

# A Structured Procedure for Assessing How Crop Models Respond to Temperature

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## ABSTRACT

Crop simulation models are widely used to analyze temperature effects on crop growth, development, and yield. Unfortunately, temperature responses of models often are not examined critically to ensure that a model is appropriate for a given research application. This paper describes a procedure for assessing how models respond to temperature. The procedure treats major processes in a balanced fashion but does not require access to source code. The results are easily interpretable by nonmodelers and readily documented and employed with different models. Sensitivity analyses are run using standardized conditions of nonlimiting water and N with regimes of constant mean temperatures from 3 to 40°C and daily range of 10°C. Daily model outputs define responses that are grouped in seven categories: crop mass (including economic yield), phenology, reproductive growth, canopy development, root growth, resource use efficiency, and water balance. To avoid interactions of duration of life cycle with growth, several responses are assessed before partitioning to reproductive growth reduces total aboveground biomass. Emphasis is on graphical analysis of individual variables vs. mean temperature, but cardinal temperatures and a response index are also estimated. When applied to the CSM-CERES-Sorghum and CSM-CROPGRO-Drybean models, the procedure readily identified differences in temperature adaptation of the two crops. Various examples were found where modeled responses appeared to differ from data from field or controlled-environment studies. The proposed procedure will require adjustments for specific situation but provides a foundation for assessing modeled responses to temperature in a structured and reproducible fashion.

PROCESS-BASED SIMULATION models are widely used to analyze crop response to environment in situations where variation in temperature has a major influence on growth and development. Examples of applications include global warming (e.g., Mearns et al., 1999; Alexandrov and Hoogenboom, 2000; Jones and Thornton, 2003), crop response to sowing dates (Acosta-Gallegos and White, 1995; Hunt et al., 1996), characterizations of production environments (Chapman et al., 2000), and regional targeting of technologies (Hartkamp et al., 2004).

Ideally, any temperature response incorporated in a model should be derived from well-documented field, controlled environment, or laboratory measurements. In practice, development of crop models involves numerous approximations and extrapolations, often because data from appropriate experiments do not exist.

Response functions and parameters must then be adapted from other crops or obtained from unrepresentative experimental conditions. Temperature studies are also subject to methodological constraints. While temperature per se is easily measured, ensuring that the observed temperature is representative for the process being examined (e.g., leaf formation, photosynthesis, respiration, or reproductive development) is often difficult, and the measurement process itself may introduce artifacts (Ritchie and NeSmith, 1991; Ehleringer, 1991). In controlled environments, temperature treatments often are adjusted in abrupt steps during the diurnal cycle, are limited in number, and result in humidity, radiation, and air speed regimes that are not found in field environments. Analyses of temperature responses may need to account for acclimation, diurnal cycles in responses, and confounding of temperature regimes with other environmental factors.

Thus, although models are widely used to examine crop responses to temperature (both explicitly and implicitly), modeled responses are less robust than one might initially expect. Unfortunately, there are few specific procedures for evaluating temperature responses, and as noted by Carbone et al. (2003), users often apply models without investigating whether the model has been tested for the intended conditions. A frequent assumption appears to be that if a model is widely used, the temperature responses have been thoroughly tested, including for extreme conditions such as considered in global warming scenarios.

Simulation models can be evaluated through various procedures, among them sensitivity analysis, whereby model inputs are varied in a controlled manner and the modeled responses are analyzed. Sensitivity analysis is widely used in simulation modeling (Sargent, 1999), including for agricultural research (e.g., Annandale and Stockle, 1994; Hartkamp et al., 2002; Heinemann et al., 2002; Xie et al., 2003). Here, we build on previous use of sensitivity analysis by outlining and assessing a standardized procedure for using sensitivity analysis to characterize the temperature responses of models and their

**Abbreviations:** CGR<sub>50</sub>, crop growth rate measured at the reference date of 50 days after emergence; DAE, days after emergence; HI, harvest index; LAI<sub>50</sub>, leaf area index at the reference date of 50 days after emergence; NUE, nitrogen use efficiency; RSI, response stability index; RUE, radiation use efficiency; RUE<sub>50</sub>, radiation use efficiency at the reference date of 50 days after emergence; SLA<sub>50</sub>, specific leaf area at the reference date of 50 days after emergence; T<sub>base</sub>, base temperature; T<sub>max</sub>, maximum temperature; T<sub>opt1</sub>, first optimal temperature; T<sub>opt2</sub>, second optimal temperature; TCM<sub>anth</sub>, total aboveground crop mass at anthesis; TCM<sub>harv</sub>, total aboveground crop mass harvest; TCM<sub>30</sub>, total aboveground crop mass at reference date of 30 days after emergence; TCM<sub>50</sub>, total aboveground crop mass at reference date of 50 days after emergence; WUE<sub>ET</sub>, water use efficiency at the reference date of 50 days after emergence, based on evapotranspiration; WUE<sub>TR</sub>, water use efficiency at the reference date of 50 days after emergence, based on transpiration.

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underlying modules. The procedure is based on readily available model outputs, including yield and yield components, days to physiological maturity, and daily crop growth and N uptake

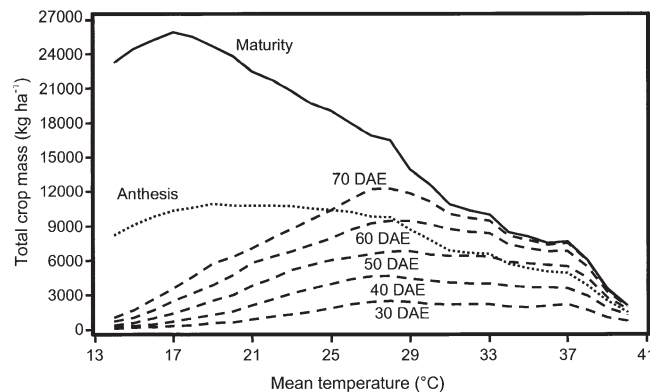
### CONCEPTUAL FRAMEWORK

The temperature response of a crop can be analyzed at levels of process detail ranging from molecular to field level, the latter potentially including interactions with pests, weeds, or pathogens. The proposed procedure focuses on responses at the whole-plant level since this scale is of principal interest to agronomists and these responses can be readily compared at this scale. Four premises underlie the recommended procedure. The first is that the analyses should provide a robust and balanced assessment of modeled responses, including not just yield but underlying processes. Second, the results of the procedure should be readily interpretable by nonmodelers who need to understand how models respond without having to analyze source code. A logical approach is to follow themes from whole-plant physiology such as growth, development, partitioning, and water and nutrient uptake and to use simple response functions to interpret the results. Third, to facilitate comparisons across models, the procedure should rely on outputs that are available from most crop models. Finally, the conditions simulated should be standardized and in a format that is easily documented and distributed, allowing other researchers to apply the procedure.

Initial assessments of crop response to temperature should focus on conditions where other resources are nonlimiting or constant across temperatures. Thus, the production conditions specified for the simulations provide constant mean temperatures with a 10°C diurnal range. It is assumed that no precipitation occurs, and daily global radiation is held constant across temperature regimes. Near-optimal levels of water and N are applied through irrigation and fertilization. While some models have options for running simulations without a soil water or N balance, to simulate nonlimiting production conditions, these options were not used to ensure that the modeled responses correspond to what would be obtained from simulating field experiments with varying water and N regimes.

Given that crop species differ substantially in their water and N requirements, especially with differences in crop duration, production conditions should be adjusted for each species—but should remain constant for comparisons across models for a single species or at least major cultivar groups. More problematic is how to select a representative cultivar, especially for crops where cultivars show large differences in duration (e.g., through thermal time requirements or photoperiod sensitivity). We suggest using reference cultivars that are photoperiod insensitive at 12 h daylength and, if required, adjusting the length of the crop life cycle to obtain values representative of commercial cultivars in major production environments.

To ensure a robust and unbiased assessment, the association between crop duration and biomass accumulation (e.g., Dalton, 1967; White and Singh, 1991) must be addressed. In the absence of constraints to season length, warmer temperatures hasten development, accelerating anthesis date and maturity, thus shortening the period for growth. While increased photosynthesis at warmer temperatures can reduce the effects of a shorter crop duration, warmer temperatures are usually associated with reduced yield. Focusing on grain yield, crop mass at maturity, or other parameters that are heavily influenced by phenology thus involves responses that are more complex than the basic effect of temperature on vegetative growth. The simplest approach to avoid the interaction between phenology



**Fig. 1. Response of total above ground crop mass to constant mean temperatures with a daily range of 10°C as simulated by CSM-CERES-Sorghum. Sample dates are for days after emergence (DAE) and for days to anthesis or maturity.**

and growth is to analyze total crop growth, measured as biomass on a dry weight basis (less roots for most crops), before partitioning to reproductive growth dominates overall growth. Thus, the procedure emphasizes responses measured when growth should be relatively unaffected by partitioning to reproductive growth. To identify this period for each model, temperature response curves for total aboveground crop mass at 10-d intervals from 30 to 80 d after emergence (DAE) are graphed for comparison [e.g., Fig. 1, which is based on simulations for sorghum [*Sorghum bicolor* (L.) Moench.] discussed in detail later]. The expectation is that the optimum temperature for growth will be higher, and constant, early in the season and shift toward a lower optimum as the temperature effect on reproductive partitioning becomes important. The most appropriate date to characterize growth independent of the effect of phenology thus is as late as possible but before effects of reproductive partitioning become important, this date being termed the “reference date.” Thus, in Fig. 1, at mean temperatures of 29°C or higher, crop mass at 60 DAE is greater than crop mass at anthesis, indicating that reproductive growth has begun earlier than 60 DAE, and 50 DAE is chosen as the reference date for sorghum.

