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Temperature Effects on the Shoot and Root Growth, Development, and Biomass Accumulation of Corn (*Zea mays* L.)

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Abstract: Temperature is a critical environmental factor regulating plant growth and yield. Corn is a major agronomic crop produced globally over a vast geographic region, and highly variable climatic conditions occur spatially and temporally throughout these regions. Current literature lacks a comprehensive study comparing the effects of temperature on above versus below-ground growth and development and biomass partitioning of corn measured over time. An experiment was conducted to quantify the impact of temperature on corn's early vegetative growth and development. Cardinal temperatures (T_{min}, T_{opt}, and T_{max}) were estimated for different aspects of above- and below-ground growth processes. Plants were subjected to five differing day/night temperature treatments of 20/12, 25/17, 30/22, 35/27, and 40/32 °C using sun-lit controlled environment growth chambers for four weeks post-emergence. Corn plant height, leaves, leaf area, root length, surface area, volume, numbers of tips and forks, and plant component part dry weights were measured weekly. Cardinal temperatures were estimated, and the relationships between parameters and temperature within these cardinal limits were estimated using a modified beta function model. Cardinal temperature limits for whole plant dry weight production were 13.5 °C (T_{min}), 30.5 °C (T_{opt}), and 38 °C (T_{max}). Biomass resources were prioritized to the root system at low temperatures and leaves at high temperatures. Root growth displayed the lowest optimum temperature compared to root development, shoot growth, and shoot development. The estimated cardinal temperatures and functional algorithms produced in this study, which include both above and below-ground aspects of plant growth, could be helpful to update crop models and could be beneficial to estimate corn growth under varying temperature conditions. These results could also be applicable when considering management decisions for maximizing field production and implementing emerging precision agriculture technology.

Keywords: corn; maize; temperature; abiotic stress; environment; root growth; shoot growth; modeling

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1. Introduction

Temperature is a major abiotic, or environmental, factor uniquely connected to agricultural production through its influence on plant growth, development, and yield. Temperature is one of the three primary environmental variables influencing plant phenology and physiology alongside solar radiation and soil moisture [1,2]. High and low temperatures have caused significant agricultural losses through the 21st century. The magnitude of lost productivity follows behind other abiotic stresses, such as drought and flooding [3,4]. However, agricultural productivity and temperature relationships vary depending on crop species, variety, soil conditions, and other weather conditions [5,6]. In addition to agronomic yield, many aspects of plant productivity are driven by temperature. These include root and shoot growth, nutrient and water uptake, and physiological processes, such as photosynthesis, respiration, and transpiration [2]. Temperatures above a plant's optimal preference have been reported to negatively affect plant physiological function, root activity, flowering and fertilization, seed set, and yield. On the other end of the spectrum, low temperatures delay seed germination [7], reduce growth rates, and negatively impact plant vigor [8]. Under extremely low temperatures, permanent frost damage can occur [9]. Temperature is also a primary driver of plant phenological development. Multiple thermal indices have been developed to predict phenological stages [10]. Therefore, a deep understanding of how agronomic crops respond to temperature throughout all growth stages is critical to support agricultural stakeholders, including producers, agronomists, and policymakers, as we work to meet the food, fiber, and energy demand for a growing global population.

Corn (*Zea mays* L.) is a major agronomic crop globally, surpassed only by wheat (*Triticum aestivum* L.) in total acreage worldwide [11]. Originating in Mexico, this C_4 plant is grown over a vast geographic area, ranging in latitude from 58° N to 40° S and elevation below sea level to over 3000 m [12]. With such widespread production, corn crops experience incredible variation in environmental conditions. Over the last half-century in the United States, corn yields have increased over eight-fold. As a result, the US is the global leader in yield and total production [4]. However, these high yields are not replicated globally. Research indicates that plant response to abiotic stress is the primary limiting factor [6,13] Thus, it can be assumed that much of the global corn production occurs under conditions exterior to corn's optimum preference. Increasing the resiliency and adaptability of corn plants to suboptimal environments will be critical for the agricultural industry to meet future global production demands.

Early vegetative growth and development are the foundation of a successful crop. Above ground, a plant establishes its capacity to produce a carbon source. Below ground, the plant extends its root system to enhance its uptake of water and nutrients. When a crop emerges, successful stand establishment is highly dependent on the ability of the emerging plants to endure stress during these early vegetative stages [13]. Vegetative growth between emergence and tassel in corn is also vital because, during tassel initiation, the potential number of kernels per ear is determined [6,14]. Vegetative growth and developmental processes, such as the initiation of new leaves, expansion of these leaves, and extension of plant height directly affect the plant's ability to intercept solar radiation throughout the growing season. In addition, research indicates that temperature can alter these processes [15].

Additionally, modern agricultural research has often ignored plant roots due to difficulty monitoring these structures in the field. Increasing our understanding of how plants respond below the soil surface to environmental variables, such as temperature will provide fundamental knowledge to build upon as we explore ways to improve abiotic stress tolerance, close the yield gap, and continue previous success in increasing agronomic yields. Moreover, understanding functional relationships between environmental factors and plant processes is critical to developing and enhancing processed-based crop simulation models. Such models could predict crop growth and simulate agricultural systems under varying conditions.

Previous research indicates vegetative growth often follows a sigmoid growth pattern as growth progresses temporally, whereby three phases typically occur: an early accelerating phase often resembling exponential growth, a middle stabilized linear phase, and a final saturation phase occurring as the process begins to reach its maximum [16]. Thus, growth rates follow a bell-shaped curve as the growing season progresses temporally, with growth per day or unit of time diminishing as maximum growth is approached [16]. To prevent growth rates and responses to temperature from being influenced by this slowing as maximum total growth is approached, this study focuses on vegetative growth during the expo-linear phase [17]

Given that all biological processes respond to temperature, three cardinal temperatures summarize the relationships between these processes and temperature. These three cardinal temperatures include the minimum temperature required for the process to occur (T_{min}), the optimal temperature at which the process occurs at its highest rate (T_{opt}), and the maximum temperature at which the process can occur (T_{max}). Temperatures falling between T_{min} and T_{opt} can be described as sub-optimal, and those falling between T_{opt} and T_{max} as supra-optimal. However, the functional relationship between biological processes and temperature between these cardinal points is difficult to portray. Typical temperature responses include an initial phase of biological activity slowly increasing as temperatures rise above T_{min}, which follows an exponential-like pattern. Then, growth typically follows a positive linear pattern as temperatures reach intermediate levels. As the temperature approaches T_{opt}, these increases begin to slow, and growth typically follows a parabola-like pattern with an apex at T_{opt}. As temperatures rise past T_{opt}, activity declines following a negative linear function until activity reaches zero at T_{max}. An ideal temperature response function should require the fewest biologically relevant parameters possible; a greater number of parameters can lead to calibration errors when modeling temperature responses, and non-biologically significant parameters are usually highly empirical [15,17]. Evidence has also suggested that ideal temperature response functions should follow smooth curves as the function transitions from low to high temperatures, not rigid transitions between multiple linear functions [18,19]. Numerous mathematical functions have been used to describe these relationships with temperature, including linear, bilinear, multilinear, quadratic, and other advanced nonlinear equations, each with unique advantages and disadvantages further discussed by Yan and Hunt [18] and Archontoulis and Miguez [20]. The beta function, a skewed probability density function in statistics, has been introduced by Yin et al. [21] as a practical non-symmetric, unimodal nonlinear function to describe temperature responses of crop development. This function was further simplified by Yan and Hunt [18] to include just two or three biologically significant parameters. Statistical parameter estimates for this simplified function can be generated using as few as three or four data points, provided these span T_{opt}.

