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Cardinal temperatures for wheat leaf appearance as assessed from varied sowing dates and infrared warming

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ABSTRACT

Accurate data on crop responses to temperature are essential for predicting the potential impacts of climate extremes. Air temperature can be precisely regulated in controlled environment chambers, but chambers seldom provide realistic radiation, photoperiod, wind and humidity regimes, which raise concerns as to whether responses quantified in such environments accurately reflect field performance. Field experiments employing sowing date (SD) and artificial warming treatments can provide a wide range of temperature regimes under otherwise natural field conditions. We analyzed temperature effects on main stem leaf appearance for the spring wheat (*Triticum aestivum* L.) cultivar Yecora Rojo using 15 sowing dates at Maricopa, AZ, USA. Six dates included infrared-based temperature free-air controlled enhancement (T-FACE) warming treatments. Mean air temperatures over the 15 periods of measurement varied from 11.6 to 33.2 °C. Our objective was to characterize the effect of temperature on leaf number, emphasizing air temperatures above 20 °C, a value often cited optimal for wheat development. An underlying concern was how different shapes of temperature responses functions might affect estimates of cardinal temperatures. For comparisons among four segmented linear functions, a quadratic function and two forms of the beta function, the best fit to the data was for a two-segment function with a base temperature (T_{base}) of 1.9 °C and an optimum (T_{optl}) of 22.2 °C. In attempting to estimate a second, upper temperature for maximum development (T_{optu}), the estimation process failed. This likely reflected the low frequency of data from mean air temperatures over 25 °C and possible severe stress responses at extreme low and high temperatures. The results further demonstrated the value of growing crops under a wide range of temperature regimes, which can be attained under field conditions through use of planting date and T-FACE treatments.

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1. Introduction

Predicting crop responses to climatic variation requires accurate data on temperature responses of component processes such as leaf development and photosynthesis. In reviewing reported effects of temperature on leaf formation in bread wheat (*Triticum aestivum* L.), few studies were found that estimated responses at daily mean air temperatures above 25 °C (Table 1). Controlled environments can provide high air temperatures, but such systems often impose regimes for radiation, photoperiod, wind and humidity that deviate substantially from field conditions. Two complementary options for exposing plant communities to a range of air temperatures are to use multiple sowing dates (e.g., Hay and Delécolle, 1989) and infrared warming with a T-FACE system (Kimball, 2005; Kimball et al., 2008).

T-FACE has been used in multiple field experiments, including a two year study at Maricopa, AZ that included 15 sowing dates, six of which had T-FACE treatments (Wall et al., 2011). Maricopa experiences large annual temperature variations, with daily maximum values that can exceed 45 °C in June. Frosts can occur in the winter, but nighttime temperatures are otherwise high enough for crop growth and development. For bread wheat at Maricopa, the recommended sowing date is from mid-November to mid-December. Slightly earlier sowings can suffer chilling or frost damage, especially in developing spikes. Late sowing reduces growth and grain yield largely due to reduced tillering, a shorter overall growth cycle, and high temperatures during grain fill (Ottman et al., 2012). The T-FACE treatments used target temperatures of 1.5 °C above ambient during the daytime and 3.0 °C at night; in practice, they warmed canopies to temperatures approximately 1.3 °C warmer in daylight hours and 2.8 °C at night (Wall et al., 2011). Previous papers reported on performance of the T-FACE system (Kimball et al., 2012a), grain yield responses (Ottman et al., 2012), leaf gas exchange and water relations (Wall et al., 2011), normalized

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Table 1

Cardinal temperatures for leaf appearance in wheat (*T. aestivum* L.) as reported in previous studies and from the sowing date and T-FACE study at Maricopa, AZ.