Seven categories of responses that correspond to major processes of crop growth, development, and resource use are examined (Table 1). Responses are further characterized by cardinal temperatures corresponding to a trapezoidal response curve and an overall temperature response index, which are explained following the description of the categories.

The first category of responses concerns overall growth and includes total aboveground crop mass at harvest ( $TCM_{harv}$ ), the reference date of 50 DAE ( $TCM_{50}$ ), 30 DAE ( $TCM_{30}$ ), and anthesis ( $TCM_{anth}$ ), as well as grain yield in relation to mean temperature (e.g., Fig. 2A for simulations of sorghum). The second category is phenology. Effects on rates of development are often easier to interpret than effects on durations of developmental phases, so three phases (germination to seedling emergence, emergence to anthesis, and anthesis to maturity) are used to calculate rates as the inverse of phase durations for seedling emergence (sowing to emergence), vegetative development (emergence to anthesis), and reproductive development (anthesis to physiological maturity). To assess how crop mass and development interact, the relations between  $TCM_{harv}$  and grain yield vs. days to maturity are also examined (Fig. 2C).

The third category relates to reproductive growth. The main response of interest is the change in harvest index (HI) with temperature, but changes in total grain numbers, unit grain

**Table 1.** Variables used to characterize the temperature response of crop models. The “reference date” refers to a constant date after emergence selected as representative of rapid vegetative growth (before the onset of sufficient reproductive growth to slow overall growth) and had a value of 50 d after emergence (DAE) for both sorghum and common bean.

Variable	Units	Definition
<b>Crop mass</b>		
Grain yield	kg ha <sup>-1</sup>	grain yield at harvest maturity expressed on a dry weight basis, where harvest maturity is considered to be when crop has dried and/or defoliated sufficiently to allow harvesting with commercial practices
Total crop mass at 30 DAE	kg ha <sup>-1</sup>	dry mass of all aboveground parts at 30 d after seedling emergence
Total crop mass at reference date	kg ha <sup>-1</sup>	dry mass of all aboveground parts at 50 DAE
Total crop mass at anthesis	kg ha <sup>-1</sup>	dry mass of all aboveground parts at anthesis
Total crop mass at harvest maturity	kg ha <sup>-1</sup>	dry mass of all aboveground parts at harvest maturity (as defined for grain yield)
<b>Phenology</b>		
Emergence rate	days <sup>-1</sup>	inverse of time from planting to seedling emergence
Vegetative development rate	days <sup>-1</sup>	inverse of time from seedling emergence to anthesis date, which is defined as when 50% of plants have at least one flower showing anthesis
Reproductive development rate	days <sup>-1</sup>	inverse of time from anthesis to physiological maturity, which is defined as when 50% of plants have reached their maximum economic yield
<b>Reproductive growth</b>		
Harvest index	kg grain kg <sup>-1</sup>	ratio of grain yield to total crop mass at maturity
Unit grain mass	mg grain <sup>-1</sup>	dry weight of an average grain at harvest
Grain number at maturity	grains m <sup>-2</sup>	number of grains at harvest maturity (as defined for grain yield)
Grain N conc.	g g <sup>-1</sup>	concentration of N in grain (dry weight basis) at harvest maturity (as defined for grain yield)
<b>Canopy development</b>		
Leaf area index at reference date	m <sup>2</sup> m <sup>-2</sup>	leaf area index at 50 DAE
Specific leaf area at reference date	cm <sup>2</sup> g <sup>-1</sup>	ratio of total leaf area to total leaf dry mass at 50 DAE
Number of main-stem nodes at reference date	nodes	number of nodes on the main stem at 50 DAE
Canopy height at reference date	m	height of the canopy at 50 DAE
Fraction radiation intercepted		mean fraction of daily global radiation intercepted by crop 45 to 54 DAE
<b>Root growth</b>		
Mass of root system at reference date	kg ha <sup>-1</sup>	dry mass of roots at 50 DAE
Depth of root growth at reference date	m	maximum depth of root growth achieved by 50 DAE
Root/shoot ratio at reference date	kg kg <sup>-1</sup>	the ratio of root dry mass to total crop mass at 50 DAE
<b>Resource use efficiency</b>		
Water use efficiency–evapotranspiration basis	kg ha <sup>-1</sup> mm <sup>-1</sup>	mean daily ratio of crop growth to evapotranspiration from 45 to 54 DAE
Water use efficiency–transpiration basis	kg ha <sup>-1</sup> mm <sup>-1</sup>	mean daily ratio of crop growth to transpiration from 45 to 54 DAE
Radiation use efficiency	g MJ <sup>-1</sup>	mean daily ratio of crop growth to intercepted global radiation from 45 to 54 DAE
N use efficiency	kg kg <sup>-1</sup>	ratio of crop dry mass to total N uptake for the interval from emergence to 50 DAE
Crop growth rate at reference date	kg ha <sup>-1</sup> d <sup>-1</sup>	mean daily crop growth rate from 45 to 54 DAE
<b>Water balance</b>		
Total irrigation	mm	total amount of irrigation water supplied from preplanting irrigation to harvest
Total evapotranspiration	mm	total water lost through evaporation and transpiration from the start of simulation to harvest
Total transpiration	mm	total water lost through transpiration during the crop cycle
Total evaporation	mm	total water lost by evaporation from the soil surface from the start of simulation to harvest

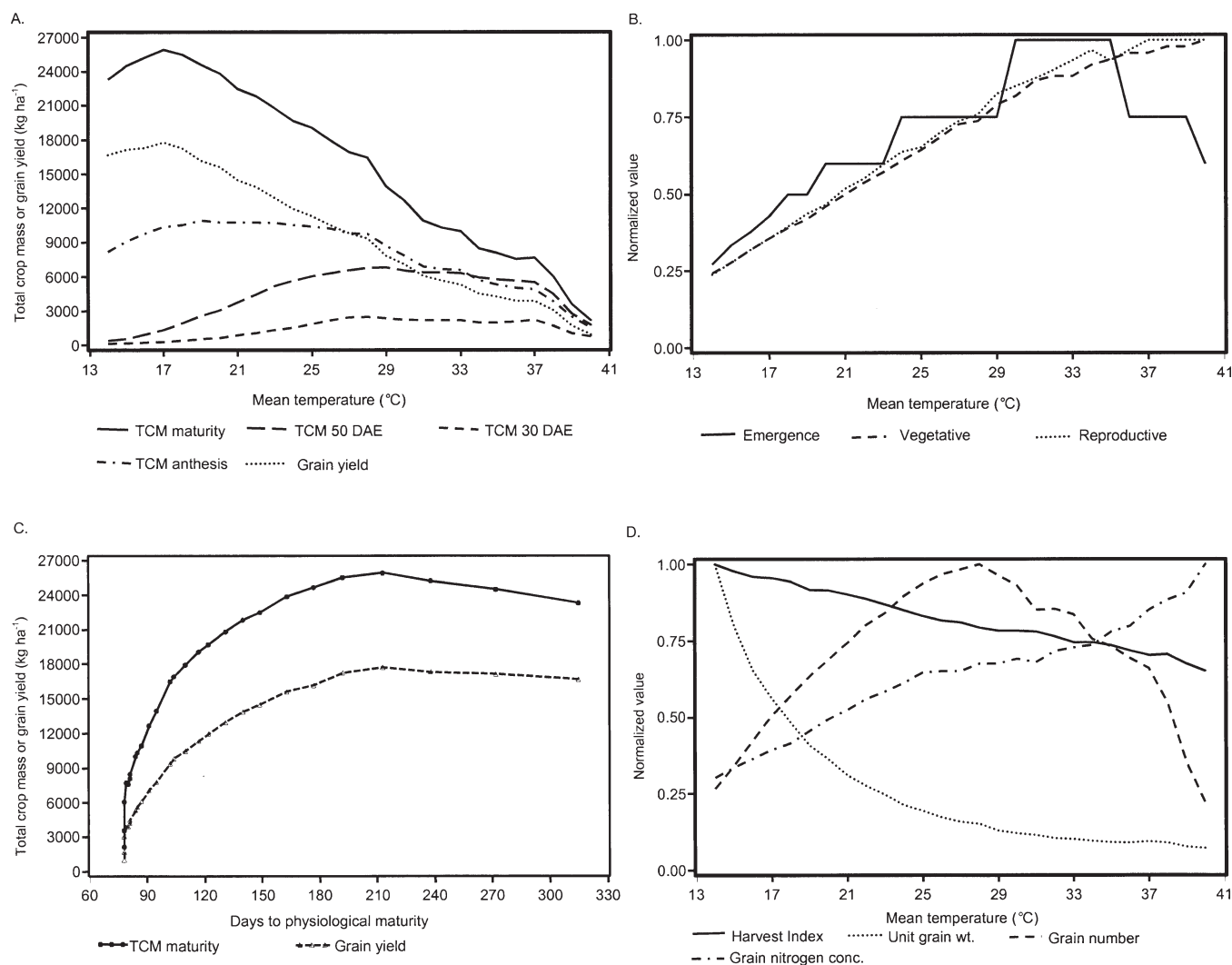
mass, and grain N concentration are included (Fig. 2D). For graphical presentation, values of these variables are normalized from 0 to 1 by dividing by the maximum value obtained across the temperature range. (Similarly, variables in subsequent categories are also normalized.)

Node formation, internode elongation, leaf expansion, and leaf thickening are often considered to be especially sensitive to temperature and form a fourth category related to leaf area development, canopy structure, and radiation interception. Variables examined are leaf area index at reference date of 50 DAE (LAI<sub>50</sub>), specific leaf area at reference date of 50 DAE (SLA<sub>50</sub>), number of main-stem nodes, and canopy height, all determined for a reference date. In addition, the fraction of radiation intercepted, integrated over an entire day, can be calculated as the mean value over 10 d centered on the reference date.

