanding of global change impact on crop production, in order to aid in model development.

The Network is envisioned to initially include studies on maize, sorghum, and millet. Modelers and experimentalists will be given equal importance in achieving the objectives.

The primary objective of the GCTE workshop was to establish the inaugural Network membership. To this end interested scientists were invited to present models and datasets suitable for model development.

Standardized descriptions (metadata) of models and datasets, which will be included as inaugural contributions to the Network, will be collated and published on the GCTE Focus 3 web site. The inaugural set will be submitted to the GCTE Scientific Steering Committee for endorsement as GCTE Core Research.²

The workshop organizers wish to acknowledge and thank CIMMYT for its support in convening and hosting the workshop.

Meeting Report

Thursday 25 April

Opening

Professor Tim Reeves (then Director General of CIMMYT) opened the proceedings and indicated the need to increase food supply in order to meet projected demands in coming decades. He emphasized the need to refine agricultural systems in order to match the high levels of productivity seen in developed countries without jeopardizing the natural resource base.

Tony Hunt presented a flow diagram showing where this meeting fit within the wider GCTE framework. It was agreed that the nascent GCTE Tropical Cereals Network would be led by Andre du Toit, with Bill Batchelor, Richard Vanderlip, and Upendra Singh acting as coordinators for maize, sorghum, and millet, respectively. These four, together with Jeff White, representing CIMMYT, would constitute the GCTE Tropical Cereals Working Group.

¹ Also published as GCTE Working Document 28. http://mwnta.nmw.ac.uk/GCTEFocus3/networks/tropical.htm

² Please see the GCTE web site (<u>http://mwnta.nmw.ac.uk/gcteFocus3/</u>) for more information about GCTE Focus 3: Agroecology and Production Systems, and about the Crop Networks in particular.

Session 1: Collation of models for maize, sorghum, and pearl millet

An informal review of models available for the target crops identified numerous examples, as summarized in Table 1.

Session 2: Developing metadata for models and data

There is a need to document models and differences in models, and it was agreed to base these efforts on the format developed for the GCTE Wheat Network. An additional field in the documentation, Model Differences, is also needed to describe differences between versions of the same model. Thus, CERES-Maize would have a single metadata description while variants of the model would be presented on a form that stated the contact individual, and highlighted or listed changes between CERES-Maize and the modified version.

Session 3: Data availability and describing data quality

Key individuals were identified as possible contacts for data (Table 2).

Table 1. Crop simulation models identified dealing with maize, sorghum or pearl millet.

Maize	Sorghum	Pearl Millet
CERES-Maize (official release) (Du Toit, Batchelor, Dardanelli, Algarswamy) CERES-Grignon (Roche) CAMS-Maize v 2.0 (Wang Futang) APSIM (Keating) Maize calculator (Jamison) Tom Sinclair's model Cropsys (Stockle) Sucros (Goudriaan) GPFARM (McMaster) STICS (Brisson) MAIS (Tolenaar) Cropsim (Hunt) Stewart model (Stewart) EPIC/ALMANAC (Kiniry) EPIC (Williams)	CERES-Sorghum (IFDC) CERES-Grignon (Gabrielle) SORKAM (Vanderlip) APSIM (G. Hammer) WINSORG (M.M. Martin) EPIC/ALMANAC GPFARM RESCAP (S. Huda)	CERES-Millet (IFDC) APSIM (Carberry) EPIC/ALMANAC

Note: Names in parentheses indicate developers or key contacts.

Indicating data quality

A section for data describing quality needs to be added to the metadata files. Several entries will be requested from the data contributors, along with several entries from model testers.

Quality Section

- SD (standard deviation) for yield and other traits
- Mean for yield and other traits
- Comments on data quality from data collector
- Consistency of data: what are the three strongest and weakest features of the data?
- Lack of model fit and causes for lack of fit
- Consistency among components (seasonal trends, water content trends, etc.)

Session 4: Evaluating models using datasets and error plots

Model Performance Using Actual Data

This analysis will be highly dependent upon what data are contributed to the group. Four types of validation are envisioned:

 Development performance – The purpose of this analysis would be to test the model's ability to capture the impact of climate on plant development. Several datasets that represent diverse environments

Table 2. Possible sources of data for evaluating crop models.