Reference	Germplasm tested[a]	Temperature regime	Environment	Response function	Cardinal temperature (°C)			Comments
					Base (T_{base})	Lower optimum or single optimum (T_{optl} or T_{opt})	Upper optimum (T_{optu})	
Friend et al. (1962)	Spring (1)	10, 15, 20, 25, 30 °C	Chambers	(None)		25		No model used. Value based on graphed responses
Gallagher (1979)	Winter (1)	1 sowing	Field	1-segment	0			
Klepper et al. (1982)	Winter (1)		Field	1-segment	3			No estimation
Baker and Gallagher (1983)	Winter (1)	7 sowings in 5 years	Field	1-segment	0			Leaf primordia
Bauer et al. (1984)	Spring (19)	7 environments	Field	2-segment	0	21		T_{opt} applied to maximum daily air temperatures (T_{max})
Baker et al. (1986)	Spring (6), winter (3)	2 years at 2 locations	Field	1-segment	0			
Del Pozo et al. (1987)	Spring (5)	5 sowings in 1 year	Field	1-segment	2.7			Leaf extension. Air temperature at 0.05 m above soil
Cao and Moss (1989)		Constant 7.5, 10, 12.5, 17.5, 20, 22.5, 25 °C	Chambers	Quadratic	0	22.5		
Hay and Delécolle (1989)	Winter (5)	15 sowings in 3 years	Field	1-segment	0			
Ritchie and NeSmith (1991)	(Not specified)	Constant plus undisclosed	Chambers plus undisclosed	3-segment	−4	16	33	Reanalysis of Cao and Moss (1989) and unpublished data
Sayed (1995)	Spring (1)	Constant 10, 20, 30 °C	Chambers	1-segment	−5.5			
Slafer and Rawson (1995)	Spring (2), facultative (1), winter (1)	Variable	Chambers	2-segment	−5.7 to −1.9	22		$T_{optu} < 25$ °C
Jame et al. (1998)	Spring (2), facultative (1), winter 5)	Constant and variable	Chambers	Beta	0	20.7–24.4		T_{base} not estimated Reanalysis of Cao and Moss (1989) and Slafer and Rawson (1995)
Jamieson et al., 2008	Spring (1)	Constant	Chambers	2-segment	0	≥31		Soil temperature
This paper	Spring (1)	15 sowings, including 6 with T-FACE	Field	1-segment 2-segment	−1.5 1.9	 22.2		Three-segment model failed to converge

[a] Number in parentheses indicates the number of lines or cultivars tested.

