

Approaches to Modeling Potato Leaf Appearance Rate

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ABSTRACT

Two approaches quantifying potato (*Solanum tuberosum* L. cv. Kennebec) leaf appearance rates were evaluated: a thermal time approach using the phyllochron, and a nonlinear temperature response approach using a modified β distribution function. Leaf appearance measurements at six temperature treatments (14/10, 17/12, 20/15, 23/18, 28/23, and 34/29°C thermoperiods with a 16/8 h cycle) were obtained from three SPAR (soil–plant–atmosphere–research) chamber experiments at 450 (D0), 370 (D1), or 740 (D2) $\mu\text{mol mol}^{-1}$ atmospheric CO_2 concentration. Independent data from a field study and the literature were obtained. The $[\text{CO}_2]$ effects on leaf appearance rate were not significant ($P \leq 0.05$). Leaf appearance rate increased from 12 to 27.2°C and declined with increasing temperature for all SPAR data except D2. Data from D0 and D1 were pooled to estimate model parameters. Phyllochrons of 28.2 and 24.3°C-d leaf⁻¹ (4°C base temperature) were obtained with all temperature treatments and without the 34/29°C treatment, respectively. Parameters for the modified β distribution function were 39.5°C for the ceiling temperature, 27.2°C for the optimum temperature at which the leaf appearance rate is maximum, and 0.96 leaves plant⁻¹ d⁻¹ for the maximum leaf appearance rate. Both approaches were comparable with values reported in the literature and were suitable for simulating leaf appearance in the field study (root mean square deviations of 3.2 and 2.6 leaves for thermal time and response function, respectively). The temperature function approach has advantages in that nonlinear relationships, particularly those at warmer temperatures, can be included in a single equation with biologically meaningful parameters.

POTATO MODELS typically simulate canopy growth and development by forecasting daily or hourly increases in total leaf area index based on inputs for environment and plant nutritional status (e.g., International Benchmark Sites Network for Agrotechnology Transfer, 1993; Kooman and Haverkort, 1995; Shaykewich et al., 1998). Conceptual C pools for total leaf and stem dry mass are then computed through the use of empirical partitioning coefficients as opposed to predicting individual leaf appearance, expansion, and duration. Models using this “big-leaf” approach have been shown to be adequate for simulating yield within the specific geographic regions for which they were developed; however, this level of detail may limit the model’s ability to accurately simulate potato production under different climates, soil types, and management practices

without extensive parameter calibration (Vos, 1995). A more mechanistic level of detail at which individual organs can be simulated will allow incorporation of recent advances in leaf-level gas exchange modeling (e.g., Kim and Lieth, 2003) and is needed for developing visual or three-dimensional canopy architectural components that can improve decision support capability (Fournier and Andrieu, 1998). Improving the level of detail in potato models will facilitate both scientific understanding of potato canopy growth and development and improve management prescriptions for farmers.

One reason for the lack of detail in modeling potato canopy development is the scarcity of published data on potato leaf appearance rates. The literature consists primarily of appearance rates measured under controlled environments in a small range of air temperatures for just a few cultivars (Cao and Tibbitts, 1995; Firman et al., 1991, 1995; Kirk and Marshall, 1992; Vos and van der Putten, 1998). To the best of our knowledge, leaf appearance data from controlled environments have not been compared with results from field studies, and leaf appearance rates are typically not measured in field work. Moreover, information on potato developmental responses to climate have been primarily limited to temperate regions (e.g., Dawes et al., 1983; Haun, 1975) even though there has been interest in potato production in tropical environments (Manrique et al., 1989).

The rate of leaf appearance in potato is primarily influenced by air temperature (Struik and Ewing, 1995; Vos, 1995). These rates are not significantly affected by day length, unlike some cereal crop responses where photoperiod effects are important (Streck et al., 2003; Xue et al., 2004). While the total number of leaves that form in a potato canopy is sensitive to photoperiod due to its effect on lateral branch formation, carbohydrate partitioning, and the number of leaves that form per stem, an effect of photoperiod on the rate of leaf appearance in potato has not been observed (Struik and Ewing, 1995). These findings have been incorporated into the “big-leaf” potato models, where early leaf area growth in potato is limited by temperature rather than assimilate supply (van Delden et al., 2000). Once canopy leaf area exceeds a predefined value, leaf area growth is then linearly related to intercepted photosynthetically active radiation (PAR) (e.g., International Benchmark Sites Network for Agrotechnology Transfer, 1993; Kooman and Haverkort, 1995; Shaykewich et al., 1998).