Root growth is characterized through the mass of roots and depth of rooting achieved at the reference date (Fig. 3B). The

root/shoot ratio at this date is provided to indicate the balance between above- and belowground growth.

Efficiency of resource use is characterized based on estimates of resource capture vs. crop growth. Water use efficiency is calculated as the ratio of the crop growth rate to water consumed by the crop, estimated based both on total evapotranspiration (WUE<sub>ET</sub>) and on transpiration alone (WUE<sub>TR</sub>). Values are averaged over the 5 d before and following the reference date (Fig. 3C). Radiation use efficiency at the reference date of 50 DAE (RUE<sub>50</sub>) for the 10-d interval is based on the mean of daily ratios of crop growth rate to intercepted global radiation. For models that do not output radiation interception, RUE<sub>50</sub> is calculated assuming complete interception of the 20 MJ d<sup>-1</sup> radiation. Nitrogen use efficiency (NUE) is calculated as the ratio of TCM<sub>50</sub> to total N uptake from planting to the reference date. This excludes possible N losses through senescence or additional gains through biological N fixation, if simulated. Including crop growth rate over the 10-d period



**Fig. 2.** Response of the sorghum model CSM-CERES-Sorghum to constant mean temperatures with a daily range of 10°C as indicated by: (A) total aboveground crop mass (TCM) at harvest maturity, a reference date (50 d after emergence, DAE), 30 DAE, and anthesis date, and grain yield; (B) normalized values (from 0 to 1) of rates of development for seedling emergence, vegetative, and reproductive phases; (C) total aboveground crop mass at harvest maturity and grain yield vs. days to physiological maturity; and (D) normalized values at harvest maturity of harvest index, grain number, unit grain mass, and grain N concentration.

[crop growth rate measured at the reference date of 50 DAE (CGR<sub>50</sub>)] helps indicate the relative importance of resource capture vs. growth rate in determining resource use efficiency.

The final category concerns the crop water balance as characterized by end-season totals of irrigation, evapotranspiration, transpiration, and soil evaporation (Fig. 3D). Total irrigation is the sum of user-specified irrigation events (but indirectly affected by modeled crop duration), but comparing irrigation to evapotranspiration allows verifying whether simulations are biased by water deficit or excess.

Analysis of the responses is based on both qualitative information from inspection of graphed responses and through quantitative indicators. Cardinal temperatures for each response curve are estimated to the extent permitted by the shape of the response. Each response is characterized by a base temperature ( $T_{base}$ ), below which the response variable has a value of 0; two optimal temperatures ( $T_{opt1}$  and  $T_{opt2}$ ) that define the interval where the maximal response occurs; and a maximum temperature ( $T_{max}$ ), above which the response is 0.

A further indicator is provided by a response stability index (RSI), which is based on the integral of the response curve,

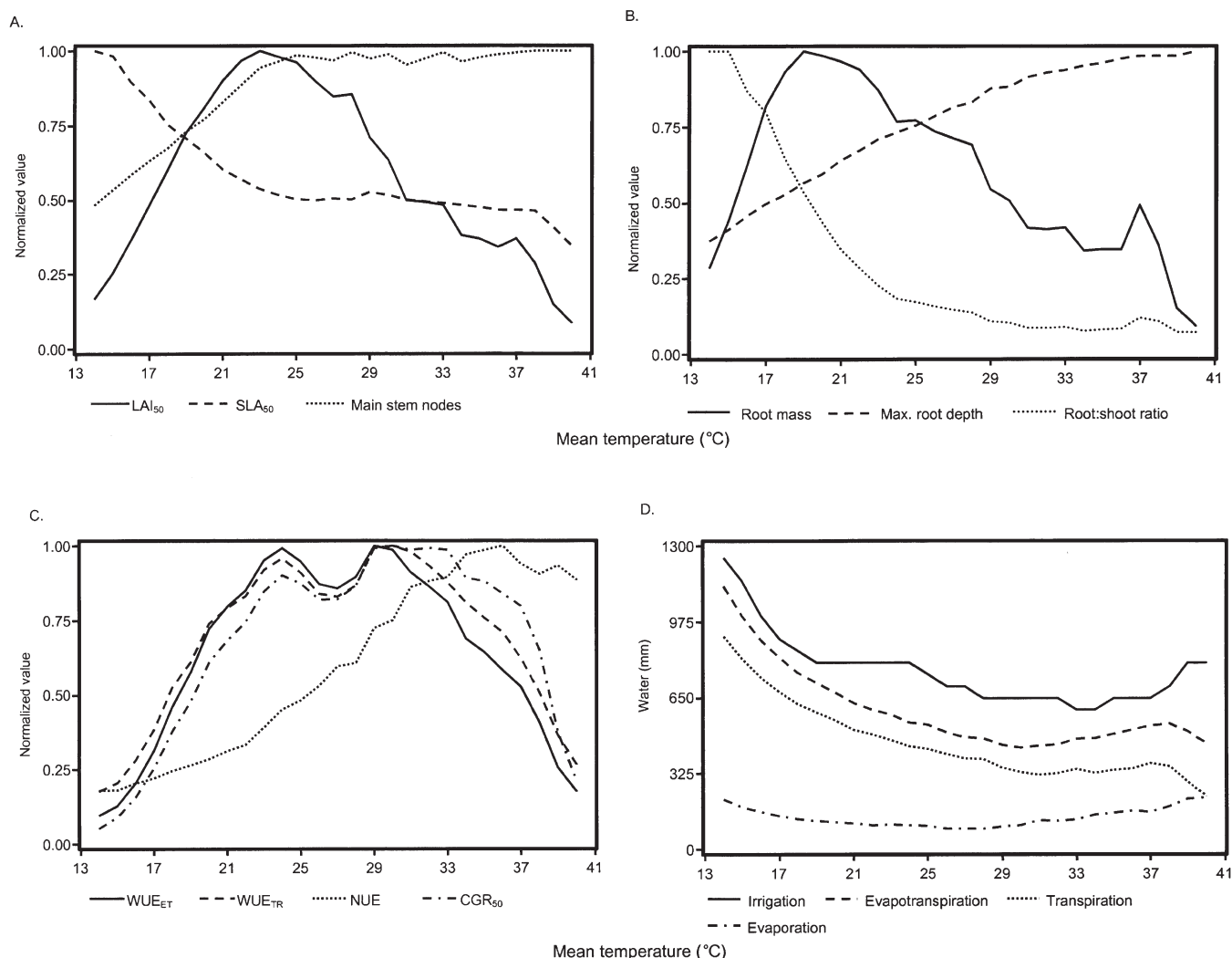
using  $T_{base}$  to  $T_{max}$  for  $TCM_{harv}$  as the end-points of the integration. (If either  $T_{base}$  or  $T_{max}$  was not reached, then the critical temperature is set equal to the minimum or maximum temperature that allowed successful simulation.) Limiting the integral to a maximum value of 1 (achieved by normalizing both the response and the temperature range to values from 0 to 1) makes RSI values comparable across processes, crops, or models. A value near 1 typically indicates a process that has a sharp rise immediately above  $T_{base}$  to a near-maximum level and maintains this value until near  $T_{max}$ . A value of 0.5 corresponds to a process with a linear increase from  $T_{base}$  to  $T_{opt1}$ ,  $T_{opt1} = T_{opt2}$ , and a linear decrease to  $T_{max}$  (e.g., an inverted V-shape response). Values of RSI less than 0.5 usually imply a very narrow response.

## MATERIALS AND METHODS

### Environmental Conditions and Management Practices

Annual sets of daily weather data were created for a hypothetical site at 0° latitude to provide a constant 12-h photo-





**Fig. 3.** Response of the sorghum model CSM-CERES-Sorghum to constant mean temperatures with a daily range of 10°C as indicated by: (A) normalized values (from 0 to 1) at a reference date (50 d after emergence) for leaf area index (LAI<sub>50</sub>), specific leaf area (SLA<sub>50</sub>), and number of main-stem nodes; (B) normalized values at a reference date for root dry mass, maximum root depth, and root/shoot ratio; (C) normalized values of water use efficiency based on evapotranspiration (WUE<sub>ET</sub>), water use efficiency based on transpiration (WUE<sub>TR</sub>), N use efficiency (NUE), and crop growth rate (CGR<sub>50</sub>); and (D) total-season irrigation, evapotranspiration, transpiration, and soil evaporation.

period. Separate files were created for mean air temperatures on a 1°C interval from 3 to 40°C, with a daily range of 10°C. To estimate soil temperatures, the CSM models require long-term values of the average annual temperature and of the amplitude of the annual temperature cycle (Jones and Kiniry, 1986). Thus, the mean temperature of each regime was also provided, and the amplitude for all regimes was assumed to be 0°C. Daily global radiation was 20 MJ m<sup>-2</sup> d<sup>-1</sup>. No precipitation was allowed. The two models tested use a modification of the Priestley-Taylor method (Priestley and Taylor, 1972) to estimate potential evapotranspiration as described by Ritchie (1998), which does not require wind speed or humidity.

The soil profile corresponded to a "medium silty loam" as provided in the DSSAT Version 4 soil profile file SOIL.SOL (Hoogenboom et al., 2004) and is summarized in Tables 2 and 3. The initial profile water content was set equal to the drained upper limit or field capacity, and initial N levels were as specified in Table 3.

Simulations were started on 1 January, and the crops were sown on 31 January. Results from simulations taking more than 365 d (due to slowed growth at low temperatures) were excluded since examining extreme slow development and

growth of such crops would provide few insights into useful model responses. Total crop mass was restricted to above-ground dry biomass and excluded senesced tissue.