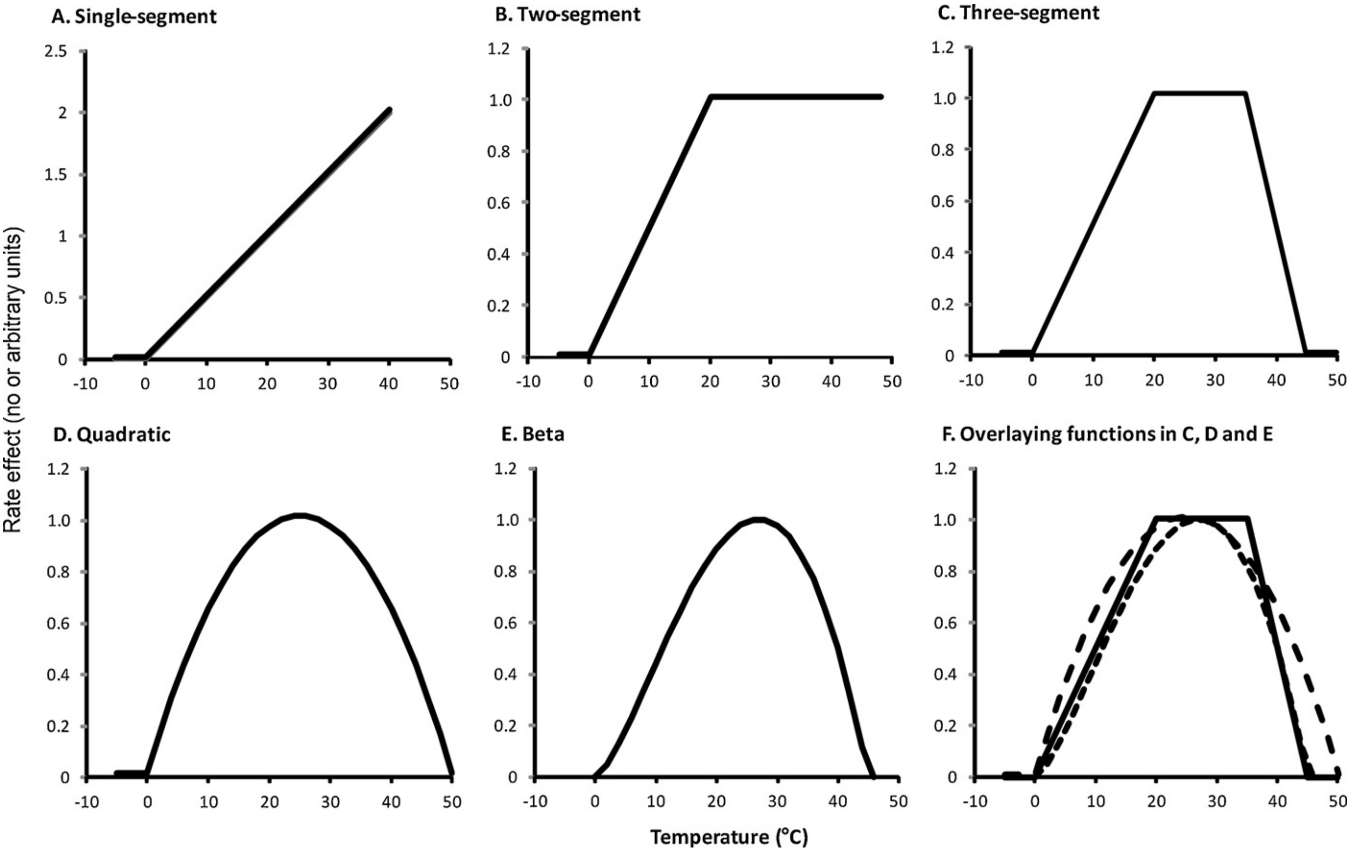

Fig. 1. Comparison of functions that were used to describe temperature effects on leaf appearance rate. The scales of the vertical axis are arbitrary, but for the functions represented in figures B–F, the scale most often varies from 0 to 1 and is used to reduce the leaf appearance rate from a maximum value.

difference vegetation index (Kimball et al., 2012b) and phenology (White et al., 2011). Large effects both of sowing dates and warming treatments were observed throughout. The analyses of phenology assessed whether the plant responses under T-FACE were comparable with those measured under the natural variation in temperature from sowing dates and concluded that the T-FACE treatments induced no artifacts (White et al., 2011).

Main stem leaf number (L) is often used to predict leaf area development and phenology, so accurate modeling of temperature effects on leaf appearance is of widespread interest (Wilhelm and McMaster, 1995). Similar to other developmental processes, L can be predicted by integrating a developmental rate over time. The leaf appearance rate (R) can be estimated from a potential, maximal rate ($R_{\max}$), which is reduced as a function of temperature (T) or other factors,

$$R = R_{\max} \times F(T) \tag{1}$$

or

$$R = R_{\max} \times K(T, x, y), \tag{2}$$

where $F(T)$ is a function of temperature and $K(T, x, y)$ is a function of temperature plus other factors such as photoperiod or water deficits, here represented by x and y. The ranges of the two functions are usually scaled from 0 to 1. If the time step for integration is one day and T is the daily mean air temperature, this approach is numerically equivalent to summing so-called thermal time or heat units. The phyllochron is equal to the inverse of R, and the phyllochron index is the inverse of $R_{\max}$. Research to improve prediction of L predominantly seeks either to improve the specification of $F(T)$ or $K(T, x, y)$ or to estimate $R_{\max}$ for specific germplasm. There is considerable uncertainty over the shape of $F(T)$ and over the necessity of using the more complex $K(T, x, y)$. Following the strategy that it is prudent to examine simpler mechanisms prior to invoking more complex hypotheses, we emphasize $F(T)$ in this report.

The simplest form of $F(T)$ involves a single linear segment above a base temperature (T_{base}), below which $R = 0$ (Fig. 1A), and is the most widely used function (Table 1). The next level of complexity is a two-segment function (Fig. 1B), where $F(T) = 1$ above the lower limit of the “optimum” temperature range (T_{optl}). The three segment function (Fig. 1C) assumes that in addition to T_{optl} there is a second, upper limit (T_{optu}) above which $F(T)$ declines linearly to a limiting temperature (T_{lim}) where leaf development ceases ($R = 0$) with any further increases in temperature. Among other forms of $F(T)$ are a truncated quadratic curve (Fig. 1D) used by Cao and Moss (1989), and the beta function (Fig. 1E; Yan and Hunt, 1999), both of which assume a single optimum (T_{opt}). Fig. 1F shows that for a hypothetical case where $T_{\text{base}} = 0$, the differences among different functions is surprisingly small for the interval from T_{base} to T_{optl} or T_{opt}.

The physiological basis for cardinal temperatures is unclear. The simplest hypothesis is that T_{base} and T_{opt} relate to enzyme kinetics (e.g., Parent and Tardieu, 2012). T_{base} thus represents the temperature below which there is no metabolic activity. T_{opt} or T_{optu}, would represent the temperature above which metabolic activity declines or ceases due to loss of enzyme function. Possible more complex mechanisms might include changes in membrane state (e.g., Raison et al., 1980; Hughes and Dunn, 1996) or the action of “thermostat genes” that regulate adaptive responses to low or high temperatures (Deal and Henikoff, 2010).