Maize (Batchelor, leader)	Sorghum (Vanderlip, leader)	Pearl Millet (Singh, temporary leader)
CERES list	ICRISAT	ICRISAT
(Batchelor)	(S. Huda, Vanderlip)	(S. Huda, Algarswamy)
CIMMYT (Risk	Kansas (Vanderlip) ¹	Kansas
Management		(Vanderlip)
Project; White)		
French data	APSIM	W. Africa
(Romain)	(Hammer)	(Kropff)
FACE Maize CO2	European Network	APSIM
experiment in	1 and 2	
Illinois (Long)	(Gabrielle, M. Martin)	
New Zealand data	INTSORMIL	C02
(Jamieson)	(Vanderlip)	(Bidinger and Vanderlip)
CIMMYT Maize Program	FACE (Kimball)	
APSIM data? (Keeting)	DSSAT data	
	(v. 3.5) (Singh)	
Canada (Tolenaar)		
Texas (Kiniry)		
Argentina (Travasso)		
¹ Mainly US data		

and that have good measurements of phenological events would be selected. The model would be run to determine the accuracy with which it can predict these events. The graph generated as a result would illustrate % error vs. measured phenological data (i.e., anthesis date, etc.). The specific phenological data selected would depend upon the data measured in the dataset.

- 2. Growth performance The purpose of this analysis would be to test the model's ability to capture the impact of climate on plant growth. Several datasets would be selected for analysis. These datasets would represent diverse environments and would have good measurements of growth characteristics, including final yield and biomass at harvest. After running the model, a plot of % error vs. data (i.e., yield, biomass, etc.) would be generated.
- 3. *Temporal performance* The purpose of this analysis would be to test the model's ability to capture the impact of climate on temporal plant growth. The model would be run for several datasets that have time series measurements of growth, and a plot of predicted and measured data (i.e., leaf, stem, seed, pod weights) vs. time would be generated for each experiment.
- 4. Water stress performance The purpose of this analysis would be to test the model's ability to respond to water stress. The model would be run for several datasets with irrigated and non-irrigated treatments. Percent error plots would be generated for any measured data.

Statistics such as RMSE, D, and r^2 could be used as indicators of accuracy for all four analyses.

Sensitivity Analysis to Climate Factors

The purpose of this analysis would be to demonstrate the general response of key model outputs to changes in climatic inputs, including daily temperature, $CO_{2'}$ daylength, and drought.

 Temperature – A dataset would be selected and the model would be run with the daily temperatures found in the dataset. A sensitivity analysis would then be conducted by modifying the daily temperature by ± 5°C. Results to be plotted include duration to flowering, duration from flowering to physiological maturity, total biomass at harvest, and yield as a function of daily temperature change.

- 2. Carbon dioxide A dataset would be selected and the model would be run with the CO_2 levels found in the dataset. A sensitivity analysis would then be conducted by modifying CO_2 levels over a certain range. Results to be plotted include duration to flowering, duration from flowering to physiological maturity, total biomass at harvest, and yield as a function of CO_2 .
- 3. Daylength A dataset would be selected and the model would be run with the weather data for a given cultivar found in the dataset. A sensitivity analysis would then be conducted by modifying parameters that affect daylength response while changing the latitude in the weather file. Results to be plotted include duration to flowering, duration from flowering to physiological maturity, total biomass at harvest, and yield as a function of the daylength and latitude parameter.
- 4. Drought A dryland dataset that shows drought effects would be selected and the model would be run with the weather data for a given cultivar found in the dataset. A sensitivity analysis would then be conducted by modifying rainfall over a range of ± X%, as well as including a fully irrigated treatment. Results to be plotted include duration to flowering, duration from flowering to physiological maturity, total biomass at harvest, and yield as a function of cumulative rainfall or water available in the season.