An initial irrigation of 100 mm was provided on 26 January to fill the soil profile. Subsequently, 50 mm was applied every 5 to 12 d as needed to avoid water deficits. The interval varied with temperature and developmental stages to match the water applied to expected losses through evapotranspiration. Additional adjustments were made to intervals to avoid excess water. Both crops were fertilized with 100 kg ha<sup>-1</sup> of N (as ammonium nitrate) at planting, with additional 40 kg ha<sup>-1</sup> as anhydrous ammonia at 40 and 60 d after planting. (Planting populations and arrangements for the two crops considered are described in the next two sections.) Additional simulations to evaluate the effect of water and N deficits were conducted for both crops using 20, 40, and 60% of irrigation amounts and applying no N fertilizer.

### Simulations for the Sorghum Model CSM-CERES-Sorghum

The temperature response of the sorghum model CSM-CERES-Sorghum model Version 4.0 (Jones et al., 2003;

**Table 2. Properties of the soil surface and properties assumed constant through the profile as used to model temperature response. Values are based on the default medium silty loam provided in DSSAT4 (Hoogenboom et al., 2004).**

Variable	Value	Definition
Albedo	0.12	albedo of bare soil
Evaporation limit	6.0 cm	potential evaporation from soil surface at maximum rate after re-wetting
Drainage rate	0.3 d <sup>-1</sup>	soil drainage parameter (assumed constant throughout profile)
Runoff curve number	79	USDA Natural Resources Conservation Service (NRCS) runoff curve number, which scales potential for runoff from 0 (no runoff) to 100 (all water lost through runoff)
Mineralization factor	1.0	0 to 1 factor to scale mineralization
Photosynthesis factor	1.0	0 to 1 factor to scale photosynthesis in soils with unspecified constraints
Clay fraction	0.1 g g <sup>-1</sup>	standard soil textural analysis for particle-size distribution in dry soil passing a 2-mm sieve
Silt fraction	0.6 g g <sup>-1</sup>	standard soil textural analysis for particle-size distribution in dry soil passing a 2-mm sieve
Sand fraction	0.3 g g <sup>-1</sup>	standard soil textural analysis for particle-size distribution in dry soil passing a 2-mm sieve
Coarse fraction	0.0 g g <sup>-1</sup>	standard soil textural analysis for particle-size distribution in dry soil, portion retained by a 2-mm sieve

Hoogenboom et al., 2004) was assessed assuming a 0.75-m row spacing with a population of 20 plants m<sup>-2</sup>. CSM-CERES-Sorghum was developed from CERES-Sorghum (Alagarswamy and Ritchie, 1991), and the growth and development routines of the model are similar to those of early versions of CERES-Maize as described by Jones and Kiniry (1986) and Ritchie et al. (1998). Briefly, vegetative growth is modeled based on a potential radiation use efficiency (RUE) factor, which may be reduced by suboptimal temperature or water or N deficits. The temperature effect on RUE is modeled as a trapezoidal response with cardinal values of 8°C (T<sub>base</sub>), 20°C (T<sub>opt1</sub>), 40°C (T<sub>opt2</sub>), and 50°C (T<sub>max</sub>), where the temperature is the sum of 0.25 × the daily minimum temperature and 0.75 × the T<sub>max</sub>. Light interception is estimated assuming a homogeneous canopy and using a conventional canopy-level extinction coefficient although the coefficient is adjusted for row width. Phenology is based on thermal time calculated from a diurnal curve estimated from the daily minimum temperature and T<sub>max</sub>, with an adjustment early in the life cycle for an effect of solar radiation.

The cultivar corresponded to Dekalb 54,<sup>1</sup> but the coefficient for the critical daylength was set to 14 h to eliminate photoperiod effects. The cultivar-specific coefficients assumed are listed in Table 4.

### Simulations for the Common Bean Model CSM-CROPGRO-Drybean

Responses of common bean (*Phaseolus vulgaris* L.) to temperature were simulated using CSM-CROPGRO-Drybean model Version 4.0 (Jones et al., 2003; Hoogenboom et al., 2004), which was developed from BEANGRO (Hoogenboom et al., 1994; White et al., 1995) and CROPGRO (Hoogenboom et al., 1992; Boote et al., 1998). The hedgerow photosynthesis

option was used, which predicts leaf photosynthesis for sunlit and shaded leaves in a canopy (Boote and Pickering, 1994). Hourly time steps are used to simulate photosynthesis and phenology in separate routines, and partitioning, water balances, and nutrient balances are simulated with daily steps. Symbiotic N fixation was simulated.

A row spacing of 0.3 m and a population of 30 plants m<sup>-2</sup> were used. The cultivar was a generic Meso American Habit 2 & 3 cultivar, which is indeterminate, day neutral, and has small seed. The cultivar-specific coefficients are listed in Table 4.

### Data Analysis

For both models, all variables required for analysis were in files of daily outputs in ASCII space-delimited format. Values at the reference date and at time of maximum leaf area index were obtained by using data-processing tools of the SAS Version 8 (SAS Inst. Inc., Cary, NC). Calculations of derived variables are explained in Table 1.

Cardinal temperatures were estimated visually due to the irregular shape of some curves. The T<sub>base</sub> and T<sub>max</sub> were assumed to have been reached if the standardized response variable was within 0.05 of 0 or the maximum value, respectively. Extrapolations of 2°C below or above the temperature range tested were allowed if responses showed clear linear trends. The interval from T<sub>opt1</sub> to T<sub>opt2</sub> was assumed to correspond to temperatures where the response variable was greater than 0.95 of the maximum value. For some variables, the response model was inappropriate (e.g., total irrigations), or the response was too irregular for estimating cardinal temperatures.

For each variable, RSI was estimated by integrating normalized response values over the range from T<sub>base</sub> to T<sub>max</sub> for TCM<sub>50</sub> or the range of temperatures that allowed successful simulations. To permit comparisons across crops or models showing different temperature intervals for TCM<sub>harv</sub>, the inte-

<sup>1</sup>Reference to a brand or firm name does not constitute an endorsement by the USDA, the University of Georgia, or the University of Guelph over others of a similar nature not mentioned.

**Table 3. Properties of individual soil layers in the profile used to model temperature response. Values are based on the default medium silty loam provided in DSSAT4 (Hoogenboom et al., 2004). Lower and upper limits correspond to -1600 and -33 kPa soil water potentials, respectively.**

Soil depth m	Soil moisture content			Root growth factor	Bulk density Mg m <sup>-3</sup>	Organic C %	Total N	NH <sub>4</sub> μg g <sup>-1</sup>	NO <sub>3</sub> μg g <sup>-1</sup>
	Lower limit	Upper limit	Saturation						
	m <sup>3</sup> m <sup>-3</sup>								
0.00–0.05	0.106	0.262	0.462	1.000	1.37	1.16	0.12	4.0	10.0
0.05–0.15	0.106	0.262	0.462	1.000	1.37	1.16	0.12	1.0	10.0
0.15–0.30	0.106	0.262	0.462	0.819	1.37	1.10	0.11	1.0	5.0
0.30–0.45	0.107	0.262	0.462	0.607	1.37	0.97	0.10	1.0	2.0
0.45–0.60	0.107	0.262	0.462	0.607	1.37	0.97	0.10	0.5	1.0
0.60–0.90	0.108	0.261	0.461	0.368	1.38	0.72	0.07	0.5	0.5
0.90–1.20	0.110	0.260	0.460	0.202	1.38	0.43	0.04	0.5	0.5
1.20–1.50	0.111	0.259	0.459	0.111	1.39	0.20	0.02	0.5	0.5

**Table 4. Cultivar-specific parameters assumed to simulate response to temperature using the CSM-CERES-Sorghum and CSM-CROPGRO-Drybean models.**

Parameter description	Value	Abbreviation
<b>CSM-CERES-Sorghum</b>		
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.	450	P1
Critical photoperiod or the longest daylength (in hours) at which development occurs at a maximum rate. At values higher than P20, the rate of development is reduced.	14	P20
Extent to which phasic development leading to panicle initiation (expressed in degree days) is delayed for each hour increase in photoperiod above P20.	110	P2R
Thermal time (degree days above a base temperature of 8°C) from beginning of grain filling (3–4 d after flowering) to physiological maturity.	700	P5
Scalar for relative leaf size.	12	G1
Scalar for partitioning of assimilates to the panicle (head).	6	G2
Phyllochron interval; the interval in thermal time (degree days) between successive leaf tip appearances.	95	PHINT
<b>CSM-CROPGRO-Drybean</b>		
Text code for the ecotype to which this cultivar belongs (as specified in a separate ecotype file).	MESIND	ECO#
Critical daylength below which reproductive development progresses with no daylength effect (hour).	12.17	CSDL
Slope of the relative response of development to photoperiod with time (1/h).	0	PPSEN
Time between plant emergence and flower appearance (R1) (photothermal days).	32	EM-FL
Time between first flower and first pod (R3) (photothermal days).	2	FL-SH
Time between first flower and first seed (R5) (photothermal days).	9	FL-SD
Time between first seed (R5) and physiological maturity (R7) (photothermal days).	21	SD-PM
Time between first flower (R1) and end of leaf expansion (photothermal days).	18	FL-LF
Maximum leaf photosynthesis rate at 30°C, 350 ppm CO <sub>2</sub> , and high light (mg CO <sub>2</sub> m <sup>-2</sup> s <sup>-1</sup> ).	1.0	LFMAX
Specific leaf area of cultivar under standard growth conditions (cm <sup>2</sup> g <sup>-1</sup> ).	320	SLAVR
Maximum size of full leaf (three leaflets) (cm <sup>2</sup> ).	133	SIZLF
Maximum fraction of daily growth that is partitioned to seed + shell.	1.0	XFRT
Maximum mass per seed (g).	0.23	WTPSD
Seed-filling duration for pod cohort at standard growth conditions (photothermal days).	14.0	SFDUR
Average seed per pod under standard growing conditions (number pod <sup>-1</sup> ).	5.2	SDPDV
Time required for cultivar to reach final pod load under optimal conditions (photothermal days).	8.0	PODUR

gral was then normalized to a value of 0 to 1 by dividing by the temperature range to obtain the final value of RSI for each response.