Cardinal temperatures for corn have been reported by many and are extensively reviewed and summarized by Sánchez et al. [6]. However, among the studies reviewed, differences exist in experimental design, temperature treatments, growth conditions, varieties, and other factors, making direct comparison of the studies difficult. Additionally, many previous studies investigating the relationship between corn growth and temperature were conducted under highly artificial conditions where natural solar radiation levels are unattainable or in outdoor situations where precise environmental control is complicated and inconsistent. To our knowledge, no single study has comprehensively unraveled the impact of temperature treatments spanning above and below T_{opt} for both above and below ground aspects of corn growth and development under natural solar radiation. Our comprehensive study allows for a more reliable comparison of the different parts of growth and development above and below ground and their response to sub- and supra-optimal temperatures.

The objectives of this study were to: (1) quantify the effect of sub and supra optimal temperatures on above and below ground aspects of corn vegetative growth and development, (2) estimate cardinal temperatures for each aspect of growth and developmental parameters by fitting the data with best-fit mathematical functions, and (3) compare the cardinal limits among all measured parameters.

2. Materials and Methods

2.1. Experimental Facilities

This study was conducted during the 2018 growing season at the Environmental Plant Physiology Laboratory at the Mississippi Agricultural and Forestry Experiment Station, Mississippi State University, MS, USA (33°28′ N, 88°47′ W). The experiment was conducted in sun-lit, controlled environment growth chambers called Soil-Plant-Atmosphere-Research [SPAR] units. These units allow precise manipulation and monitoring of growing conditions, such as temperature, CO_2 concentration, soil moisture, and nutrient levels while growing plants under natural solar radiation. Each unit consists of a soil bin to hold pots, a heating/cooling unit, and a 1.27 cm thick Plexiglas canopy, allowing 97% of the visible solar radiation to pass. The specifications and operation of SPAR units have been detailed by Reddy et al. [22].

2.2. Experimental Setup

Seeds of corn hybrid Agrigold A6659 (Agrigold Inc., St. Francisville, IL, USA) were sown into 30.5 cm (height) × 15.2 cm (diameter) polyvinyl chloride (PVC) pots. These were filled with a soil medium consisting of a 3:1 ratio by volume of pure fine sand and ground topsoil (87% sand, 2% clay, 11% silt). These pots contained a 0.5 cm drain hole at the bottom and were initially filled with one inch of pea gravel to aid drainage. Thirty pots were placed in each SPAR unit with a temperature set point of 30/22 °C, day/night, 70% relative humidity, and 420 ppm CO_2 to create optimum growing conditions for emergence. Pots were watered thrice per day with full strength Hoagland's nutrient solution [23] to ensure plant growth optimal nutrient and moisture levels. Initially, each pot was watered for 60 s each irrigation event. Irrigation volume was adjusted continuously throughout the experimental period based on treatment-based evapotranspiration measured daily [22]. Each SPAR unit is sun-lit; thus, all plants were grown under natural day lengths for Mississippi State, MS (33°28′ N, 88°47′ W) during the experimental period. A similar methodology has been used to study temperature effects on cotton [5], sweetpotato [24], and cover crops [25].

2.3. Treatments

Upon emergence, plants were thinned to one per pot, and temperature setpoints were adjusted to five different day/night settings (20/12, 25/17, 30/22, 35/27, and 40/32 °C). These setpoints were maintained throughout the experimental period (5 DAS to 33 DAS). Temperature treatments were selected to cover a range above and below previously reported optimal temperatures for corn, but within a range, the growth chambers could effectively, mechanically maintain. For all temperature treatments, daytime temperature setpoints were maintained from sunrise to sunset, and temperatures transitioned between day/night set points over 30 min. The incoming daily solar radiation (285–2800 nm) was continuously monitored throughout the experimental period using a pyranometer (Model 4–8; The Eppley Laboratory Inc., Newport, RI, USA). Black shade cloths with variable density were placed around the edge of each growth chamber and regularly raised as plants grew in height to simulate the effect of natural shading by border plants.

2.4. Data Collection

Upon imposition of the five temperature treatments (5 DAS), multiple aspects of corn growth and development, hereafter termed parameters, were destructively measured on six randomly selected plants every seven days. After each harvest, the plant spacings were adjusted throughout the experiment to maintain uniformity. At each measurement event, hereafter termed harvest, plant height (PH, cm $plant^{-1}$) was measured by hand with a standard metric ruler as the distance from the soil surface to the highest leaf collar. Leaf number (LN, no. $plant^{-1}$) was counted as the total leaves with a collar. The aboveground plant components were cut from the root system at the soil level. Leaves were separated from the stem at the point of the leaf collar and measured for leaf area (LA, cm^2 $plant^{-1}$) using an LI-3100 leaf area meter (LiCor Inc., Lincoln, NE, USA). Root systems were then gently removed from the PVC pots and washed with a gentle stream of water over a wire mesh sieve to remove soil media until roots were clean. Individual root systems were floated in a 400 × 300 cm acrylic tray filled with 5 mm water. Roots were carefully untangled using plastic forceps to minimize roots' overlap to ensure quality imagery. Trays were placed upon an Epson Expression 11000XL (Epson America, Inc., Long Beach, CA, USA) scanner, and images were acquired at a resolution of 800 dpi. These images were analyzed by WinRHIZO Pro 2009C software (Regent Instruments, Inc., Québec, QC, Canada). The digitized output from analysis quantified multiple root growth and development parameters for each plant: root tips (RT, no plant^{-1}), root forks (RF, no. plant^{-1}), total root length (TRL, cm plant^{-1}), root surface area (RSA, cm^2 plant^{-1}), and root volume (RV, cm^3 plant^{-1}). Once plant components were analyzed to the extent mentioned above, the separated leaves, stems, and roots were placed into individual paper bags. Samples were oven-dried on-site at 80 °C for three days to ensure a constant weight was reached. These samples were weighed individually for dry weight estimation of the leaves, stems, and roots.

2.5. Statistical Analysis and Curve Fitting

2.5.1. Growth Trends and Analysis of Variance of Observed Data

This experiment was a split-plot design with temperature treatments as the main plot and measurement date as the subplot. PROC GLM of SAS (SAS Institute, Cary, NC, USA) was used to conduct ANOVA for treatment effects, harvest, and interaction. Temperature effects were separated using the LSMEANS statement within PROC GLM at an alpha level of 0.05. Means of each measured growth and development parameter from each treatment at each sampling period were plotted to days after treatment imposition (DAT) to allow visual analysis and representation of growth trends over time using Sigmaplot 13 (Systat Software, Inc., San Jose, CA, USA).

2.5.2. Cardinal Temperature Estimation

Means of each treatment within each sampling period were plotted as a function of average daily temperature. These values were fitted to a modified beta function [Equation (1)] similar to the one described by Yan and Hunt [17] using the user-defined equation option in the Regression Wizard program of Sigmaplot 13. We derived three biologically significant statistical parameters for each harvest by fitting a simplified modified beta function to the data.

$$g = G_{max}\,(T_{max} - t/T_{max} - T_{opt})(t/T_{opt})\ \hat{}\ (T_{opt}/T_{max} - T_{opt}) \tag{1}$$

where g is the growth of the plant process in question, G_{max} is the maximum growth achieved at temperature T_{opt}, T_{max} is the maximum temperature at which the process could occur, T_{opt} is the optimal temperature at which maximum growth occurs, and t is the average daily temperature of the treatment.