Standard Output File

A standard output file could be created by each model to facilitate developing the graphs discussed above. This file would have the following information:

- Anthesis date
- Physiological maturity date
- Biomass at maturity
- Yield
- Level of the factor used for the sensitivity analysis
- Some identification of the dataset

Session 5: Model runs for different experiments and sensitivity analysis

Datasets from Hawaii and South Africa were supplied by Upendra Singh of IFDC and Andre du Toit of ARC-GCI, respectively. These data represent tropical and semi-arid environments and include low- to highwater stress environments. It became evident from the exercise that there is a need to revisit the definition on physiological maturity and clarify any possible confusion in this regard. The simulations should be seen as a starting point and a practical indication of possible problems. The experiments took longer to set up than expected, and it became evident while running the experiments that it was quite easy to use the wrong soil and genotype input files. While it is clear that more analysis will be needed before it will be possible to indicate model differences, the exercise proved valuable in launching the process and identifying where more work is needed.

Friday 27 April

Session 6: Next steps/actions

Meta-database for crop growth experiments

The meta-database should include a further question (Q15), "What do you consider to be the strongest (and weakest) points of this experiment/dataset?" Respondents should follow the standard GCTE format provided (GCTE Crop Networks: Metadata format for crop growth experiments) and return information to crop coordinators by 15 May. If a full report is not feasible, at least a preliminary report could be sent. Crop coordinators are to follow up with contributors and/or the contacts for the datasets.

Metadata sets

Potential contributors for metadata were identified as:

Maize (Leader Bill Batchelor)

CERES-Maize standard data (15)

Contributors/contacts for other datasets:

Jeff White, Peter Jamieson, Steve Long, Maria Travasso, Romain Roche, B. Keating, J. Kiniry, T. Tolenaar, Jorge Bolaños

Sorghum (Leader Richard Vanderlip)

- CERES-Sorghum standard data (2) Contributors/contacts for other datasets: Richard Vanderlip, S. Huda, B. Kimball, G.
 - Hammer, Gabrielle, M. Martin, Scott Chapman

Millet (Leader Upendra Singh) Contributors/contacts for datasets: Richard Vanderlip, S. Huda, G. Alagarswamy, M. Kropff, F. Bidinger, APSIM.

Meta Database for Crop Growth Models

Respondents should follow the standard GCTE format provided (GCTE Crop Networks: Metadata format for crop growth models). For different versions of models, or for models derived/developed from an existing model, the appropriate contact person and the major differences from the original model should be indicated. In addition, the model itself (in the form of an .exe file with user instructions) should be provided to crop coordinators for independent model runs, etc.

General Actions for Network and Crop Coordinators

- Invite other modelers to participate in the network (Network Coordinator)
- Send friendly reminders, provide pressure, etc. to get datasets from contributors/contacts
- Send datasets that meet MDS requirements to participating modelers
- Set established procedures for data and model evaluation
- Distribute results of model performance, sensitivity analyses, and quality checks among members
- Discuss above progress in approximately 12 months

Topics for Next Meeting

- Formalizing the structure of network with all participating members
- Constraints to progress
- Examination of procedures for ongoing model evaluation
- Gaps in data coverage
- Funding of data collection when there is no member in a region
- Funding for less popular crops (ie, millet)
- Funding of members from developing countries

Network Members

A few points were noted regarding potential Network Members:

- Membership would be comprised of volunteer/ invited experimenters and modelers who value the scientific interactions and relationships that develop in the Network. These activities would offer opportunities for publications.
- Being voluntary, the priority given to Network activities may be low, and deadlines may not be met on time.
- The long-term membership will comprise of a highly motivated group that views the benefits as outweighing the additional time commitment.

Session 7: Outcomes from GCTE Tropical Cereals Working Group meeting

The indications are that the GCTE Tropical Cereals Network will initially consist of about 15 members.

Specific actions include:

- 1. Andre du Toit will set up a web page to host the different datasets. The web page will be password protected.
- 2. Jeff White will put a map together to indicate the spatial distribution of the different data points.

- 3. The next workshop was to be held at CIMMYT within 12 months time, with ICRISAT as an option for a meeting venue in 2003. However, due to changes in GCTE Focus Group 3 management, the 2002 workshop was not held.
- 4. The next meeting will complete the present work and start looking at tillage-climate interactions.

Participants: See combined list for CIMMYT Modeling Workshop and GCTE Workshop.

Note: Full details on how to apply to join the gcte tropical crops network, as well as downloadable forms, can be found on the GCTE Focus 3 web site: http://mwnta.nmw.ac.uk/ GCTEFocus3/networks.htm.

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