## RESULTS

### CSM-CERES-Sorghum

Simulations with the CSM-CERES-Sorghum model were run successfully from 14 to 40°C. At temperatures below 14°C, predicted crop duration was over 330 d, so these results were excluded. By 40°C, growth was near zero (Fig. 2A). As temperatures increased, development accelerated (Fig. 2B), which hastened time to anthesis and to maturity and reduced crop mass (Fig. 2A). However, the decline in grain yield and crop mass for maturity dates under 100 d (Fig. 2C) indicated that growth rates per se also declined at higher temperatures.

Harvest index declined almost linearly with temperature from 0.72 at 15°C to 0.47 at 40°C (Fig. 2D). Unit grain mass decreased rapidly from 204 mg to a low of 15 mg over the same temperatures. Related to the large grain size at low temperatures, total grain number was low at 15°C, reached a maximum value of 30 600 grains m<sup>-2</sup> at 27°C, and then declined rapidly at higher temperatures. Grain N concentration rose almost linearly from a value of 0.8% at 14°C to 2.5% at 40°C (Fig. 2D).

Leaf area production, as indicated by LAI<sub>50</sub>, showed a narrow optimum from 22° to 25°C and declined in a somewhat irregular fashion to values near 0 at 41°C (Fig. 3A). This drop is attributable to reduced leaf mass since SLA<sub>50</sub> was practically constant above 24°C (Fig. 3A). Main-stem nodes increased from 14 to 24°C and then remained relatively constant around 19 nodes. CSM-CERES-Sorghum did not simulate canopy height and did not output radiation interception.

Root growth showed a lower optimum than leaf growth, with T<sub>optl</sub> occurring at 19°C (Table 5 and Fig. 3B). Maximum root depth increased smoothly with temperature, reaching the maximum value allowed by the soil profile description of 1.3 m at 36°C. The ratio of root to shoot dry mass declined from a maximum value of 1.3 at 14°C to values around 0.1 above 32°C (Fig. 3B).

Responses of WUE<sub>ET</sub>, WUE<sub>TR</sub>, and CGR<sub>50</sub> were similar across the range of temperatures tested. All three parameters increased from 14 to 24°C, then showed a dip in values at 25 to 27°C, and after reaching a second maximum at 29°C, declined to less than 25% of maximum values by 40°C (Fig. 3C). Nitrogen use efficiency increased from 14 to 36°C, reached a maximum of 95 kg kg<sup>-1</sup>, and then declined slightly up to 40°C (Fig. 3C). Water use was greatest at low temperatures (Fig. 3D), reflecting the long crop duration. Irrigation exceeded total evapotranspiration over the entire temperature range, indicating that minimal water deficit occurred.

Values of RSI were as high as 0.82 for HI and 0.89 for main-stem nodes (Table 5) with most values falling between 0.6 and 0.8. Unit grain mass and root/shoot ratio had values less than 0.3, reflecting skewed responses (Fig. 2D and Fig. 3B). Grain yield had an RSI of only 0.56 due to the peak in yield at 18°C (Fig. 2A).

### CSM-CROPGRO-Drybean

For the common bean model CSM-CROPGRO-Drybean, the greatest initial growth was obtained at mean temperatures around 25°C (Fig. 4A), but due to the effects of delayed flowering and maturity, grain yield and crop mass at anthesis and at harvest maturity were maximal at 13°C or lower. Below 10°C, the model predicted that the crop would require over 330 d, so results

**Table 5.** Cardinal temperatures, maximum values, and response sensitivity index (RSI) for variables used to assess temperature responses. Cardinal temperatures are in units of °C and correspond to fitted trapezoidal-shaped response functions with a base ( $T_{\text{base}}$ ), two end-points of the optimal range ( $T_{\text{opt1}}$  and  $T_{\text{opt2}}$ ), and a maximum ( $T_{\text{max}}$ ). Reference date for both species was 50 d after emergence (DAE).

Variable	Units	Sorghum						Common bean					
		Cardinal temperatures				Max.	RSI	Cardinal temperatures				Max.	RSI
		T <sub>base</sub>	T <sub>opt1</sub>	T <sub>opt2</sub>	T <sub>max</sub>			T <sub>base</sub>	T <sub>opt1</sub>	T <sub>opt2</sub>	T <sub>max</sub>		
		°C						°C					
Crop mass													
Total crop dry mass at harvest maturity	kg ha <sup>-1</sup>	<14	16	19	42	25 920	0.62	<10	11	14	31	16 300	0.66
Total crop dry mass at reference date	kg ha <sup>-1</sup>	<14	27	30	42	6 830	0.69	10	22	25	32	5 860	0.65
Total crop dry mass at 30 DAE	kg ha <sup>-1</sup>	14	27	29	>40	2 480	0.61	10	23	25	33	1 780	0.56
Total crop dry mass at anthesis	kg ha <sup>-1</sup>	<14	16	19	42	9 590	0.76	<10	13	15	31	6 680	0.56
Grain yield	kg ha <sup>-1</sup>	<14	15	18	42	17 740	0.56	<10	12	16	31	8 300	0.68
Phenology													
Emergence rate	days <sup>-1</sup>	<14	30	35	>40	0.333	0.72	<8	24	33	42	0.200	0.75
Vegetative development rate	days <sup>-1</sup>	<14	36	ND	ND	0.022	0.69	<10	25	34	>40	0.024	0.74
Reproductive development rate	days <sup>-1</sup>	<14	34	ND	ND	0.033	0.71	<10	27	38	>40	0.048	0.68
Reproductive growth													
Harvest index	kg grain kg <sup>-1</sup>	ND	ND	17	ND	0.72	0.82	<10	15	28	35	0.56	0.94
Unit grain mass	mg grain <sup>-1</sup>	ND	ND	14	ND	204	0.24	ND	ND	14	36	410	0.66
Grain number at maturity	grains m <sup>-2</sup>	10	26	29	42	30 600	0.74	<10	19	19	31	2 380	0.74
Grain N concentration	g g <sup>-1</sup>	<14	40	ND	ND	2.5	0.63	ND	29	34	35	.041	0.86
Canopy development													
Leaf area index at reference date	m <sup>2</sup> m <sup>-2</sup>	12	22	25	42	6.0	0.62	10	18	21	32	7.4	0.65
Specific leaf area at reference date	cm <sup>2</sup> g <sup>-1</sup>	ND	ND	15	ND	262	0.57	ND	22	27	ND	366	0.88
Number of main-stem nodes at reference date	nodes	<14	24	ND	ND	19.3	0.89	<10	22	38	ND	14.0	0.78
Canopy height at reference date	m	ND	ND	ND	ND	ND	ND	<10	24	26	ND	1.4	0.61
Fraction radiation intercepted	–	ND	ND	ND	ND	ND	ND	<10	18	28	ND	0.99	0.82
Root growth													
Root system dry mass at reference date	kg ha <sup>-1</sup>	12	19	21	42	1780	0.62	<10	18	20	34	550	0.67
Maximum root depth at reference date	m	<14	34	ND	ND	1.3	0.78	<10	29	34	ND	1.3	0.75
Root/shoot ratio at reference date	kg kg <sup>-1</sup>	ND	ND	15	ND	1.32	0.28	ND	ND	ND	ND	0.64	0.17
Resource use efficiency													
Water use efficiency–ET† basis	kg ha <sup>-1</sup> mm <sup>-1</sup>	<14	23	30	ND	47	0.69	10	19	23	32	49	0.70
Water use efficiency–transpiration basis	kg ha <sup>-1</sup> mm <sup>-1</sup>	<14	24	31	ND	57	0.73	<10	18	22	34	54	0.77
Radiation use efficiency	g MJ <sup>-1</sup>	<14	29	33	ND	1.19	0.72	<10	19	25	34	1.09	0.78
N use efficiency	kg kg <sup>-1</sup>	<14	34	36	ND	95	0.71	ND	ND	ND	ND	67	0.41
Crop growth rate at reference date	kg ha <sup>-1</sup> d <sup>-1</sup>	12	29	33	42	237	0.72	10	20	25	32	215	0.68

† ET, evapotranspiration.

for those temperatures are not presented. Above 29°C, growth and yield declined rapidly, reaching values of  $T_{\text{max}}$  at 31 to 33°C, depending on the response variable considered (Table 5).

Contrasting with the sorghum model, developmental rates were reduced not only by low temperatures but also by temperatures above 33 to 38°C (Fig. 4B). This resulted in a more complex relation between dry matter accumulation and time to physiological maturity (Fig. 4C) although a comparison of Fig. 4A and 4C reveals that from 16°C to 30°C, growth and yield decreased with temperature, largely due to the effect on developmental rates.

The HI varied less than 15% between 12 and 29°C and declined rapidly beyond either of these extremes (Fig. 4D). Unit grain mass declined from 410 mg at 10°C to 54 mg at 35°C. Grain number was comparatively constant from 12 to 25°C with the exception of a spike at 19°C. Grain N concentration increased slowly from 3.5% at 8°C to 4.1% at 34°C, above which no grain was produced (Fig. 4D).