This function assumes a T_{min} of 0 °C, which may seem unrealistic at first thought as previous research has indicated the minimum temperature for plants, such as corn is well above 0 °C. However, Yan and Hunt [18] argue and provide evidence that this assumption can be helpful as the equation still presents biological activity at a very low level as temperatures approach zero. Additionally, the ascending linear phase of the beta function has an x-intercept above zero. This intercept lowers in correlation with a lower T_{opt}, suggesting that lower T_{opt} paired with a T_{min} fixed at zero could indicate greater cold tolerance. Additionally, due to the nature of the beta function, a greater range between T_{opt} and T_{max} could indicate greater adaptability to a broader range of temperatures.

For each measured parameter, means from the 20/12 °C, 25/17 °C, and 30/22 °C treatments were fitted to a linear function [Equation (2)] using Sigmaplot 13. Statistical parameters generated from this function were used to estimate T_{min} by extrapolating the x-intercept of the function [Equation (3)].

$$Y = mx + b \tag{2}$$

$$T_{min} = -b/m \tag{3}$$

where m and b are regression constants generated from Sigmaplot 13.

2.5.3. Parameter Comparison

To compare the impact of average daily temperature on each parameter, estimated cardinal temperatures from each harvest were treated as replicates and analyzed using the CONTRAST function and LSMEANS at an alpha level of 0.05 within PROC GLM of SAS. Parameters were pooled into four categories for further comparison among aspects of the shoot and root growth and development: shoot growth (PH, LA, LDW, StDW), shoot development (LN), root growth (TRL, RSA, RV, RDW), and root development (RT, RF). If no differences were found within the individual categories, mean cardinal temperatures (T_{opt} and T_{max}) were used to generate a simplified beta function [Equation (4)], also introduced by Yan and Hunt [18]. This equation represents the fractional temperature response relative to potential G_{max} on a scale of 0 to 1.

$$g/G_{max} = (T_{max} - t/T_{max} - T_{opt})(T/T_{opt})\hat{}(T_{opt}/T_{max} - T_{opt}) \tag{4}$$

3. Results

The treatments selected for this study represent temperatures above and below those previously reported for optimum corn growth and development. We successfully created five differing average daily growing temperatures by utilizing SPAR units set to five different day/night temperature set points, which remained stable throughout the experimental period (Figure 1). Environmental variables were continuously monitored throughout the experimental period, and mean values for each are provided in Table 1.

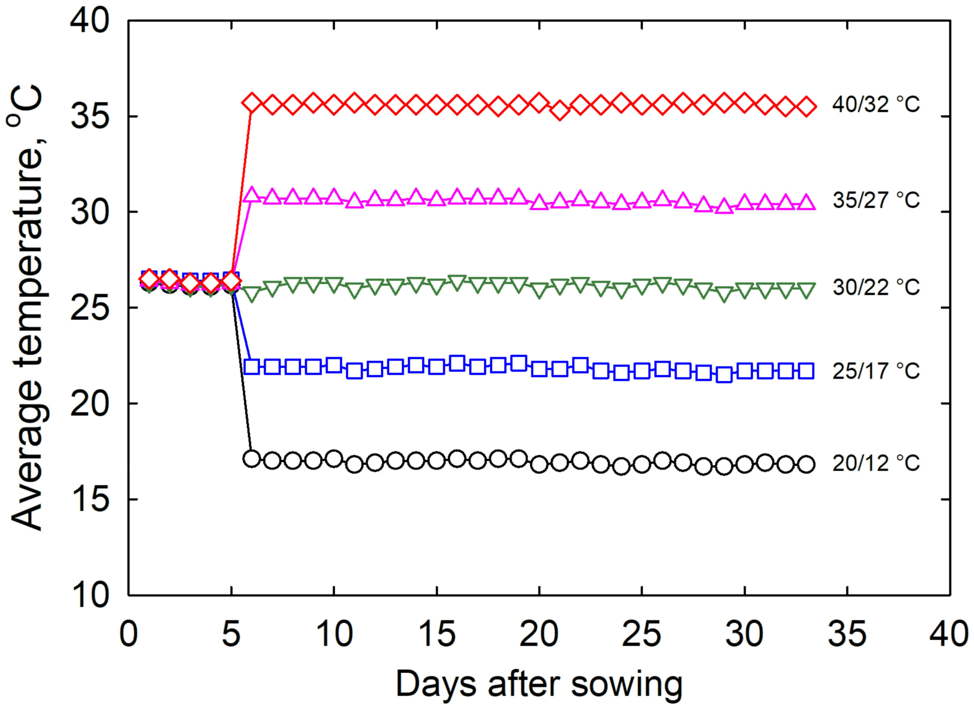

Figure 1. Average daily temperatures were recorded for five temperature treatments during the corn experiment.

Table 1. Environmental parameters recorded during the experimental period: average day, night, and day/night temperatures, average day chamber CO_2 concentration, and average day/night vapor pressure deficit (VPD) during the experimental period of 28 days.

Set Temperature (°C)	**Measured Temperature (°C)**			**CO_2 (µmol mol^{-1})**	**VPD (kPa)**	
Day/Night	**Day**	**Night**	**Day/Night**	**Day**	**Day**	**Night**
20/12	20.18 ± 0.03	12.66 ± 0.02	16.9 ± 0.02	441.19 ± 1.37	0.62 ± 0.01	0.60 ± 0.01
25/17	25.19 ± 0.03	17.42 ± 0.01	21.79 ± 0.03	458.61 ± 1.31	0.66 ± 0.01	0.64 ± 0.01
30/22	29.36 ± 0.03	21.95 ± 0.02	26.12 ± 0.03	424.97 ± 1.59	0.71 ± 0.02	0.68 ± 0.01
35/27	33.71 ± 0.03	26.39 ± 0.01	30.53 ± 0.03	439.39 ± 1.39	0.83 ± 0.04	0.76 ± 0.03
40/32	38.87 ± 0.02	31.35 ± 0.02	35.59 ± 0.01	456.43 ± 1.96	0.92 ± 0.06	0.83 ± 0.04

This experiment is the first study to investigate the temperature effects on root growth during the vegetative development of a corn plant using these methods. All measured aspects of growth and development were significantly affected by temperature and the duration of growth, except for the number of root tips, leaf allocation percentage, and root allocation percentage (Table 2). However, these three aspects were significantly affected by growth duration and temperature independently. This interaction indicates that although these parameters were impacted by temperature, some plant growth occurred exponentially, and the magnitude of the impact of temperature depended on harvest timing. When fitting the data to the beta function [Equation (1)], this change in magnitude is accounted for by an increase in G_{max}. In addition, all parameters continuously increased as the experimental period prolonged, indicating that the five treatments in this study were within corn's minimum and maximum temperature range.

Table 2. Summary of analysis of variance across the harvest date (H), temperature treatment (T), and their interaction (H × T) on different root and shoot growth, physiological, and developmental traits measured weekly after emergence. Values are the mean of six replications for each harvest date at each temperature treatment. Plant height (PH), leaf number (LN), leaf area (LA), leaf dry weight (LDW), stem dry weight (StDW), root dry weight (RDW), the root to shoot ratio (RS), total dry weight (TDW), total root length (TRL), root surface area (RSA), root volume (RV), root tips (RT), root forks (RF); and leaf (L%), stem (S%), and root (R%) dry weight as a fraction of total dry weight.