A thermal time approach is frequently used to characterize the rate of leaf appearance in many crops using the phyllochron, which is measured as the number of degree days (°C-d) required to produce a new leaf (Cao

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Abbreviations: DAE, days after emergence; MBD, mean bias difference; PAR, photosynthetically active radiation; RMSD, root mean square difference; SPAR, soil–plant–atmosphere–research.

and Moss, 1989). Developmental rate is assumed to be linearly proportional to increases in air temperature within a specified range. Although simple to compute and apply, the phyllochron approach is not used by potato models, presumably due to (i) the aforementioned lack of data on leaf appearance; (ii) the need to establish linearity of response between temperature and leaf appearance rate; and (iii) the need for additional equations to describe leaf appearance rate, should the desired temperature values for modeling purposes lie outside the specified range.

Nonlinear temperature response functions have also been used to simulate leaf appearance rate in other crops (e.g., Jame et al., 1998; Streck et al., 2003; Wang and Engel, 1998; Xue et al., 2004). Maize leaf appearance rate was accurately simulated using a modified β distribution function by Yan and Hunt (1999). The modified β function was also shown to describe a variety of other crop responses (including rates of seedling growth, leaf elongation, and dry matter production) across a wide range of temperatures and required fitting of three parameters, namely, the maximum rate of development, the highest temperature at which development ceases, and the temperature at which developmental rate is at maximum. This approach has an advantage over thermal time in that a nonlinear relationship with temperature and appearance rate can potentially be incorporated and described with a single continuous curve in which all parameters have a clear biological meaning (Yin et al., 1995).

Potato is an indeterminate crop where vegetative growth can continue well after floral initiation. Main stems terminate in an inflorescence, at which point typically two apical lateral branches develop from the axils of the second and third leaf below the inflorescence. Each of the apical lateral branches will also terminate in an inflorescence and give rise to additional orders of branching, depending on the plant assimilate supply and environmental conditions (Vos, 1995). Because of this growth pattern, relevant potato studies focus on leaf appearance on both main and apical lateral stems (Cao and Tibbitts, 1995; Vos and Biemond, 1992; Vos and van der Putten, 1998). Our objectives were to (i) provide data on potato main stem and apical lateral branch leaf appearance across a broad range of air temperatures for the Kennebec cultivar, (ii) derive expressions for potato leaf appearance rates using thermal time and nonlinear temperature response function approaches, and (iii) evaluate the suitability of the nonlinear temperature response vs. the thermal time approach for simulating leaf appearance using independent data sets from SPAR chambers and field data.

MATERIALS AND METHODS

Growth Chamber Experiments

Three growth chamber experiments (D0, D1, and D2) were conducted at the USDA-ARS facilities located in Beltsville, MD, in the summer of 2003 (D0) and 2004 (D1 and D2). Experiments used certified potato (cv. Kennebec) seed tubers planted in a 50:50 peat/vermiculite potting medium in 15-L

pots at a depth of 5 cm. Cut seed pieces of 12-mm diam. (10.0 g mean fresh weight) were used in D0 and whole tubers (54.9 g) in D1 and D2. Plants were grown in reach-in growth chambers (Environmental Growth Chambers, Chagrin Falls, OH) maintained at a 20°C day–night thermocycle with a 16-h photoperiod and 550 $\mu\text{mol m}^{-2} \text{s}^{-1}$ photosynthetic photon flux density (6.61 MJ PAR $\text{m}^{-2} \text{d}^{-1}$) until 5 DAE (days after emergence) in D0 and D1 and 12 DAE in D2. Plants were selected for uniformity based on the main-stem node count, thinned to a single main stem per pot, and relocated to one of six outdoor SPAR chambers at a density of 9 pots per chamber in D0 and 12 pots per chamber in D1 and D2.

The SPAR chambers were constructed with clear acrylic transparent to natural sunlight, were 2.3 m tall, and had a 1.0-m² cross-sectional area (horizontal production area of 1.0 m²) and a total chamber volume of 3360 L. Air was constantly recirculated in a closed loop at 3 m s⁻¹. Air temperature and relative humidity were monitored and controlled with TC2 controllers (Environmental Growth Chambers). Air temperature was controlled and water vapor removed by operating solenoid valves that injected chilled water through the cooling coils located in the air handler of each chamber. A dedicated Sun SPARC 5 work station (Sun Microsystems, Mountainview, CA) logged environmental data (air and soil temperatures, relative humidity, atmospheric CO₂ concentration ([CO₂]), and solar radiation) every 300 s. Mass flow controllers (Omega Engineering, Stamford, CT), located in the air ducting in each chamber, and a feed-forward, feed-back proportional-integral-derivative control algorithm were used to maintain [CO₂]. Pure CO₂ was supplied from a compressed gas cylinder. Thermocouples for measurement of air temperatures were shielded and aspirated. Photosynthetically active radiation, both ambient and inside each chamber, was measured with quantum sensors (LI-190 SA, Li-Cor, Lincoln, NE). Additional details may be found in Reddy et al. (2001).