The temperature response of  $\text{LAI}_{50}$  was somewhat narrower than radiation interception (Fig. 5A). Variation in  $\text{SLA}_{50}$  was less than 20% from 17 to 35°C, so most of the variation in  $\text{LAI}_{50}$  reflected changes in leaf mass. The number of main-stem nodes increased from 3 to 14 nodes from 8 to 24°C, dropped slightly from 25 to 34°C, and reached the maximum value at 37°C

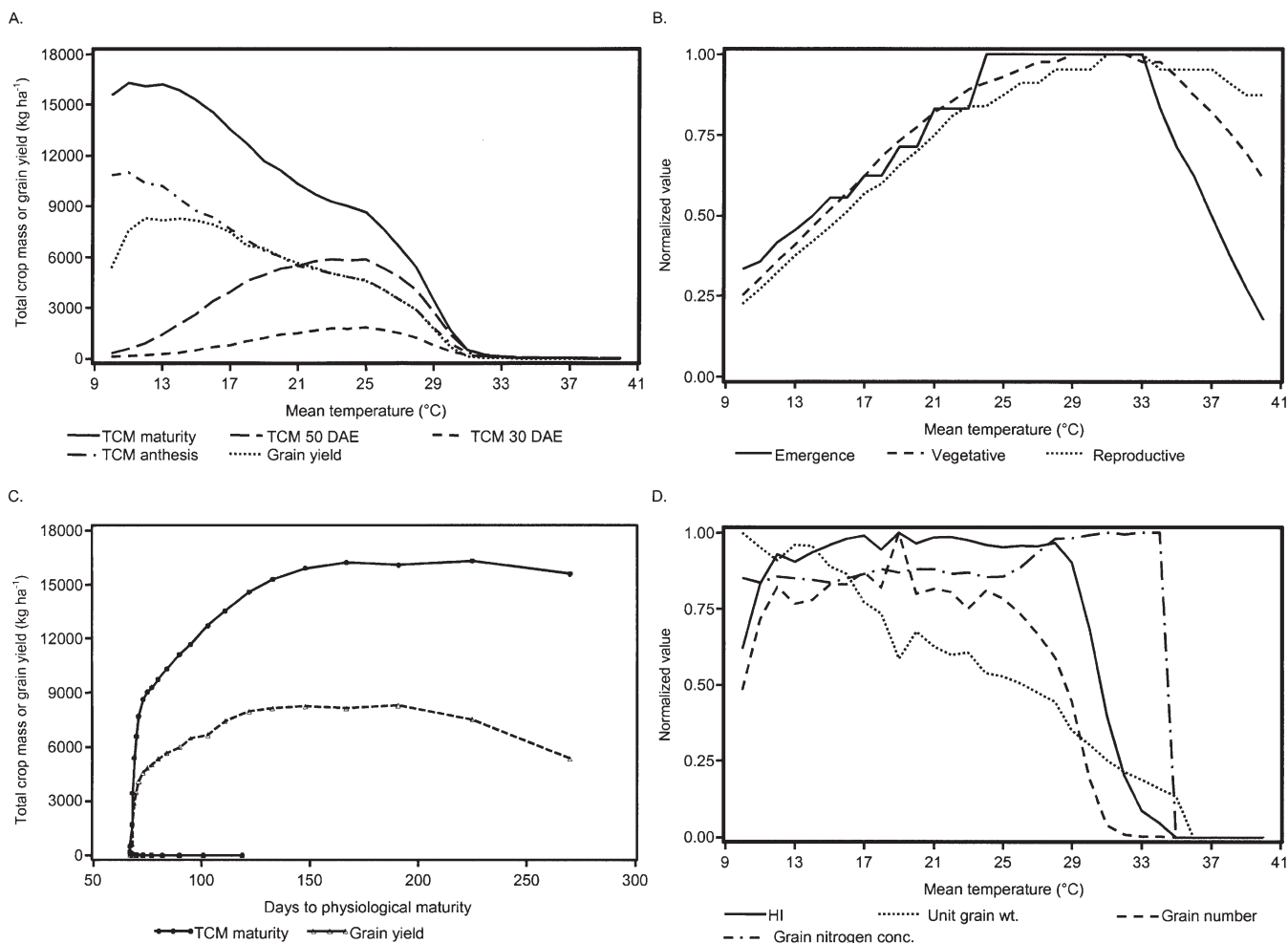
(Fig. 5A). Similarly, canopy height had a maximum of 1.4 m at 25°C, decreased to 0.96 m at 35°C, and increased again to 1.2 m at 38°C and then decreased.

The greatest root mass at the reference date occurred between 18 and 20°C, with values over 500 kg ha<sup>-1</sup>, and dropped rapidly away from this optimum (Fig. 5B). In contrast,  $T_{\text{opt1}}$  and  $T_{\text{opt2}}$  for maximum root depth were 29 and 34°C, respectively. The root/shoot ratio reached its highest values at extremely high temperatures, corresponding to very restricted shoot growth (Fig. 5B and Fig. 4A). Minimum values of 0.07 occurred around 24°C.

Temperature responses of  $\text{WUE}_{\text{ET}}$ ,  $\text{WUE}_{\text{TR}}$ ,  $\text{RUE}_{50}$ , and  $\text{CGR}_{50}$  were similar, having maximum values from 18 to 25°C and dropping rapidly away from this plateau (Fig. 5C). The response of NUE was quite different, being fairly constant for temperatures from 10 to 32°C and then rising rapidly at temperatures that severely restricted growth.

The highest values of RSI (Table 5) were for HI (0.94), grain N concentration (0.88), and  $\text{SLA}_{50}$  (0.83). Most other parameters had values of RSI between 0.6 and 0.8. The lowest values were for root/shoot ratio (0.17) and NUE (0.44), both of which showed U-shaped responses (Fig. 5B and 6C). Total aboveground crop mass at reference date of 30 DAE and  $\text{TCM}_{\text{anth}}$  had RSI values of 0.56, but optimal temperatures for  $\text{TCM}_{30}$  were about 10°C warmer than for  $\text{TCM}_{\text{anth}}$ .





**Fig. 4.** Response of the common bean model CSM-CROPGRO-Drybean to constant mean temperatures with a daily range of 10°C as indicated by: (A) total aboveground crop mass (TCM) at harvest maturity, a reference date (50 d after emergence, DAE), 30 DAE, anthesis date, and grain yield; (B) normalized values (from 0 to 1) of rates of development for seedling emergence, vegetative, and reproductive phases; (C) total aboveground crop mass and grain yield vs. days to physiological maturity; and (D) normalized values at harvest maturity of harvest index, grain number, unit grain mass, and grain N concentration. HI, harvest index.

### Effects of Water and Nitrogen Deficits

To examine whether other stresses would affect the responses, water and N deficit conditions were simulated by reducing the irrigation amounts or eliminating the N applications. For CSM-CERES-Sorghum, decreased water availability reduced crop mass at maturity and grain yield more at cooler temperatures (where crop duration was extended due to slowed development), thus resulting in a shift in optima toward warmer temperatures for TCM<sub>harv</sub> and grain yield (Fig. 6). Similarly, eliminating the N application reduced growth and yield below 31°C. The response to water deficits was similar with CSM-CROPGRO-Drybean, but presumably due to capacity for N fixation, eliminating the N application had minimal effect (data not shown).

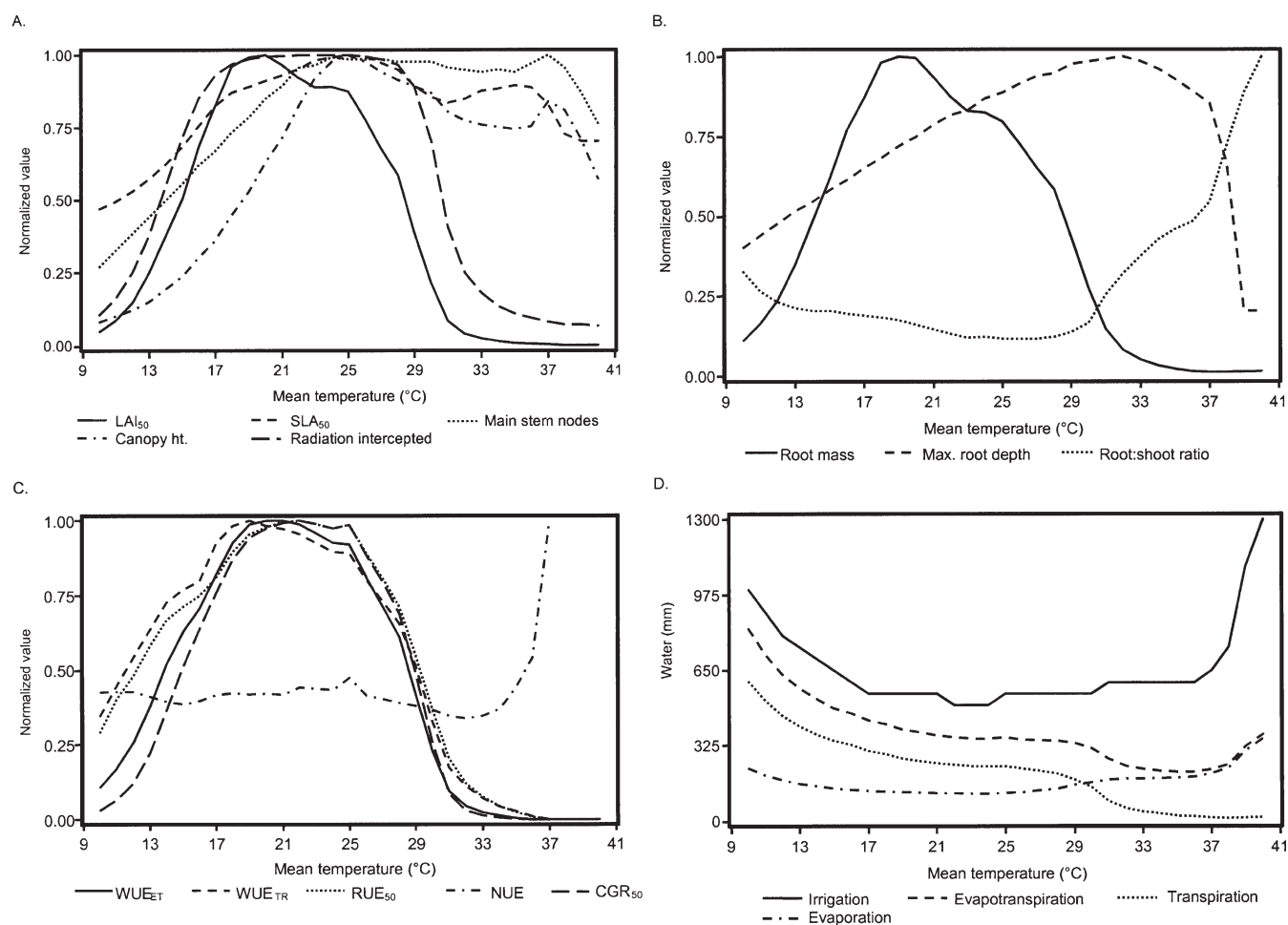
### DISCUSSION

The main objective of this paper was to determine whether a structured procedure using sensitivity analysis with standardized inputs and readily accessible model outputs can provide significant insights into how models