Our objective was to characterize the effect of temperature on R with emphasis on mean daily air temperatures near or above 20 °C, which is often reported as an appropriate value of T_{optl}.

Table 2

Air temperatures for each sowing date including whether heaters were used. For daily mean temperature (T_{mean}), values are the mean, maximum and minimum over the period when leaf number was measured. Extreme daily values are the largest value among maximum daily air temperatures (T_{max}) and the lowest value among daily minimums (T_{min}) measured for a given sowing date and treatment.

Sowing date[a]	Warming treatment	Air temperature over the period of measurement (°C)				
		T_{mean}			Extreme daily values	
		Mean	Maximum	Minimum	T_{max}	T_{min}
13-Mar-2007	Control/reference	18.3	23.4	12.0	33.9	3.2
13-Mar-2007	T-FACE	20.5	25.6	14.5	35.8	6.0
19-Apr-2007	Control	25.6	29.4	18.0	39.5	9.4
12-Jun-2007	Control	33.2	35.0	29.4	45.1	17.4
25-Jul-2007	Control	31.5	35.2	26.4	43.3	21.8
17-Sep-2007	Control/reference	21.6	28.5	16.6	35.9	5.4
17-Sep-2007	T-FACE	23.0	29.2	17.4	36.3	6.4
30-Oct-2007	Control	11.6	21.6	4.2	32.3	−5.0
02-Jan-2008	Control/reference	11.9	21.4	4.7	30.7	−5.0
02-Jan-2008	T-FACE	13.7	23.5	7.0	32.5	−2.3
13-Feb-2008	Control	16.1	23.7	10.5	33.0	−0.2
10-Mar-2008	Control/reference	18.9	24.1	11.6	36.1	0.5
10-Mar-2008	T-FACE	21.0	26.0	13.7	37.2	3.0
28-Apr-2008	Control	23.1	31.9	14.7	41.7	8.9
25-Aug-2008	Control	28.8	31.2	25.7	41.3	16.6
29-Sep-2008	Control/reference	17.1	24.9	8.9	36.2	0.2
29-Sep-2008	T-FACE	19.4	27.1	10.7	37.8	3.0
27-Oct-2008	Control	12.5	18.7	3.8	30.7	−2.3
01-Dec-2008	Control/reference	11.9	19.7	3.8	29.3	−2.3
01-Dec-2008	T-FACE	13.9	21.8	6.2	30.2	0.4
12-Jan-2009	Control	14.3	21.3	7.5	31.9	−1.2

[a] Seed were sown in dry soil, so the reported sowing date corresponds to the effective date, which was the date of the first irrigation.

However, in reviewing the literature for effects of temperature on leaf development, differences in cardinal temperatures were found (Table 1), which were associated with differences in assumed $F(T)$, as well as experimental conditions and germplasm. An underlying hypothesis was that different versions of $F(T)$ would result in substantial differences in estimates of cardinal temperatures. The work takes advantage of the unusually wide range of natural air temperatures attained in the Maricopa sowing date and T-FACE study.

2. Materials and methods

The spring wheat cultivar Yecora Rojo (Qualset et al., 1985) was sown on a Trix clay loam [fine-loamy, mixed (calcareous) hyperthermic Typic Torrifluvent] at Maricopa, AZ, USA (33.07°N lat; 111.97°W long; elevation 360 m) on 15 dates from March 2007 to January 2009 (Table 1), six of which included T-FACE treatments. Field conditions and management were detailed by Wall et al. (2011). Relevant aspects of the study are summarized below.

The T-FACE system of Kimball et al. (2008) was arrayed as follows. Warmed plots contained six 1000-W infrared ceramic heaters (Model FTE-1000,[1] Mor Electric Heating Association, Inc., Comstock Park, MI, USA) positioned in a 3-m-diameter hexagonal array and elevated 1.2 m above the wheat canopy. Individual heaters measured 24.5 cm × 6.0 cm and were housed in reflectors measuring 25.4 cm long × 9.9 cm wide × 8.9 cm high. The target warming was +1.5 °C during the daytime and +3.0 °C at night. Warming was controlled by comparing canopy temperatures, measured by infrared thermometry, on the warmed and reference plots (Kimball, 2005; Model IRR-PN, Apogee Instruments Inc., Logan, UT, USA).