The SPAR chambers were set to one of six different day/night temperature regimes: 14/10 (T1), 17/12 (T2), 20/15 (T3), 23/18 (T4), 28/23 (T5), and 34/29°C (T6) with a 16- and 8-h day/night thermoperiod. Average 24-h air temperatures (“observed” temperature) throughout the experiment and average, minimum, and maximum daily light integrals throughout the sample period for each treatment are reported in Table 1. A minimum of 450 $\mu\text{mol mol}^{-1}$ [CO₂] was maintained at all times during the day for D0, 370 $\mu\text{mol mol}^{-1}$ for D1 and 740 $\mu\text{mol mol}^{-1}$ for D2. Nighttime [CO₂] was uncontrolled and ranged between 370 and 771 $\mu\text{mol mol}^{-1}$ in all experiments. All other conditions were identical for each chamber. Fiberglass shading material, graded to match canopy depth, was erected around each chamber at DAE 14 and raised twice per week to match canopy height to minimize border effects. Plants were irrigated once per day with tap water (approximately 2 L per pot). Each pot received 500 mL of nutrient solution, as described in Robinson (1984), twice per week before 30 DAE and 1000 mL after 30 DAE.

Field Data

Field data were collected from a USDA-ARS experimental field at Beltsville, MD, in 2004. The 0.18-ha field was planted with potato (cv. Kennebec) using certified seed tubers (54.9 ± 10.04 g mean fresh weight). The field soil, classified as a Downer loamy sand (coarse-loamy, siliceous, mesic Typic Hapludult), is a very deep, well-drained soil with a low available water holding capacity. Potatoes were planted at a depth of approximately 20 cm in rows spaced at 0.76 m, and average plant spacing in rows was 0.38 m; planting density was 3.6 plants m⁻². The potatoes were not irrigated. Nitrogen fertilizer treat-

Table 1. Observed average 24-h air temperature (T_{air} with standard deviations in parentheses) and average, minimum, and maximum daily light integrals (photosynthetically active radiation, PAR) from emergence through the number of days corresponding to the last data point used in the analysis of the particular temperature treatment (Day no.). Relative humidity was maintained at 75% and the photoperiod was approximately 14.3 h. Treatment refers to temperature day/night setpoints on growth chambers (T1, 14/10; T2, 17/12; T3, 20/15; T4, 23/18; T5, 28/23; T6, 34/29°C).

Treatment	Day no.	T_{air} °C	PAR		
			Avg.	Min.	Max.
			MJ m ⁻² d ⁻¹		
D0, T1	31	14.5 (0.06)	8.0	2.4	11.9
D0, T2	31	16.3 (0.06)	8.0	2.4	11.9
D0, T3	28	18.7 (0.08)	8.4	3.4	11.9
D0, T4	31	21.5 (0.09)	8.0	2.4	11.9
D0, T5	31	25.0 (0.21)	8.0	2.4	11.9
D0, T6	28	29.7 (0.06)	8.4	3.4	11.9
D1, T1	23	14.2 (0.58)	8.1	3.2	11.2
D1, T2	27	16.2 (0.64)	8.1	3.2	11.2
D1, T3	28	19.3 (0.29)	7.9	2.2	11.8
D1, T4	34	21.8 (0.15)	7.8	2.1	11.8
D1, T5	41	26.0 (0.23)	7.8	1.7	11.8
D1, T6	41	30.9 (0.36)	7.8	1.7	11.8
D2, T1	29	15.6 (0.78)	7.0	1.9	10.6
D2, T2	36	17.0 (0.15)	6.5	1.9	10.6
D2, T3	33	19.6 (0.07)	6.4	1.9	10.6
D2, T4	33	21.4 (0.12)	6.4	1.9	10.6
D2, T5	33	24.5 (0.02)	6.4	1.9	10.6
D2, T6	36	28.3 (0.10)	6.5	1.9	10.6

ments, ranging from 0 to 280 kg N ha⁻¹, were applied throughout the field (17 DAE and immediately incorporated into the soil by hilling). Air temperatures during the leaf measurement period (9 May–28 June 2004) ranged from a minimum of 15.4°C to a maximum of 26.6°C, with an average daily value of 22.1 ± 2.87°C. Precipitation during this time was approximately 15.6 cm. Thirty-year normal values for the Beltsville area are 16.7°C minimum, 25.8°C maximum, and 16.8°C average temperatures, and 20.7 cm of precipitation. Photosynthetic irradiance ranged from a minimum of 1.7 to a maximum of 15.2, with an average daily value of 9.9 ± 3.29 MJ PAR m⁻² d⁻¹.

Other Data

Data published in Kirk and Marshall (1992), referred to as KM, were used to provide an additional independent dataset of potato leaf appearance rates from potato grown at varying temperature regimes. The data consists of appearance rates from controlled environment experiments ranging from 9 to 29°C average temperature with cv. Maris Piper.