respond to temperature. This proposition can be tested by considering whether the procedure revealed features of the two models, CSM-CERES-Sorghum and CSM-CROPGRO-Drybean, that would not be detected from documentation or validation procedures. Thus, model performance is reviewed briefly in the context of published data on growth and development of the two crops. We emphasize that this is not a full review of temperature responses of the two species or of the two models.

The expected better adaptation to warmer conditions of sorghum (e.g., Peacock and Heinrich, 1984) compared with common bean (Masaya and White, 1991) was visible in the range of cardinal temperatures (Table 5). Values of  $T_{opt1}$  and  $T_{opt2}$  for TCM<sub>50</sub>, LAI<sub>50</sub>, and CGR<sub>50</sub> of sorghum were typically 4 to 5°C higher than in common bean, with the notable exception of root mass where  $T_{opt1}$  and  $T_{opt2}$  had similar values. This overall temperature difference is similar to that between commonly used values of  $T_{base}$  for thermal time for development of 10°C for sorghum (Gerik et al., 2003) and 5°C for common bean (Miller et al., 2002).

Seed germination studies can indicate temperature



**Fig. 5.** Response of the common bean model CSM-CROPGRO-Drybean to constant mean temperatures with a daily range of 10°C as indicated by: (A) normalized values (from 0 to 1) at a reference date (50 d after emergence) for leaf area index ( $LAI_{50}$ ), specific leaf area ( $SLA_{50}$ ), and number of main-stem nodes; (B) normalized values at a reference date for root dry mass, maximum root depth, and root/shoot ratio; (C) normalized values of water use efficiency based on evapotranspiration ( $WUE_{ET}$ ), water use efficiency based on transpiration ( $WUE_{TR}$ ), radiation use efficiency ( $RUE_{50}$ ), N use efficiency (NUE), and crop growth rate ( $CGR_{50}$ ); and (D) total-season irrigation, evapotranspiration, transpiration, and soil evaporation.

responses of seedling emergence (Brar and Stewart, 1994), and such studies often consider a wider range of temperatures than applied to whole plants. Germination in sorghum shows a  $T_{base}$  near 10°C and  $T_{opt1}$  varying from 22 to 35°C, depending on cultivar and other factors (Peacock and Heinrich, 1984; Brar and Stewart, 1994). Extrapolating emergence rate in Fig. 2B to a value of 0 would also result in an estimate of  $T_{base}$  near 10°C, and the estimated value of  $T_{opt1}$  of 30°C (Table 5) is in the middle of the range from germination studies. The review by Peacock and Heinrich (1984) gives values of  $T_{opt2}$  around 35°C, the same value given in Table 5. These authors suggest lethal temperatures are from 40 to 48°C while our estimate is >40°C (Table 5). For common bean, White and Montes (1993) estimated values of  $T_{min}$ ,  $T_{opt1}$ , and  $T_{opt2}$  of 8, 28, and 35°C, respectively, but noted that  $T_{max}$  was not estimable because seed quickly decayed at temperatures over 35°C. Extrapolating emergence rate to 0 in Fig. 4B suggests a value of 5°C or lower. The estimated value of  $T_{opt1}$  was 24°C (Table 5), 4°C lower than the value of White and Montes (1993), but  $T_{opt2}$  was estimated as 33°C, similar to the 35°C value

of White and Montes (1993). Table 5 gives a value of  $T_{max}$  of 42°C, considerably above the 35°C limit for onset of seed decay. Comparisons of constant temperature regimes, as typically used in germination studies, with diurnally varying field conditions where air and soil temperatures may differ are known to be problematic, but the review of cardinal temperatures for germination and emergence confirms that the proposed model assessment procedure can readily identify issues that merit further study.

Focusing on sorghum, the high value of HI at 14°C and nearly linear decrease with increasing temperature (Fig. 2D) contrasts with the general stability of the HI in field trials (e.g., Muchow, 1988) and the finding of Hammer and Broad (2003) that HI decreased at lower temperatures. Unit grain mass in sorghum can vary from 8 to 35 mg (Martin, 1970), but values for commercial materials grown under diverse environments vary much less, typically from 15 to 25 mg (e.g., Hammer and Broad, 2003). Simulated values declined from 204 mg at 14°C to 15 mg at 40°C, and even for the interval from 20 to 30°C, values ranged from 74 to 25 mg (Fig. 2D).

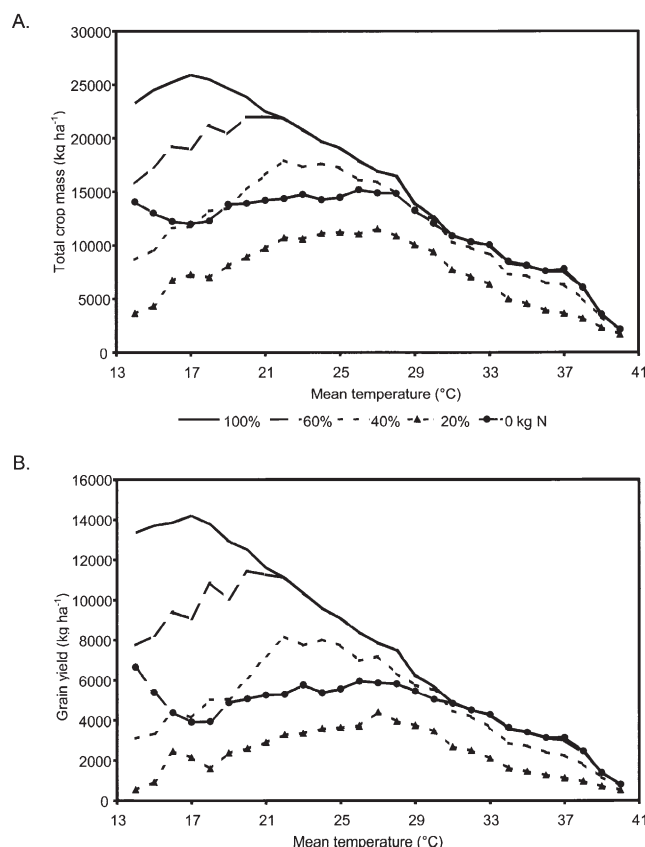


Fig. 6. Response of the sorghum model CSM-CERES-Sorghum to constant mean temperatures with a daily range of 10°C as affected by water or N deficits. Water deficit levels are percentage of full irrigation, and N deficit if no N applied. (A) Total aboveground crop mass at maturity. (B) Grain yield.

This response also conflicts with the interpretation of Peacock and Heinrich (1984) that compensation between reduced grain-filling period but more rapid rate of filling results in “little change in grain size” for mean temperatures from 23 to 28°C. Similarly, for common bean, grain mass declined from 406 mg at 10°C to 54 mg at 35°C (and from 360 mg at 15°C to 210 mg at 25°C), contrasting with the reported stability of grain mass in common bean (Adams, 1967).

Water and N were intended to be nonlimiting, which might lead to inefficiency in resource use. Both models showed  $WUE_{ET}$  and  $WUE_{TR}$  varying directly with  $CGR_{50}$ , but for sorghum,  $NUE$  increased with temperature while for common bean,  $NUE$  was nearly constant up to temperatures that were limiting growth and then more than doubled in value (Fig. 3C and 5C). Such contrasting responses could have major implications for estimations of impacts of global warming on crop production and suggest a need for more detailed analyses of N dynamics at high temperatures.

Cardinal temperatures for leaf appearance and leaf expansions rates from Peacock and Heinrich (1984) suggest a  $T_{base}$  of 14°C,  $T_{opt2}$  of 33 to 34°C, and  $T_{max}$  over 43°C ( $T_{opt1}$  was not extractable from their descriptions). Modeled responses for  $LAI_{50}$  and main-stem node number indicated values of  $T_{base}$  substantially below 14°C. The

$T_{opt2}$  for  $LAI_{50}$  was only 24°C, and for main-stem node number, values remained maximal to 41°C (Fig. 3A).

These examples are only indicative of the types of comparisons that are possible with the assessment procedure, but they demonstrate that a structured procedure can reveal diverse features of crop models that are not readily obtained from descriptions of the models per se. Thus, the procedure appears to satisfy the goal of providing a balanced assessment of modeled responses to temperature without requiring access to model source code. Where issues are identified, the models can be tested in more detail, and further information from experiments can be sought to guide interpretation, possible model revisions, and research prioritization.