For the six sowing dates that included T-FACE treatments, plots were arrayed as 3 × 3 Latin squares with control, warmed and reference plots. The reference plots differed from control plots by including the infrared thermometers and an array of dummy heaters consisting of empty reflector housings. For sowing dates with only the control treatment (no real or dummy heaters), plots were replicated three times.

Plots were sown in strips 11 m wide × 37 m long, allowing three 11 m × 11 m plots per strip. In the center of each plot, a 3-m-diameter hexagonal area was delineated for measurements (Ottman et al., 2012). The wheat was sown on the flat in rows 0.19 m apart at a rate of 134 kg ha^{-1} (288 seeds m^{-2}) to produce a final target stand of approximately 200 plants m^{-2}. The crop was managed to provide near-optimal conditions within the constraints posed by the sowing dates. Crops were fertilized at sowing with monoammonium phosphate sulfate (16-20-0), providing 54 kg ha^{-1} of nitrogen (N) and 67 kg ha^{-1} of phosphorus (P_2O_5). Additional nitrogen was supplied as urea–ammonium nitrate through drip irrigations, at a rate of approximately 50 kg nitrogen ha^{-1} per application. Surface drip irrigation was used except for one sowing date where initially, sprinkler irrigation was included to improve seedling emergence. Plots were irrigated uniformly to avoid water deficit with the exception of T-FACE plots which also received supplemental irrigations amounts calculated to equal their realized evapotranspiration as expected with future global warming, assuming air warming but a constant relative humidity (Kimball, 2005, 2011). Kimball (2005) estimated a factor of 1.063 times the amount of evapotranspiration from the reference plot per degree of warming. Thus, for 1.5 °C of daytime warming, supplemental amounts of 10% were applied to T-FACE plots. Maximum (T_{max}) and minimum (T_{min}) values of daily air temperatures were obtained primarily from a weather station in the experimental area. When temperature data were unavailable, data were obtained from a station located 1.2 km from the experiment and were adjusted to match the on-site station values using a regression procedure. Both stations had a temperature sensor height of 2 m. Daily mean air temperature (T) was calculated as $T = 0.5 \times (T_{max} + T_{min})$.

Main stem leaf number was measured from plants in two 1 m-long rows within the plot area. Leaves were counted as emerged based on Haun stage (Haun, 1973). Initial evaluations were based on visual averages of plants on the 1 m-long rows, but at approximately the fourth leaf stage (Haun 4.0), four plants per row were

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[1] Mention of a specific trade name is made for identification only and does not imply endorsement by the United States Department of Agriculture over similar products not mentioned.

Table 3
Cardinal temperatures for leaf number as estimated for different temperature response functions using the Maricopa, USA dataset. Also given are the estimated phyllochron index and the root mean squared error (RMSE) for predicted leaf number. Phyllochron index was calculated as the inverse of the maximum leaf appearance rate.

Function	Cardinal temperatures (°C)								Phyllochron index (°C leaf^{-1})	RMSE (leaves plant^{-1})
	Base (T_{base})		Lower optimum (T_{optl}) or optimum (T_{opt})		Upper optimum (T_{optu})		Limiting (T_{lim})			
	Value	SE	Value	SE	Value	SE	Value	SE		
One-segment	−1.5	0.8							108	0.35
Two-segment	1.9	0.7	22.2	0.9					83	0.31
Three-segment	−0.1	0.6	23.4	1.2	30	NA[b]	50[c]		81	0.32
Inverted-V	2.6	0.4	23.5	NA			45[c]		79	0.33
Quadratic	3.7	0.6	34.8	3.3					115	0.33
Beta, $T_b = 0$	0[c]		27.5	0.8			43.9	1.9	109	0.32
Beta, T_b varied	−1.9	4.3	29.4	4.3			44.7	2.8	123	0.32

[a] Includes optimum for models with only optimal temperature.
[b] Not available because the estimation failed to converge.
[c] Value assumed fixed for estimation of other temperatures.

marked for subsequent counts. To avoid problems due to more rapid emergence of the first two leaves (Peterson et al., 1988), data for L less than 1.6 were excluded. Similarly, wheat plants often differ in final L (L_f), which is attributed to the existence of sub-populations of plants that differ for R (Hay and Delécolle, 1989). If some plants reach L_f earlier than others, the mean value of L declines relative to the expected trend. Thus, values of $L > 7$ were also excluded.