Leaf Appearance Measurements

In monocotyledonous species, leaf appearance from the leaf sheath is observable (Gallagher, 1979). In dicotyledonous species such as potato, there are no distinct morphological events to mark the appearance of leaves. A minimum leaf length of the unfolded leaf from the apical bud is typically used to indicate appearance of the leaf rather than initiation (Cao and Tibbitts, 1995; Kirk and Marshall, 1992). A measurement of 0.5 cm in length from the stem to the tip of the leaf was used to indicate whether a leaf had appeared (Vos and Biemond, 1992). Leaf appearance measurements from growth chamber experiments D0, D1, and D2 were recorded for five plants from each chamber twice per week—starting on the day in which plants were transferred into the SPAR chambers—on the main stem and the uppermost apical lateral stems, including all secondary and tertiary branches. Leaf appearance measurements

from the field experiment were made six times during the growing season on potato main stems and the uppermost apical lateral stem at 6, 9, 16, 26, 30, and 51 DAE on the same plants. Nitrogen, at the concentration used in the experiment, does not influence leaf appearance rate (Vos and van der Putten, 1998; Vos and Biemond, 1992). Thus, measured plants were pooled among N treatments at each measurement date. Growth temperature strongly influences branching behavior in the potato canopy, where warmer temperatures facilitate the formation of higher orders of branching from apical stems and extend the period during which new leaves are added to the plant (Struik and Ewing, 1995; Vos, 1995). Measurements were stopped for each treatment based on the time at which leaf appearance on the apical branches ceased. An average ratio of 0.83 leaves on the second apical stem for every leaf on the uppermost apical stem was obtained from D1 and D2. Leaf counts on the second uppermost apical stem in D0 and field experiments were estimated using this factor (the least squares mean separation technique [PROC GLM from SAS Institute, 2001] indicated no significant differences between treatment means [data not shown]).

Data Analysis

Thermal time was calculated according to Eq. [1] using a base temperature of 4°C (Firman et al., 1991; Kirk et al., 1985) starting from DAE 0 for D0, D1, and D2. Leaf appearance data, consisting of the total number of main stem and apical branch nodes at each observation date, were regressed against the corresponding thermal time. The phyllochron (°C-d leaf⁻¹) was computed as the inverse of the slope of the regression line fitted to this plot. The REG procedure in SAS (SAS Institute, 2001) was used for this analysis. Observed average 24-h temperature (T_a) was calculated as the mean of all 5-min temperature observations within each 24-h period. The T_a for the field study was calculated from 15-min measurements from an automated weather station located <0.4 km away from the field.

$$TT = \sum_{i=1}^n (T_{a_i} - T_b) \quad i = 1 \dots n \quad [1]$$

where T_a is average 24-h temperature for day i (°C), T_b is baseline temperature (4°C), n is the total number of time steps (d) for calculation, and TT is thermal time in degree days from emergence (°C-d). The nonlinear temperature response approach used the modified β distribution function (Eq. [2]) discussed by Yan and Hunt (1999). The observed average daily temperature during the experiment (T) was obtained by averaging T_a from Eq. [1] across the time period for which leaf appearance rates were measured. Leaf appearance rates (leaves plant⁻¹ d⁻¹) were obtained as the slope of the regression of leaf numbers vs. time for each temperature treatment. Nonlinear optimization using the modified Gauss–Newton method in the NLIN procedure in SAS (SAS Institute, 2001) was then used to obtain the parameter values for T_{max} , T_{opt} , and R_{max} .

$$r = R_{\text{max}} \left(\frac{T_{\text{max}} - T}{T_{\text{max}} - T_{\text{opt}}} \right) \left(\frac{T}{T_{\text{opt}}} \right)^{\frac{T_{\text{opt}}}{T_{\text{max}} - T_{\text{opt}}}} \quad r = 0 \text{ at } T \leq 0$$

$$r = 0 \text{ at } T \geq T_{\text{max}} \quad [2]$$

where r is the leaf appearance rate (leaves plant⁻¹ d⁻¹), R_{max} is the maximum leaf appearance rate (leaves plant⁻¹ d⁻¹), T_{max} is the ceiling temperature where $r = 0$, T_{opt} is the optimum temperature where $r = R_{\text{max}}$, and T is the observed average daily temperature during the experiment (°C).

Table 2. Leaf appearance rates (LAR), correlation coefficients (r^2), and standard errors for each growth chamber experiment. Regression coefficients were: intercept -1.41 (leaves plant $^{-1}$ d $^{-1}$, SE = 0.25), linear 0.175 (leaves plant $^{-1}$ d $^{-1}$ °C $^{-1}$, SE = 0.023), and quadratic -0.0033 (leaves plant $^{-1}$ d $^{-1}$ °C $^{-2}$, SE = 0.0005) for analysis of leaf appearance rate vs. temperature between experiments.