For both models, the assessments identified issues related to what might be termed “unrealistic responses” occurring under conditions of near-zero or negative growth. For CSM-CROPGRO-Drybean, examples included grain N concentration reaching a value of 0% at 35°C and the fluctuations in  $SLA_{50}$ , main-stem node number, and canopy height from 35 to 40°C. Similar problems involve linkages between growth and development. Models usually assume that phenology is unaffected by biomass accumulation or, at most, is modified only by severe water or N deficits. This approach works remarkably well, but when growth is severely reduced due to thermal stress, the approach may be problematic. In common bean, while  $TCM_{harv}$  had a  $T_{max}$  of 31°C, all three phases of development continued to at least 40°C (Fig. 4B). Similarly, in both models, root elongation continued at temperatures where root mass was declining rapidly (Fig. 3B and 5B). There is a need for research to clarify interactions of crop processes at near-lethal temperatures.

The question arises of how best to evaluate the modeled responses against data from field or controlled-environment studies. For some variables, the responses can be compared against published data, as illustrated above. A logical source of additional evaluation data is studies using locations or sowing dates to obtain a range of temperature regimes (e.g., White et al., 1992; Ogoshi, 1995), but there are limitations to the temperature regimes obtainable from natural environments. Figure 7A presents variation in mean temperature of the six warmest months for 1000 sites in the Americas from 26°S to 35°N latitude based on data from the FAOCLIM 2.01 database (FAO Agrometeorology Group, 2001). Even at sea level, few locations have six-month mean temperatures over 30°C (Fig. 7A). An additional concern is within-season temperature variation. If one accepts a difference of no more than 2°C among monthly means in a six-month period, sites should be sought primarily in latitudes below 23°C (Fig. 7B) with due consideration to adequacy of soils, protection from excessive precipitation, and access to research facilities. Another alternative would be to combine an elevation gradient with treatments to artificially influence the temperature, such as by heat tunnels (Schrope et al., 1999) or infrared heating (Harte et al., 1995). Controlled environments are another option but, as noted in the introduction,

can introduce artifacts that limit their usefulness for studying crop-level responses.

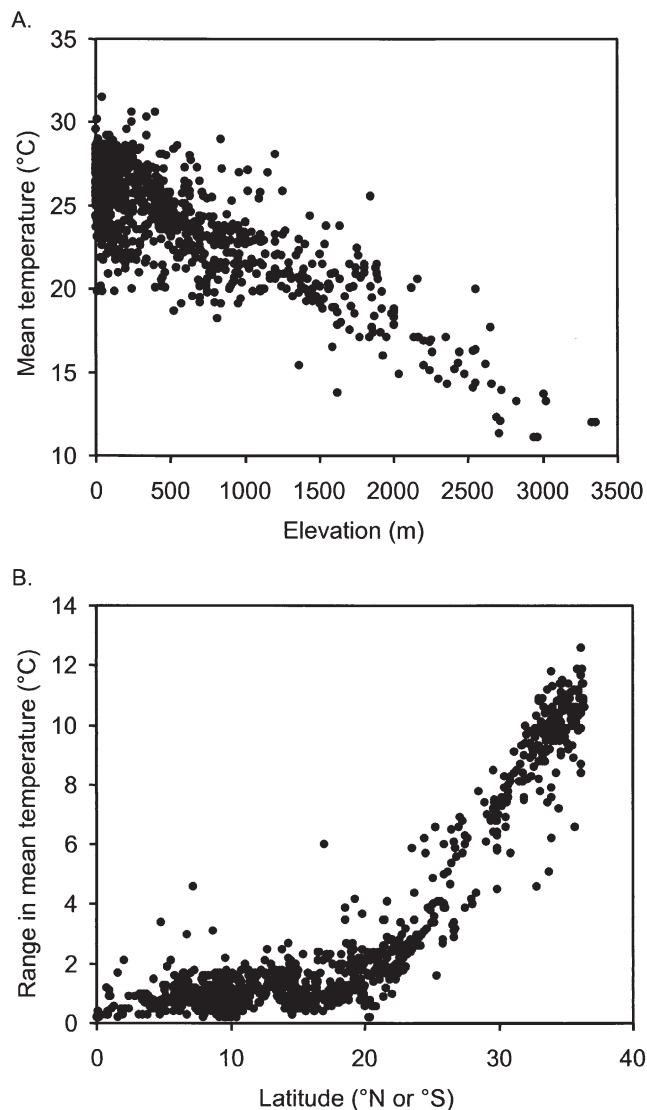
The suggested procedure for assessing temperature dependencies of models is seen as a set of guidelines that should evolve through testing and use. Improvements that might be sought include characterizing partitioning among leaf, stem, and root growth and the balance among photosynthesis, respiration, and senescence. Considering both above- and belowground crop mass might provide a more accurate measure of crop mass, reducing irregularities in curves due to variation in partitioning to roots vs. shoots. This appeared to be an issue, for example, in curves of  $TCM_{30}$ ,  $TCM_{50}$ , and  $CGR_{50}$  in sorghum (Fig. 2A and 3C).

For common bean, the shapes of the curves for the root/shoot ratio and NUE were strongly concave (Fig. 5B and 5C), making it impossible to define cardinal temperatures and resulting in arguably misleading values of RSI. Calculating parameters based on their reciprocals (i.e., a shoot/root ratio and kg of N required per kg of dry mass produced) might resolve this problem. However, given that the values for the root/shoot ratio and NUE for sorghum were less problematic, it seems prudent to wait until more models are assessed or field data are available to suggest whether the two curves for common bean are sound.

Another concern is how well irrigation and fertilizer regimes can be matched to crop requirements, which might result in smoother response curves. Given that models differ in how they estimate water and N dynamics, these inputs may have to be adjusted to ensure that no model is favored. For models that require atmospheric humidity and wind speed as inputs, a consensus would be needed on appropriate values to assume for weather inputs.

If standard conditions are agreed on for responses without effects of water or N deficits, then it should be easy to extend the overall approach to examine temperature response under water deficits or N deficits. The preliminary tests conducted with the sorghum (Fig. 6) and common bean models suggest that responses at lower temperatures, where greatest growth occurs, will show the largest effect of water or N deficit. This seems counterintuitive given the usual expectation that high temperatures exacerbate effects of abiotic stresses but is at least partially attributable to the large effect of a longer crop cycle and delayed maturity on crop growth and hence demand for water and N. The procedure could also be extended to short-term stresses, such as brief periods of elevated temperatures, although the need to consider stress acclimation, timing of onset, duration, and intensity would necessarily complicate the conditions used in the sensitivity analysis.

Recognizing that the seven categories might be too "information dense" for some users, it is also worth considering whether a simplified or preliminary assessment can be used to document model response with a smaller set of parameters. These might be  $TCM_{50}$ ,  $TCM_{harv}$ , grain yield, days to anthesis, and days to maturity on one graph and normalized values of HI, unit grain mass, grain number, and grain N concentration on a second



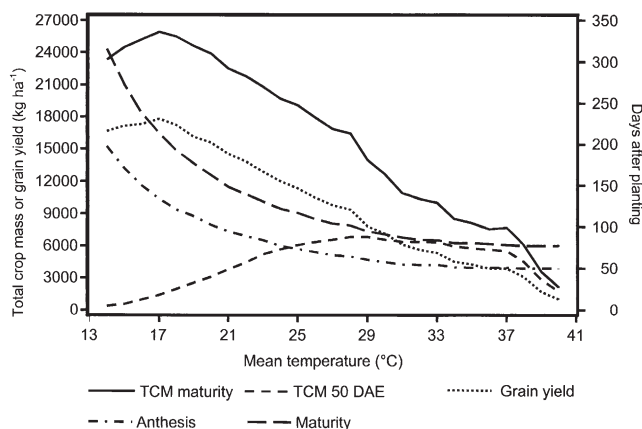
**Fig. 7. Relation between regimes of monthly mean temperature during the six warmest months for 1000 stations from 26° S to 35° N latitude in the Americas. Long-term monthly means are from FAOCLIM2.01 (FAO Agrometeorology Group, 2001). (A) Mean temperature vs. elevation. (B) Temperature range (warmest to coolest of the six warmest months) vs. absolute value of latitude.**

graph (as presented in Fig. 2D and 4D). These can be presented as a set of two graphs, using two y-axes in the first graph. By using absolute rather than normalized values for crop mass, grain yield, and phenology, the need for a table with maximum values is reduced, and interpretation is simplified, as shown in Fig. 8 for sorghum.

## CONCLUSIONS

Conducting sensitivity analyses with standardized inputs and considering the seven categories of temperature responses provided a robust and easily understood framework for evaluating model performance. Graphical representations were essential to the analysis, but quantifying responses through cardinal temperatures and the RSI facilitated comparisons across response categories and models. Relying on readily accessible





**Fig. 8. Response of the sorghum model CSM-CERES-Sorghum to constant mean temperatures with a daily range of 10°C as indicated by total aboveground crop mass (TCM) at a reference date (50 d after emergence) and harvest maturity and by grain yield and days to anthesis and to maturity.**

model outputs limits comparisons across models, but the data available from the sorghum and bean models were adequate to generate a wide range of insights into model performance. Such evaluations have clear value in guiding selection of models for specific applications and in suggesting priorities for further research and model development, especially when combined with complementary information from field or controlled-environment studies.

To facilitate performing similar analyses, the experimental conditions were specified using formats compatible with the DSSAT Version 4.0 shell (Hoogenboom et al., 2004), which partially implements standards developed by the International Consortium for Agricultural Systems Applications (Hunt et al., 2001). As other models and crop species are assessed, additional data sets and summary reports will be made available. A set of procedures for the statistical analysis program SAS Version 8 (SAS Institute Inc., Cary, NC, USA) is available from the first author to conduct the analyses, including graphing the responses, identifying cardinal temperatures, and calculating RSI values.

### ACKNOWLEDGMENTS

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