Source	**PH**	**LN**	**LA**	**LDW**	**StDW**	**RDW**	**TRL**	**RSA**	**RV**	**RT**	**RF**	**L%**	**S%**	**R%**
Harvest Date (H)	***	***	***	***	***	***	***	***	***	***	***	***	***	***
Temperature (T)	***	***	***	***	***	***	***	***	***	***	***	***	***	***
H × T	***	***	***	***	***	***	***	***	***	NS	***	NS	**	NS
Temperature $^{+}$														
20/12 °C	e	e	e	e	d	d	e	d	c	c	d	d	c	a
25/17 °C	d	d	d	d	c	b	c	b	b	b	c	c	b	b
30/22 °C	b	c	b	b	a	a	b	a	a	ab	a	c	a	c
35/27 °C	a	a	a	a	a	a	a	a	a	a	a	b	a	c
40/32 °C	c	b	c	c	b	c	d	c	c	b	b	a	b	c

, * represent significance levels at $p \leq 0.01$, and $p \leq 0.001$, respectively and NS represents non-significant. $^{+}$ The different letters within a column for a given parameter show significant between or among the temperature treatment at $p \leq 0.05$.

Visual representation of the effects of temperature on shoot and root growth and development are shown in Figure 2. Corn plants grew taller with a greater number of leaves with greater leaf area as temperatures increased from the 20/12 °C treatment to the 35/27 °C treatment. Slight decreases in above-ground plant size can be witnessed for the 40/32 °C treatment. Below the soil surface, similar visual trends were observed. Root systems appeared longer, thicker, and denser as temperatures rose to the 30/22 °C treatment. As temperatures rise 30/22 °C, root systems become thinner and less dense but not necessarily shallower.

Figure 2. Pictorial representation of corn shoot and root growth under five temperature treatments harvested 21 days after treatment or 26 days after sowing.

3.1. Shoot Growth and Development

Plants grown at low temperature showed a linear trend over the 28-day experimental period and increases in height became exponential in growth pattern as temperature increased (Figure 3A). Plant height (PH) was the greatest under the 35/27 °C treatment throughout the experiment, followed by the 30/22 °C and then 40/32 °C treatment, indicating that this growth parameter may be more sensitive to supra-optimal temperatures than sub-optimal temperatures (Table 2). Fitting our data to the modified beta function determined PH to be the greatest at 30.2 °C (T_{opt}), with growth estimated to reach zero at a maximum of 38.9 °C (T_{max}) and a minimum of 11.5 °C (T_{min}) (Figure 3D, Table 3).

Table 3. Modified beta function parameter estimates and cardinal temperatures (T_{opt} and T_{max}). Estimated minimum temperature (T_{min}) was calculated as the intercept of a linear function of the mean values for the first three harvest measurements. All cardinal temperature estimates are the mean of estimates at all four harvests for all growth and developmental parameters: PH—plant height, LN—Lean number, LA—whole plant leaf area, LDW—whole plant leaf dry weight, StDW—whole plant stem dry weight, RDN—root dry weight, TRL—total root length, RSA—root surface area, RV—root volume, Rt—root tips, and RF—root forks.

Parameters	T_{opt}	T_{max}	R^2	**Est** T_{min}	R^2
PH	30.21	38.85	0.8995	11.47	0.8995
LN	34.62	55.08	0.8992	−0.38	0.8992
LA	30.65	38.27	0.97	11.93	0.97
LDW	30.81	38.1	0.9689	12.68	0.9503
StDW	30.57	37.43	0.9588	13.27	0.9269
RDW	28.66	39.1	0.8911	7.55	0.8837
TRL	28.93	40.35	0.9175	3.92	0.8858
RSA	28.28	40.14	0.8972	1.89	0.8764
RV	28.13	38.91	0.8847	4.11	0.8566
RT	30.47	41.71	0.8912	8.31	0.8243
RF	29.96	39.68	0.8421	9.33	0.821