Treatment	D0			D1			D2		
	LAR	r^2	SE	LAR	r^2	SE	LAR	r^2	SE
	leaves plant $^{-1}$ d $^{-1}$			leaves plant $^{-1}$ d $^{-1}$			leaves plant $^{-1}$ d $^{-1}$		
T1 (14/10°C)	0.57	0.76	0.056	0.40	0.79	0.039	0.47	0.91	0.029
T2 (17/12°C)	0.61	0.65	0.078	0.46	0.94	0.021	0.46	0.87	0.028
T3 (20/15°C)	0.73	0.88	0.051	0.71	0.97	0.020	0.68	0.97	0.029
T4 (23/18°C)	0.84	0.89	0.051	0.84	0.96	0.028	0.75	0.89	0.022
T5 (28/23°C)	1.01	0.90	0.059	0.98	0.93	0.038	0.96	0.95	0.036
T6 (34/29°C)	0.82	0.85	0.065	0.89	0.94	0.032	1.05	0.97	0.022

The Proc Mixed procedure (Littell et al., 1996) in SAS was used to regress leaf appearance rate against temperature and [CO₂]. Experimental data were analyzed as a repeated measures design with temperature as a continuous fixed effect, growth chamber as subject, and D0, D1, and D2 (corresponding to three different [CO₂] levels) as the repeated measure. An unstructured covariance was used.

Leaf appearance data from D0 and D1 were used for initial model building, data from D2 and Kirk and Marshall (1992) were used for comparison under various temperature regimes, and field data were used for testing under typical potato growth conditions in Maryland. Goodness of fit between predicted and observed leaf numbers with time for thermal time and temperature response approaches were evaluated by computing the mean bias difference (MBD, Eq. [3]) and root mean square difference (RMSD, Eq. [4]):

$$\text{MBD} = \frac{\sum_{i=1}^n (\text{observed}_i - \text{predicted}_i)}{n} \quad [3]$$

$$\text{RMSD} = \sqrt{\frac{\sum_{i=1}^n (\text{observed}_i - \text{predicted}_i)^2}{n}} \quad [4]$$

RESULTS

Leaf appearance rates are summarized in Table 2 for all SPAR experiments. Regression coefficients from the analysis of [CO₂] and temperature effects on leaf appearance rates between D0, D1, and D2 are also provided. A quadratic fit vs. observed daily average temperature was used in the analysis. Common linear and quadratic slopes and intercept for all three experiments were obtained ($P \leq 0.05$), indicating no significant

temperature \times [CO₂] interaction or [CO₂] effect on leaf appearance rate was present.

The modified β response function (Eq. [2]) was fit to D0, D1, D2 data separately and to D0 and D1 pooled together (Table 3). Parameter values of $T_{\text{max}} = 39.5^\circ\text{C}$, $T_{\text{opt}} = 27.2^\circ\text{C}$, and $R_{\text{max}} = 0.96$ leaves plant $^{-1}$ d $^{-1}$ were obtained for pooled D0 and D1 (Fig. 1). Data from D0, D1, D2, and KM are also plotted vs. observed average daily temperature in Fig. 2.

Phyllochrons for each SPAR experiment and for pooled D0 and D1 data are summarized in Table 3 with and without the T6 (34/29°C) treatment. As an example, temperature treatment data vs. thermal time for D1 are shown in Fig. 3. For D1 only, phyllochron values were obtained on leaf appearance data for each individual temperature treatment. The values are plotted against observed average daily temperature to indicate their stability with changes in average growth temperature (Fig. 4).

Thermal time and the modified β response approaches, developed from data from D0 and D1, are compared with field data in Table 4. Two thermal time approaches were evaluated: Phyllochron 1 includes all temperature treatment data, and Phyllochron 2 includes all data except for T6 (34/29°C treatment). The β approach used all temperature treatment data.

DISCUSSION

Leaf appearance rates were nonlinearly correlated with temperature when the entire range of observed daily temperature values were used (Fig. 1 and 2). Rates increased with temperature until an optimum value of

Table 3. Phyllochrons, modified β response function parameters, and standard errors (in parentheses) for growth chamber experiments. Phyllochrons are expressed with a 4 or 0°C base temperature with all treatment data (T) or all treatment data except the 34/29°C group T6 (–T6).