The utility of the five functions presented in Fig. 1 were tested by using them to model L. An "inverted-V" function was included by fitting the three segment model but assuming that $T_{optl} = T_{optu}$. Cardinal temperatures were estimated using the NLIN procedure of the SAS statistical package (V9.2, SAS Institute; Cary, NC, USA) as appropriate for the formulation of $F(T)$. For each function, cumulative growing degree days (GDD) were calculated as the sum from sowing onward, applying restrictions to the sums as per the version of $F(T)$ being tested. The values of GDD were then used to estimate L as:

$$L = a + b \times \text{SD} + c \times \text{GDD} + \varepsilon \qquad (3)$$

where a is the intercept, b is a vector of coefficients for effects of sowing date (SD), c is the linear response to GDD, and ε is the random error. This model is equivalent to fitting a series of parallel lines for L vs. GDD but assuming different intercepts for each SD. The slope c is equivalent to R_{max}. The assumption of different intercepts accounted for possible differences in seedling emergence that might reflect effects of sowing depth, initial soil conditions, or seed dormancy for different sowing dates.

Regressions testing the relative performance of different functions were conducted using the GLM procedure of SAS. Versions of $F(T)$ were compared through linear regression using sequential entry of effects, providing Type I sums of squares (White et al., 2007).

3. Results

For the period of observations of L, the sowing date and T-FACE treatments provided mean daily air temperatures ranging from 11.6 to 33.2 °C (Table 2). The warmest single-day value was 35.2 °C, and the maximum air temperature for any day was 45.1 °C (Table 2). For the six sowings with T-FACE treatments, the mean increase in air temperature was 1.6 °C.

Using the one-segment form of $F(T)$, T_{base} was estimated as −1.5 °C (Table 3). For the two-segment function, T_{base} was 1.9 °C

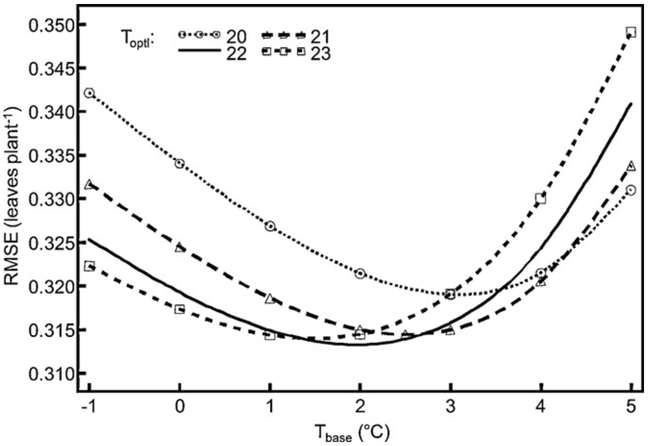

Fig. 2. Variation in root mean squared error (RMSE) for predicted main stem leaf number assuming a two-segment function defined by a base temperature (T_{base}) and a lower optimum temperature (T_{optl}) values varied on a 1 °C × 1 °C grid. The measured values of leaf number are from 15 sowing dates at Maricopa, USA, six of which included infrared warming (T-FACE) treatments.