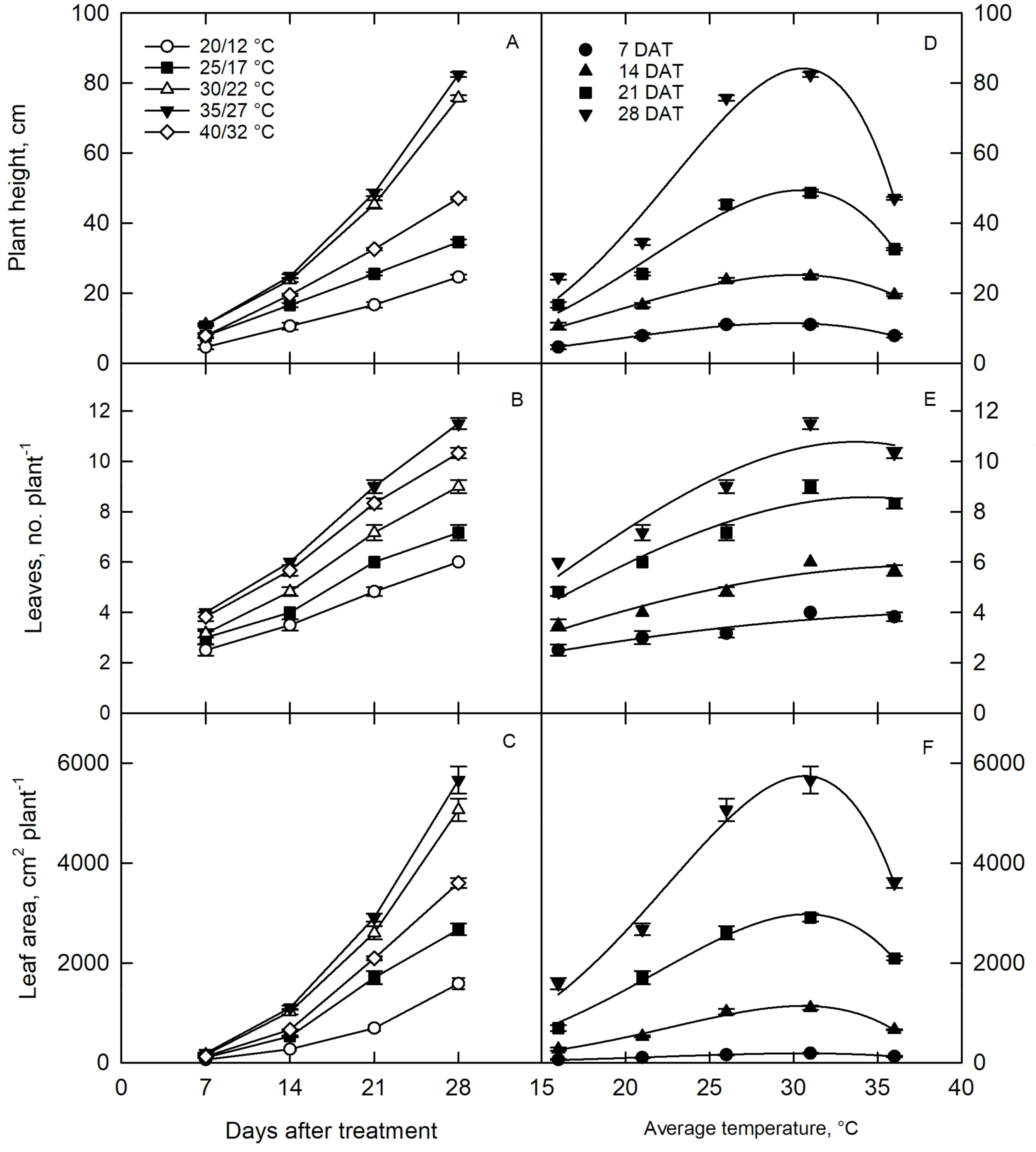

Figure 3. Temporal trends of above-ground corn growth and developmental parameters, (**A**) plant height, (**B**) the number of leaves, and (**C**) leaf area under five differing temperature treatments and estimated growth rates from the weekly measurements as a function of average temperature for (**D**) Stem elongation rate, (**E**) leaf additional rate, (**F**) leaf area expansion rate. The above-ground growth and leaf addition rates fit a modified beta function model. All values are the mean ± standard error of six replications at each harvest under each treatment.

Plants increased their number of collared leaves per plant during the 28-day experimental period linearly as time progressed for all treatments (Figure 3B). Leaf number (LN) was greatest under the 35/27 °C treatment, followed by the 40/32 °C and the 30/22 °C treatment. This suggests that corn leaf development may be less sensitive to higher temperatures than lower temperatures. Previous research indicates that plant phenological events, such as leaf initiation and development are a function of accumulated units of heat beginning at planting. Thus, as opposed to other parameters being fit to the average daily temperature during the experimental period (5 DAS to 33 DAS), leaf number development was fit to Equation (2) as a function of cumulative average temperature post sowing (0 DAS) at each harvest. Therefore, the average cumulative temperature for some treatments changed as the experiment prolonged as plants were grown at a temperature setpoint of 30/22 °C from sowing until emergence. Leaves did not show any visual damage at the high temperatures and developed the fastest at an average T_{opt} of 32.5 °C, and leaf addition rate ceased below a T_{min} of 5.5 °C and above a T_{max} of 46 °C (Figure 3E, Table 3).

Leaf area (LA) per plant increased during the experimental period following classical expo-linear growth typical for many biological processes. Leaf area showed the greatest growth occurring under the 35/27 °C treatment and the lowest growth occurring at the 20/12 °C treatment (Figure 3C). The relationship between average temperature during the experimental period and LA was described by a T_{opt} of 30.7 °C, T_{max} of 38.3 °C, and T_{min} of 11.9 °C (Figure 3F, Table 3).

3.2. Root Growth

Total root length (TRL) increased over time for all treatments following a mostly linear growth pattern (Figure 4A). TRL was the greatest under the 35/27 °C treatment, followed by the 30/22 °C treatment. Only the 20/12 °C treatment had a lower TRL on average than the 40/32 °C treatment, suggesting that corn root length growth may be severely limited by higher than optimal temperatures (Table 1). TRL had a T_{min}, T_{opt}, and T_{max} of 3.92 °C, 28.93 °C, and 40.35 °C, respectively (Figure 4D, Table 3).

Differing from root growth in length, root surface area (RSA) expanded as time progressed, following a pattern resembling expo-linear growth (Figure 4B). RSA was the greatest at both the 30/22 °C and the 35/27 °C treatment. This aspect of root growth may be optimized at a broader range of temperatures than the total root length (Table 1). RSA had a T_{opt} and T_{max} similar to TRL, 28.3 °C and 40.1 °C, respectively; however, T_{min} for RSA was estimated lower than TRL at 1.9 °C (Figure 4E, Table 3).

Roots expanded their volume following expo-linear growth as time progressed through the experimental period (Figure 4C). Similar to root surface area expansion, root volume (RV) was the greatest under the 30/22 °C and 35/27 °C treatment, and the lowest values were observed under the 20/12 °C treatment (Table 1). The optimum temperature for RV expansion was like other aspects of root growth with an estimated T_{opt} of 28.1 °C. However, RV had a lower T_{max} (38.9 °C) than TRL and RSA. The T_{min} for RV was estimated to be 4.1 °C, which is higher than RSA (Figure 4F, Table 3).

3.3. Root Development

Over time, root tip (RT) development appeared to follow a linear trend throughout the experimental period. In contrast, root fork (RF) development followed an exponential pattern, with growth becoming more linear from 14 DAT to 28 DAT (Figure 5A). The development of RT was the greatest under the 35/27 °C treatment, although this treatment was not significantly different from the 30/22 °C treatment. Values under the 30/22 °C treatment were closely related to the 25/17 °C and 40/32 °C treatment (Table 1). For RT development, carinal temperatures T_{min}, T_{opt}, and T_{max} were estimated to be 8.3 °C, 30.5 °C, and 45.7 °C, respectively (Figure 5C, Table 3). Similar to root growth aspects of RSA and RV, root fork (RF) development was the greatest under the 30/22 °C and 35/27 °C treatment (Figure 5B). RF development was estimated to have a T_{opt} of 30.0 °C, a T_{max} of 39.7 °C, and a T_{min} of 9.3 °C (Figure 5D, Table 3).