	D0		D1		D2		D0 & D1	
	Value	r^2	Value	r^2	Value	r^2	Value	r^2
Phyllochron, °C-d leaf $^{-1}$								
Base 4°C, T	26.8 (0.88)	0.80	28.2 (0.94)	0.94	28.2 (0.90)	0.90	28.2 (0.87)	0.87
Base 4°C, –T6	22.7 (5.87)	0.89	23.5 (0.98)	0.98	25.4 (0.91)	0.91	24.3 (0.91)	0.91
Base 0°C, T	31.3 (0.61)	0.92	32.2 (0.95)	0.95	32.1 (0.93)	0.93	32.6 (0.88)	0.88
Base 0°C, –T6	27.6 (0.69)	0.89	27.6 (0.99)	0.99	30.3 (0.92)	0.92	29.2 (0.90)	0.90
β response †								
T_{max} , °C	35.7 (1.69)	0.98	39.9 (1.67)	0.98	40.2 (4.94)	0.99	39.5 (1.58)	0.98
T_{opt} , °C	25.4 (0.55)	0.98	28.0 (0.61)	0.98	29.5 (2.53)	0.99	27.2 (0.55)	0.98
R_{max} , leaves plant $^{-1}$ d $^{-1}$	0.97 (0.04)	0.98	0.98 (0.03)	0.98	1.06 (0.07)	0.99	0.96 (0.03)	0.98

$^\dagger T_{\text{max}}$ —ceiling temperature at which leaf appearance rate ceases; T_{opt} —temperature at which leaf appearance rate is maximum; R_{max} —maximum leaf appearance rate.

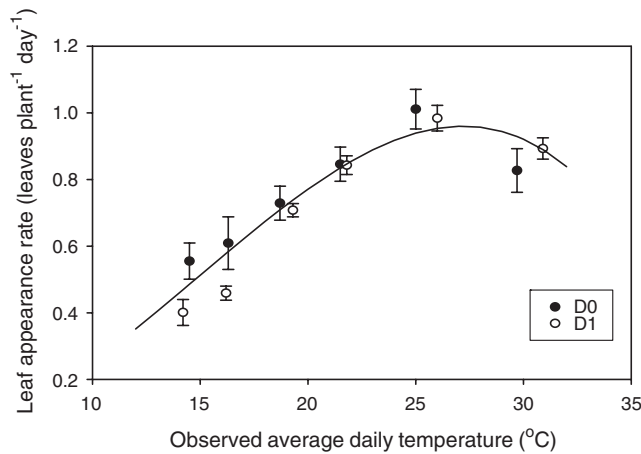


Fig. 1. Leaf appearance rates with standard errors vs. observed average daily temperature for experiments D0 and D1. The nonlinear temperature response model based on the modified β distribution parameters (Table 3) is shown as the solid line.

27.2°C was reached (Table 2) and then subsequently declined for D0, D1, and KM data (Fig. 2). Similar values were observed for D0, D1, D2 (Table 2), and KM vs. average daily temperatures between 12 and 26°C. Research by Kirk and Marshall (1992) and Firman et al. (1995) supports the nonlinear correlation that was observed with leaf appearance rate across the full range of temperatures evaluated in this study. Kirk and Marshall (1992) concluded that potato leaf appearance rates are linear with increasing temperature up to ~25°C. Firman et al. (1995) suggested that rates were linear between 11 and 19°C but significant variability among cultivars was reported. Firman et al. (1995) also reported that potato plants at temperatures >28°C showed an increased phyllochron value, and thus a decrease in leaf appearance rates above this temperature.

The D0, D1, and KM data decline at temperatures >27°C, while the rates in D2 appear to increase (Fig. 2). In D2, [CO₂] was nearly double the level used in D0

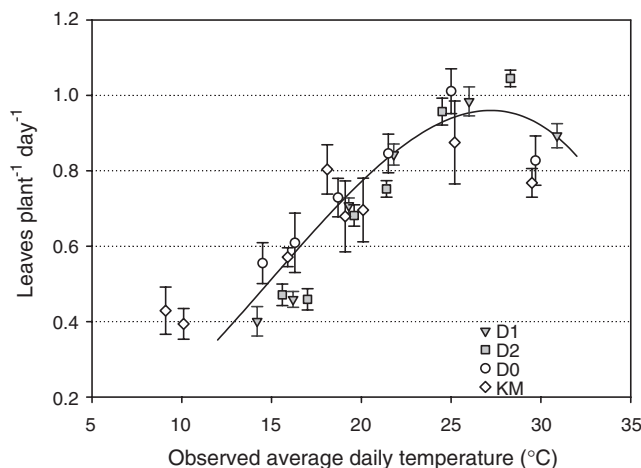


Fig. 2. Comparison of leaf appearance rates (with standard errors) vs. observed average daily temperature for D0, D1, D2, and the data of Kirk and Marshall (1992; KM). The nonlinear temperature response model based on the modified β distribution parameters (Table 3) is shown as the solid line.