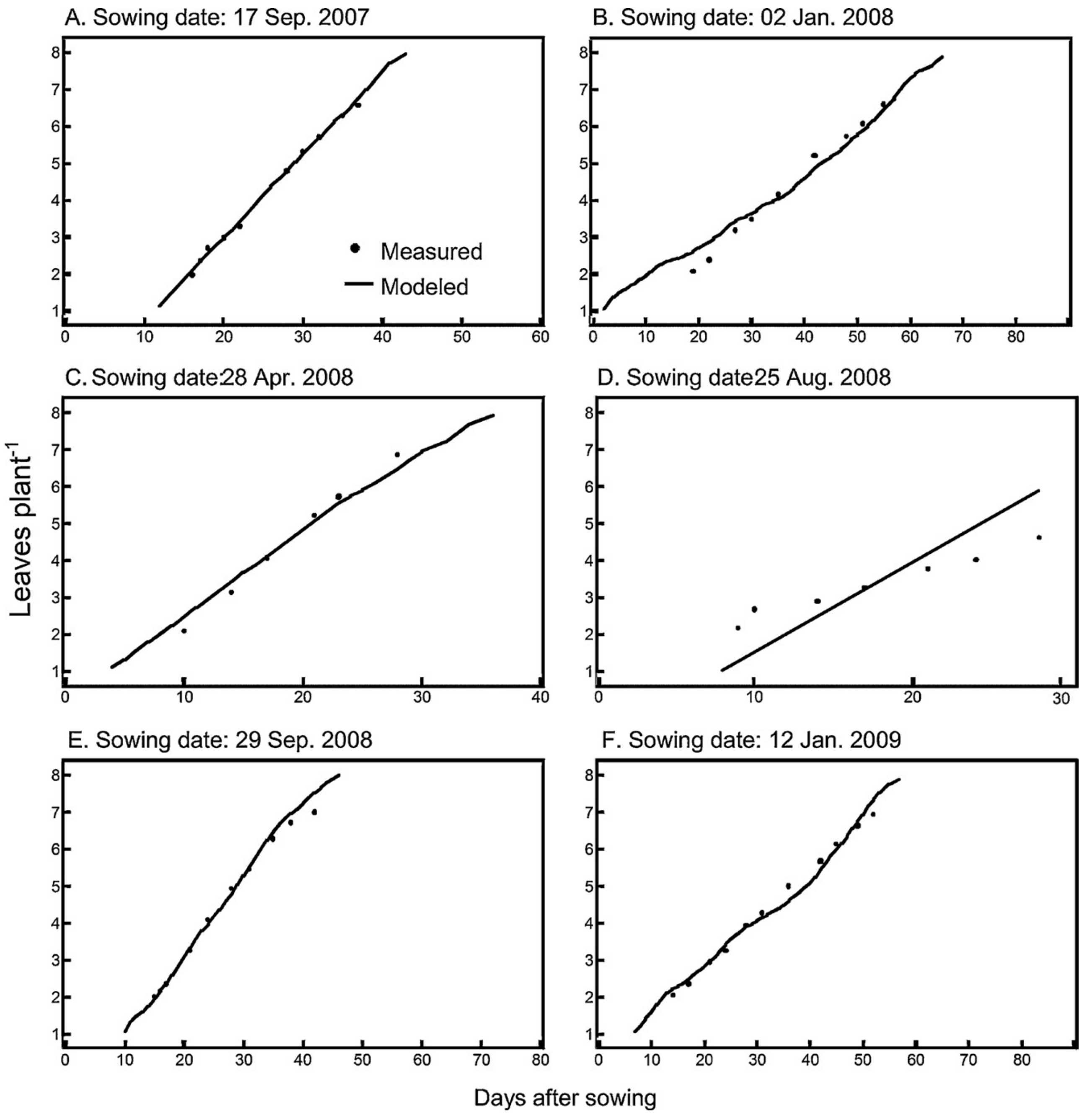

Fig. 3. Examples of measured and modeled leaf numbers vs. calendar days for six sowing dates. The two-segment temperature function assumed a base temperature of 1.9 °C and lower optimum of 22.2 °C. All data are means of control plots (and of reference plots, if present).

and T_{optl} was 22.2 °C (Table 3 and Fig. 2). In testing the potential benefit of including an upper optimum (T_{optu}) and an absolute upper limit (T_{lim}), respectively, the optimization process failed (non-convergence) even after attempts to fit an equation where individual cardinal temperatures were assigned fixed values. We then assumed a value of 50 °C for T_{m} and used it to fit the values for T_{base}, T_{optl}, and T_{optu} listed in Table 3. For an inverted V-function, the optimization also failed (Table 3).

The quadratic function had a T_{base} of 3.7 °C and a single optimum at 34.8 °C (Table 3), but the RMSE was greater than for the one- and two-segment functions. The beta function fitted with $T_{\mathrm{base}} = 0$ °C had an optimum at 27.5 °C and T_{lim} at 43.9 °C. Allowing T_{base} to vary with the beta function, estimated T_{base} as −1.9, T_{opt} as 29.4 and T_{lim} as 44.7, but the standard errors of these estimates were large, indicating no improvement over assuming $T_{\mathrm{base}} = 0$ for the beta function (Table 3). As with the quadratic function, RMSE values were larger than for the one- and two-segment functions.

An analysis of variance testing for sequential improvement with more complex versions of $F(T)$ showed that the two-segment function explained 1.2% of the Type I sums of squares (SS) over the 82.4% attributed to the one-segment function, whereas the three-segment function explained less than 0.1% of the remaining SS (Table 4). The 11.9% of SS attributable to sowing dates is also of note (Table 4), suggesting important, unexplained effects of sowing date.

Fig. 3 compares selected sets of measured and modeled L, using the two-segment function. While overall agreement appeared good, the plots evidenced systematic biases that differed in timing and direction over the sowing dates considered.