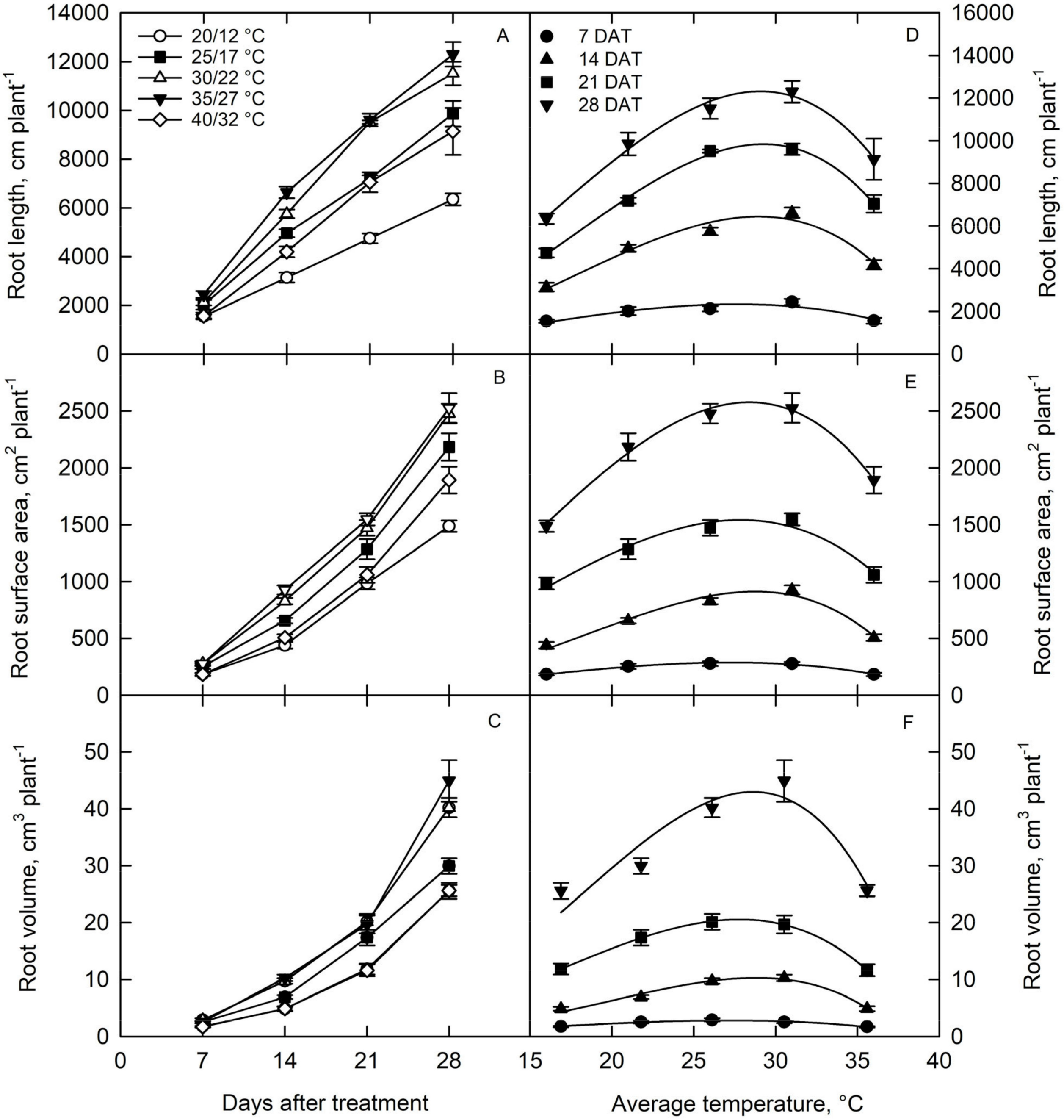

Figure 4. Temporal trends of corn (**A**) total root length, (**B**) root surface area, and (**C**) root volume under five temperature treatments over days after treatment and estimated mean growth rates from the weekly measurements as average function temperature for (**D**) total root length, (**E**) root surface area, and (**F**) root volume. A modified beta function model best described the biomass accumulation rates of various root growth parameters as a function of temperature. All values are the mean ± standard error of six replications at each harvest under each treatment.

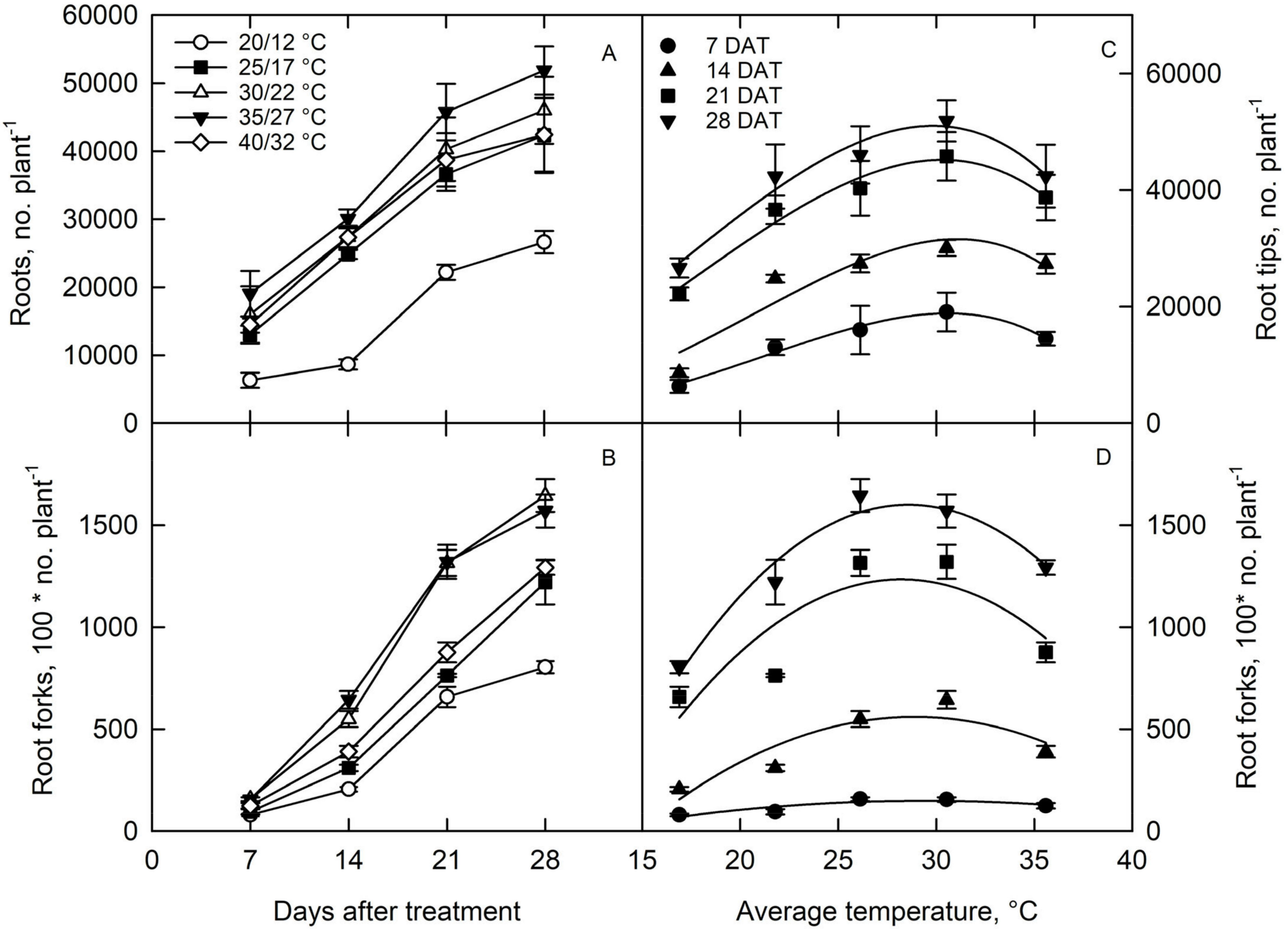

Figure 5. Temporal trends of corn root developmental parameters (**A**) root tips and (**B**) root forks under five differing temperature treatments over days after treatment and estimated mean root developmental rates measured at weekly intervals presented as a function of average temperature for (**C**) root tips and (**D**) root forks as a function of temperature at different times periods. A modified beta function model best-described biomass accumulation rates of various root developmental rates as a function of temperature. All values are the mean ± standard error of six replications at each harvest under each treatment.

3.4. Biomass Accumulation

In this study, all aspects of dry weight accumulation increased following classical exponential or linear growth and developmental patterns, depending on the parameter, during the 28-d experimental period (Figure 6). Temperature effects on leaf dry weight (LDW) accumulation were like those observed for plant height and leaf area expansion, with the highest values observed under the 35/27 °C treatment followed by the 30/22 °C treatment. LDW accumulation was estimated to have a T_{min} of 12.7 °C, T_{opt} of 30.8 °C, and T_{max} of 38.1 °C (Table 3). Stem dry matter (StDW) accumulation treatment effects differed from LDW accumulation, with the greatest accumulation occurring under the 30/22 °C and 35/27 °C treatment and second-highest accumulation occurring under the 40/32 °C treatment (Table 1). StDW accumulation was estimated to have similar cardinal temperatures to LDW, with a T_{opt}, T_{max}, and T_{min} of 30.6, 37.4, and 13.3 °C, respectively (Table 3). Root dry weight (RDW) accumulation was the greatest for plants grown under the 30/22 and 35/27 °C treatment (Table 2). Cardinal temperatures for RDW accumulation were estimated to be 28.7 °C for T_{opt}, 39.1 °C for T_{max}, and 7.6 °C for T_{min} (Table 3).