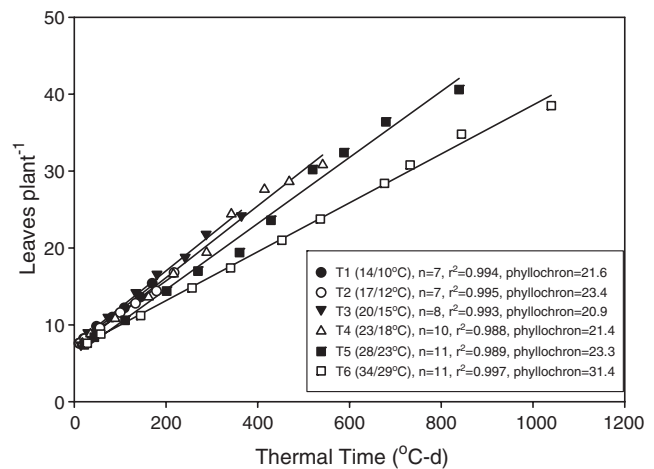


Fig. 3. Leaf appearance data separated for each temperature treatment (T1 through T6) in experiment D1. Data points are the averaged value of five observations at each measurement date (error bars not shown for clarity).

and D1. Differences due to irradiance and atmospheric [CO₂] between experiments can influence leaf expansion and duration; however, the rate of leaf appearance is thought to be independent of these effects for potato (Kirk et al., 1985). Results from regression analysis (Table 2) indicated that no significant differences were obtained between D0, D1, and D2 across the range of temperatures studied despite the difference in [CO₂]. Further evaluation of D2 (not shown), however, indicated that leaf appearance rates actually increased following flowering of the main stem at the higher temperatures. Taub et al. (2000) found that elevated [CO₂] protected photosynthesis from damage due to high temperatures, indicating that further experiments should be conducted to elucidate the effects on leaf appearance rates at temperatures >27°C.

Small differences between KM, D0, and D1 values were also observed above 26°C (Fig. 2). The KM and D0 values were 0.76 and 0.82 leaves plant⁻¹ d⁻¹, respectively, at ~28°C and the D1 value was 0.89 at 31°C. A constant day/night temperature of 28°C was used for the KM data at this point. Although the daily observed temperature

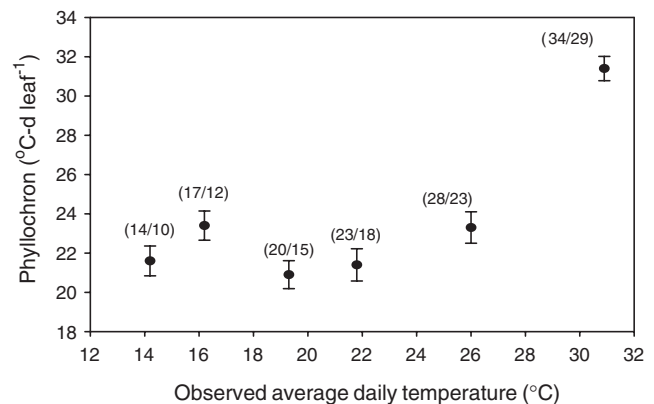


Fig. 4. Phyllochrons (with standard errors) obtained from leaf appearance data for each temperature treatment from D1 vs. observed average daily temperature. Treatment day/night temperatures (°C) are shown in parentheses above each value.

Table 4. Average leaf appearance values (with SD) for potato stems at different days after emergence (DAE) from a USDA-ARS Beltsville, MD, 2004 field study and test statistics mean bias difference (MBD) and root mean square difference (RMSD) for model comparisons. Simulated leaf values for thermal time (Phyllochron 1 and Phyllochron 2) and nonlinear response functions (β) are shown.

DAE	Observed	Phyllochron 1	Phyllochron 2	β
		leaves plant ⁻¹		
6†	9.6 ± 0.56	10.5	10.5	7.6
9†	11.2 ± 0.77	12.5	12.8	10.3
16‡	13.7 ± 1.48	17.3	18.4	16.4
26§	19.9 ± 3.03	23.3	25.4	24.4
30‡	22.7 ± 3.73	25.3	27.6	27.0
51‡	43.02 ± 13.7	39.2	43.8	45.1
Model test statistics				
MBD	-	-0.97	-2.42	-1.34
RMSD	-	2.64	3.20	2.60

† Sample size of 27 plants.

‡ Sample size of 44 plants.

§ Sample size of 132 plants.

average for the 34/29°C treatment was higher in D1, the nighttime temperature for D0 was an average of 1.1°C warmer than for D1. It has been shown that warmer daytime air temperatures, such as 25°C and above, require a larger day/night temperature differential (i.e., increasingly cooler nighttime temperatures) to encourage canopy development in potato (Benoit et al., 1986). Differences between KM, D0, and D1 may be attributed to differences in warmer nighttime air temperatures, and possibly cultivar response for the KM data.

Comparison of modified β function predictions at 9 and 10°C with KM data indicate that these values are underpredicted by ~40% (Fig. 2); however, these temperatures lie outside the range of data used to develop the model (Table 1). The modified β function used in this research is a simplified version of the β function and forces developmental response to equal 0 at 0°C. More data on potato growth at temperatures <12°C is needed to fully test whether the modified or full version of the β function is more suitable across all temperatures.