Table 4
Analysis of variance for prediction of leaf number using three versions of the segmented temperature response functions. Sources of variation are introduced sequentially (Type I sums of squares) to test for incremental improvement in explanatory power through use of more complex models (White et al., 2007). The one-segment model assumed a base (T_{base}) of −1.5 °C, the two-segment function assumed T_{base} = 1.9 °C and a lower optimum (T_{optl}) of 22.2 °C, and the three-segment function assumed T_{base} = −0.1 °C, T_{optl} = 23.4 °C, an upper optimum of 30.0 °C and a limiting value of 50 °C.

Source	df	SS	SS (%)	*F*	*F*-probability
Sowing date	14	84.8620	11.7	61.81	<0.0001
1-segment	1	613.7949	84.5	6258.53	<0.0001
2-segment	1	7.4729	1.0	76.20	<0.0001
3-segment	1	0.0011	0.0	0.01	0.9154
Residual	271	26.5779	3.7		

Values of the estimated phyllochron index ($1/R_{\max}$) are given in Table 3. As expected, these tended to increase with the range between the base temperature and lower or absolute optimum (r = 0.96, P < 0.01).

4. Discussion

Our results, based on a single spring wheat cultivar and location, support use of a two-segment function with T_{base} of 2 °C and T_{optl} of 22 °C (Figs. 2 and 3) over the alternative functions considered. A value of 2 °C for T_{base} is higher than most of the estimates in Table 1. One explanation is that in failing to consider T_{optl} or its equivalent, some estimates of T_{base} may be biased lower, as we found when our data were tested with the one-segment vs. two-segment functions (Table 3). A second cause may relate to differences between air and plant temperatures. Under the low humidity and clear sky conditions of Maricopa, canopy surface temperatures averaged 4.5 °C lower than air temperatures (Kimball et al., 2012b). Thus, an air temperature of 2 °C at Maricopa might affect plant development similar to 0 °C air temperature (or cooler) in an environment where daily mean air and plant temperatures were closer. A similar mechanism might explain values of T_{base} as low as −5 °C from growth chambers, where soil temperatures can be warmer than chamber air temperature by several degrees (Watts, 1975). A third explanation is that the cultivar grown, Yecora Rojo, is adapted to winter-sown spring wheat production systems and may simply be adapted to warmer conditions than germplasm tested in other studies.

As emphasized by Jamieson et al. (2008), further improvements in predicting L likely require more accurate measurements of temperatures in the shoot apex and expanding leaf tissue. Given the various sources of uncertainty, we also argue that other than the need to consider an optimal temperature for L, there is as yet insufficient data to test for improved prediction using different functions such as presented in Fig. 1, or of considering additional factors such as photoperiod or water deficits. An important corollary of this uncertainty is that debates on the constancy of the phyllochron index (Jamieson et al., 2008) have limited value because estimates depend on the assumed form and parameter estimates for $F(T)$ (Table 3).

Four sowing dates experienced mean air temperatures above 25 °C (Table 2). Two of these failed to reach flag leaf stage. For the 25 July 2007 treatment, L_f was 3.9, and for 25 August 2008, it was 4.6. In Fig. 3D, it appeared that while the first two leaves emerged rapidly, subsequent leaves were much slower to develop. Since the primordia of the first two to four leaves exist in the embryo (Williams, 1960; Peterson et al., 1988), high-temperature effects on R may involve different temperature responses for expansion of preformed primordia and for initiation of new leaves.

Table 4 indicates that about 12% of variation in L was attributable to differences in SD exclusive of the temperature effect. GDD was calculated from SD onward, so the data imply a need to understand factors affecting germination and seedling emergence. For sowing date experiments, this might include considering slight differences in soil tilth and moisture content that affect depth of sowing and initial physical contact between the seed and soil.

The results confirm the value of using multiple sowing dates to expose plants to a wide range of temperature regimes. For future studies at locations similar to Maricopa, a possible improvement would be to include more sowing dates that expose plants to mean temperatures over 25 °C. However, based on our experience, crop failures due to excessive heat (instantaneous air temperatures over 40 °C) would occur with some sowings. T-FACE treatments also can provide additional temperature combinations.

5. Conclusions

Analysis of wheat leaf appearance data from the 15 sowing dates, six of which included T-FACE treatments, suggested a value of 2 °C for T_{base} and of 22 °C for T_{optl} and that there was no benefit from using more complex forms of $F(T)$. Nonetheless, there is considerable uncertainty in the value of T_{optu}, and hence, the utility of more complex functions. Thus, there is need for additional research under field conditions with mean air temperatures well above 25 °C. Such conditions are readily achievable at Maricopa through sowing dates outside of the normal dates for commercial wheat production. T-FACE treatments can usefully extend the temperature range of temperatures.

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