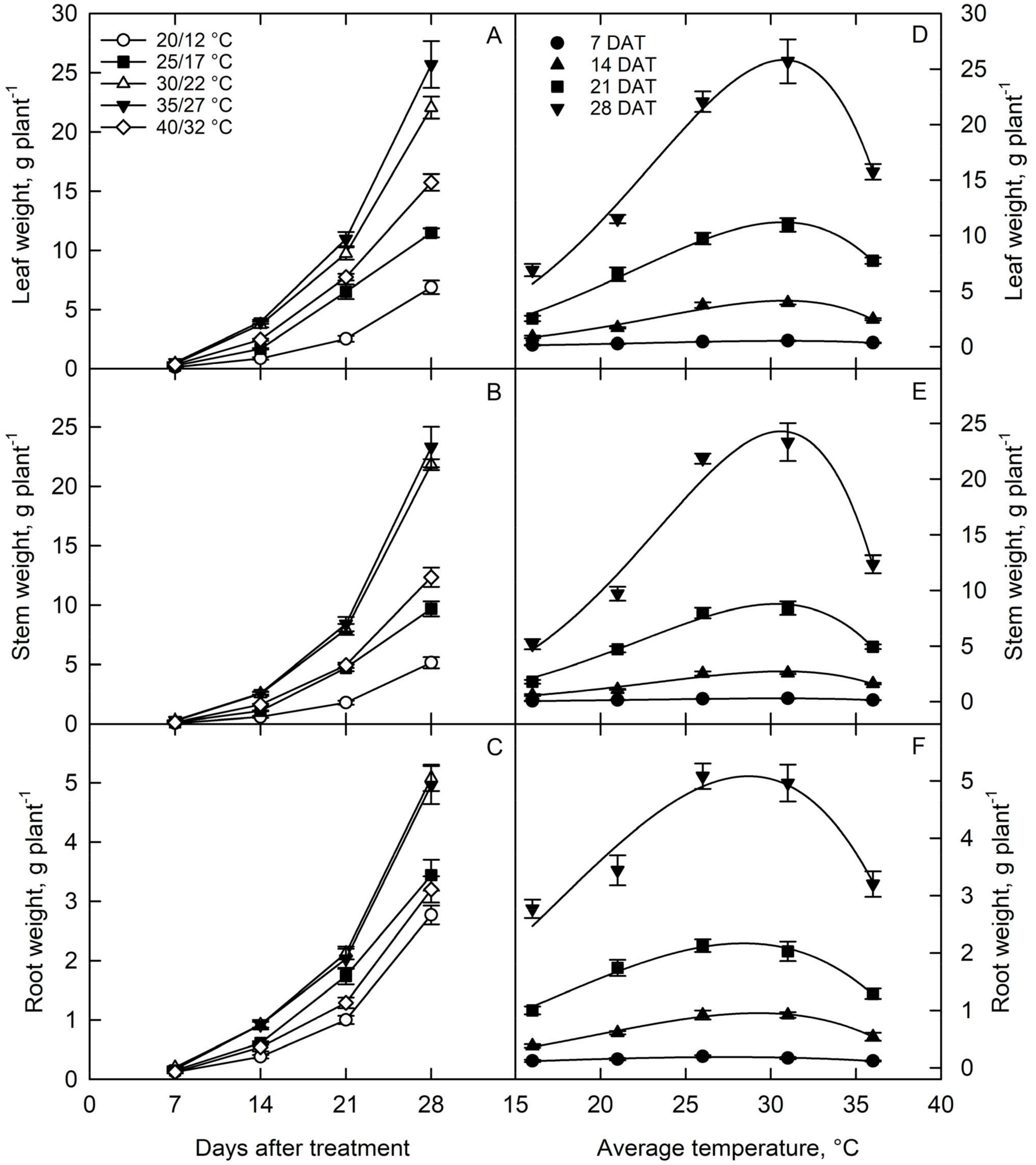

Figure 6. Temporal trends of plant dry weight components, (**A**) leaf dry weight, (**B**) stem dry weight, and (**C**) root dry weight for plants grown at different temperatures as function days after treatment, and mean biomass accumulation rates of various plant components, (**D**) leaf, (**E**) stem, and (**F**) roots as a function of temperature at different time periods. A modified beta function model best described the biomass accumulation rates of various plant components as a function of temperature. All values are the mean ± standard error of six replications at each harvest under each treatment.

3.5. Biomass Partitioning

Leaf biomass allocation percentage temporally remained stable throughout the experimental period for plants grown at high and low temperatures and declined for plants grown at more optimal temperatures as time progressed (Figure 7). On average, throughout the entire experimental period, leaves acquired the largest percentage of total plant biomass under the warmest temperature treatment, 40/32 °C, and the lowest percentage biomass under the coolest treatment. Stem biomass allocation percentage was the lowest 7 DAT and increased slightly as time progressed. The largest increase occurred between the 7 DAT and 14 DAT sampling periods. Stem biomass allocation percentage was the highest under the 30/22 °C and 35/27 °C treatment and the lowest under the coolest treatment, 20/12 °C. Root biomass allocation percentage was the highest at 7 DAT and decreased before stabilizing from 14 DAT to 28 DAT. Differing from leaf and stem biomass allocation percentages, root allocation was the highest under the 20/12 °C treatment and the lowest under the 30/22, 35/27, and 40/32 °C treatment (Figure 7).