A baseline temperature of 4.4°C was obtained when a regression line fit to the linear portion of the pooled data from D0 and D1 in Fig. 1 was extended to the x axis (not shown). The experimentally derived baseline temperature was consistent with those reported elsewhere for potato (Firman et al., 1991; Kirk et al., 1985). To compare phyllochrons from the SPAR experiments with other published values in the literature, however, phyllochrons were expressed at base 0°C (Table 3). When all temperature treatments were used in the analysis, phyllochrons of 31, 32, and 32°C-d leaf⁻¹ were obtained from experiments D0, D1, and D2, respectively (Table 3). For a variety of potato cultivars, phyllochrons of 30.8 and 34.3 (Firman et al., 1995), 31 (Kirk and Marshall, 1992), 30 (Cao and Tibbitts, 1995), 30 (Vos and van der Putten, 1998), and 28°C-d leaf⁻¹ (Vos and Biemond, 1992) have been reported; however, these published values were developed for temperature studies of potato development below 25°C. When the highest temperature treatment, T6, was removed from the SPAR data, phyllochrons of 28, 28, and 30°C-d leaf⁻¹ values were computed. These are consistent with the reported values.

Data from D0 and D1 were pooled for the purpose of testing thermal time and nonlinear response approaches against the field data (Table 4). The MBD statistic represents the average number of leaves over- or under-predicted for all observation dates and the RMSD statistic represents the average deviation from measured values at each observation date. Models are more accurate when both statistics approach zero. All three approaches approximated the field data accurately (Table 4). Negative MBD values indicated that leaf numbers were overpredicted. Potato main stem flowering and termination, followed by initiation and development of the apical branches, occurred during DAE 16 through 26 (Table 4). Because of the difficulties in distinguishing the newly initiated branches from the main stem, some of the model deviations may be attributed to measurement error during this time frame. The RMSD values were similar for each modeling approach (Table 4).

Leaf appearance in potato is not correlated with other phenological events (e.g., flowering, or tuber initiation) unlike crops such as wheat (*Triticum aestivum* L., Streck et al., 2003; Wang and Engel, 1998; Xue et al., 2004). Leaf growth typically ceases once the demand for carbohydrates by tubers approaches the daily growth rate of the plant. This point in time is simulated by potato models as a combination of cultivar and cumulative environmental factors. Thus, errors introduced by under- or overestimating leaf number in potato would be reflected in predictions of canopy leaf area expansion. The average number of leaves per plant at DAE 51 in the field study was 43 (Table 4)—all modeling approaches were within four leaves of this value. Alternatively, minimum and maximum 24-h temperatures from the field study were 15 and 22.6°C during the period of interest (not shown). Corresponding leaf appearance rates range between 0.5 and 0.95 leaves plant⁻¹ d⁻¹. This means chronological development with regard to the total leaf number on an average potato plant could be off by 2 to 3.6 d. These errors would not be expected to be significant since the final, fully expanded areas of leaves that appear at later stages of potato growth (such as those at DAE 51) tend to be much smaller than those that appear at earlier stages. It may be possible to quantify such errors once the leaf appearance rate approaches are integrated with equations for leaf expansion and duration, and compared with “big-leaf” potato model simulations of overall canopy leaf area.

The phyllochron values obtained from each temperature group in D1 varied with growth temperature, but only markedly so at the highest value (Fig. 3 and 4). This instability with phyllochron values has been reported for other crops such as maize (*Zea mays* L., Birch et al., 1998) and wheat (Xue et al., 2004) and indicates that the phyllochron concept may not have a biologically sound basis when the assumption of linearity is violated. Cutforth et al. (1992) showed that phyllochron was also dependent on temperature in wheat, and Cao and Tibbitts (1995) indicated that phyllochron for potato increased slightly with a temperature change from 17 to 22°C. Contrary to the work by Kirk and Marshall (1992)

and Firman et al. (1995), where leaf appearance rate was assumed to be linear with temperatures $<25^{\circ}\text{C}$, Borah and Milthorpe (1962) found that leaf appearance in potato was more rapid at 20 than 15 or 25°C . Phyllochron values can also differ significantly for the same crop if grown in regions that have similar mean daily temperatures but different daily temperature extremes (Birch et al., 1998; Loomis and Connor, 1996). The modified β function avoids many of these problems because it allows for nonlinear temperature responses by using a single, continuous curve and can be modified to account for large fluctuations in daily temperature values by using a time step <24 h. For example, analyzing the field data at a 15-min time interval with the β approach (not shown) results in an improved predicted leaf number at DAE 51 of 44.1 leaves. The modified β approach can also be parameterized to incorporate additional factors that influence potato leaf appearance rates, such as drought stress. These results suggest that potato leaf appearance rates can be modeled successfully with a thermal time or nonlinear temperature response function approach. Additional comparisons with leaf appearance rates at different growing locations will be required to fully validate the robustness of the approaches presented here, particularly for tropical climates experiencing wider extremes of temperature.

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