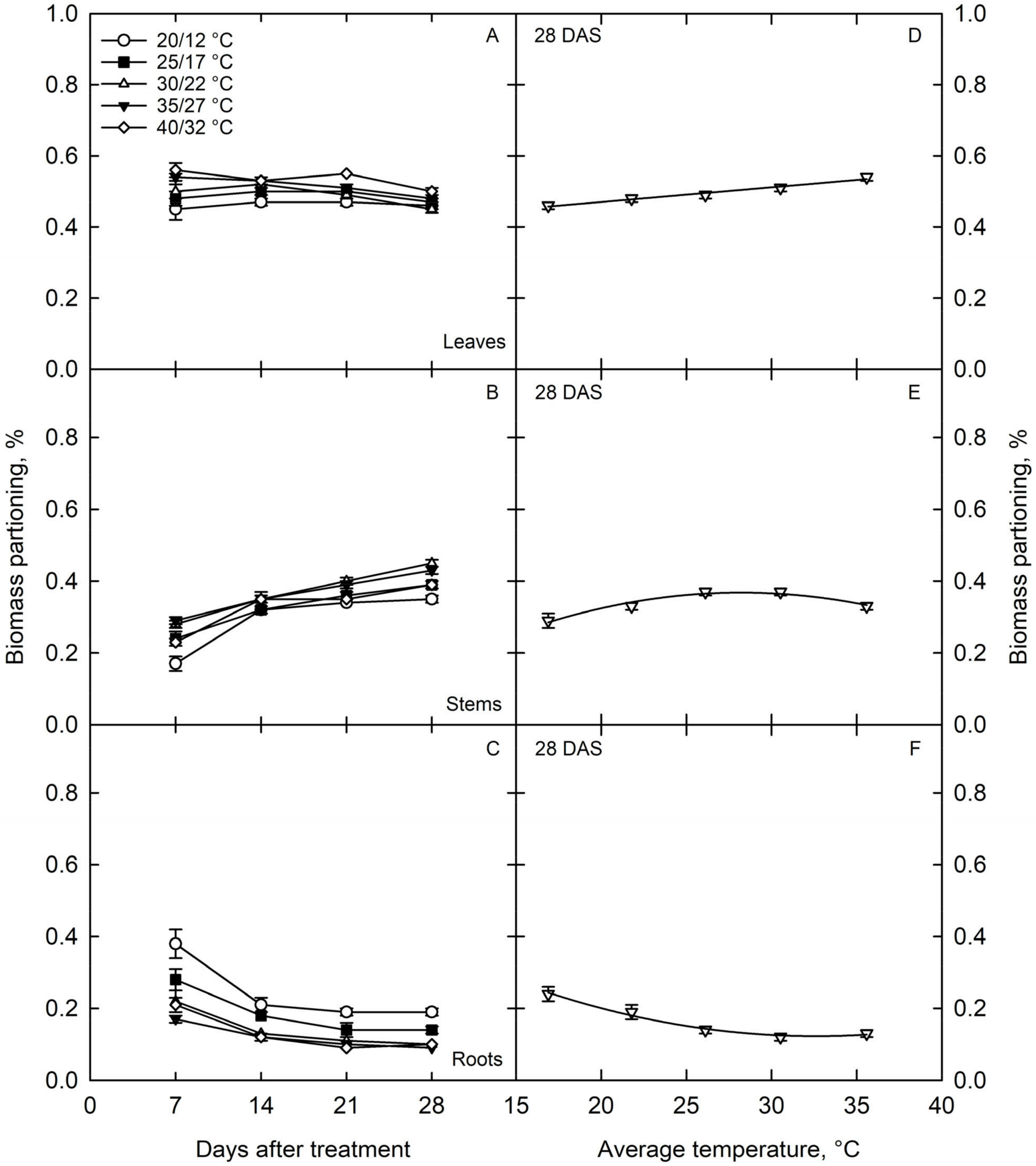

Figure 7. Temporal trends of corn biomass allocation to various plant components; (**A**) leaves, (**B**) stems, and (**C**) roots and average biomass partitioning as a function of temperature for (**D**) leaves, (**E**) stems), and (**F**) roots at various time periods as a function of temperature.

4. Discussion

Vigorous shoot growth and leaf development during early vegetative growth are crucial to establishing a crop's photosynthetic capacity and competitiveness against pests. In addition, these are critical foundations of yield potential and stress tolerance throughout the growing season. Therefore, factors controlling the production of new leaves, the duration of leaf area expansion of each leaf, and stem extension could affect yield [26,27].

In agreement with our results, Bos et al. [28] found that as temperatures decreased from their highest temperature treatment of 28/23 °C, corn leaf growth rates declined as well. Yan and Hunt [18] fit data from an experiment conducted by Barlow et al. [29] to a modified beta function and determined leaf elongation to have a T_{opt} of 32.6 °C and a T_{max} of 40.1 °C, both higher than the values estimated from this experiment. However, in this experiment, whole plant LA was measured as opposed to Barlow et al. [29], who measured the rate of individual leaf elongation. Whole plant LA is a function of leaf initiation and the expansion of those initiated leaves. In a study conducted using similar experimental facilities (SPAR units) as ours, Kim et al. [1] found the optimal and maximum temperature for leaf addition rate to be 32 °C and 44 °C, respectively. However, this study used slightly different methods to determine leaf number and considered leaf addition rate as the appearance of leaf tips. Yan and Hunt [18] fit leaf appearance data from experiments conducted by Tollenaar et al. [30] and Warrington and Kanemasu [31] to a modified beta function and estimated a T_{opt} and T_{max} for leaf appearance rate of around 31.5 °C and 41 °C. These estimates are lower than our findings and Kim et al. [1].).

The mean cardinal temperatures of PH, LA, LDW, and StDW were calculated to represent an overall summary of shoot growth. Our results conclude a T_{min} of 12.5 °C, a T_{opt} of 30.5 °C, and a T_{max} of 38.9 °C. In reviewing temperature effects on corn, Sánchez et al. [6] provided estimated cardinal temperatures for shoot growth derived from literature. These reported values included a T_{min} of 10.9 °C, lower than our results; a T_{opt} of 31.1 °C, higher than our results; and a T_{max} of 38.9 °C, precisely in line with our results.

The only shoot development aspect measured in this study was LN; thus, shoot development had a T_{min}, T_{opt}, and T_{max} of 5.5, 32.5, and 46.0 °C, respectively. It is widely understood that temperature drives phenological development in plants. Therefore, particularly in crops of agronomic importance, thermal indices use heat units to estimate the progress a plant has made throughout its life cycle. In corn, vegetative growth stages are commonly described by providing the number of collared leaves the plant has formed. Thus, by measuring the impact of temperature on leaf development, we measure the impact of temperature on shoot development and the impact of temperature on the plant's overall phenological development.

However, our results indicate that corn may maintain some development outside the range of temperatures used for thermal indices, such as the corn growing degree day (GDD) model explained by Angel et al. [10]. In this corn GDD model, a base temperature of 10 °C is used, well above the estimated T_{min} calculated in this study. The model also assumes that optimal development occurs around 30 °C and that supra-optimal temperatures do not negatively impact development. Our results estimate that vegetative development rates continue to increase until a T_{opt} of 32.5 °C is reached, and further increases in average daily temperature result in a decline in developmental rates.

A plant's productivity is directly related to its root system's ability to explore soil and forage for moisture and nutrients and its morphological capacity to uptake water and nutrients. Total root length, root surface area, and root volume are good indicators of root size and function and represent the vastness of soil the root system can access, and therefore, are helpful to evaluate nutrient and water uptake efficiency and performance under stressful conditions [5,32].

Overall cardinal temperatures for root growth were calculated as the average of TRL, RSA, RV, and RDW. These averages resulted in a T_{min} of 3.7 °C, a T_{opt} of 28.3 °C, and a T_{max} of 38.9 °C. The previous reporting of cardinal temperatures on root growth is limited, but Sánchez et al. [6] presented estimates derived from multiple studies. These findings were much higher than ours were for T_{min} (12.6 °C), lower than our results for T_{opt} (26.3 °C), and higher than our results for T_{max} (40.2 °C). Other studies have observed similar responses of root growth to temperature. As temperatures decreased from 30.5 to 15 °C, Cutforth et al. [13] reported a decrease in root growth rate; however, no supra-optimal temperatures were included in the treatments. Lal [33] reported that maize seedlings grown at constant temperatures above 35 °C significantly declined in shoot and root growth. Wijewardana et al. [8] found that when corn hybrids were grown at 29/21 °C, 25/17 °C, and 21/13 °C, decreasing temperature led to significant declines in all rooting parameters, including RT and RF development.

Water and nutrient uptake occur more predominately near the root tips due to the high expression of nutrient transporters and water channels than other parts of the root system; thus, these plant structures are critical for a healthy, productive plant [34]. Root forks can be a good indicator of root branching, and the complexity of a plant's root system architecture and root system branching provides a means to increase the expanse of soil reached and explored by a plant. Root system branching can exponentially increase the number of root tips and thus active absorptive surface area compared to root elongation alone [34]. Cardinal temperatures for root development were calculated as the mean of RT and RF with a T_{min}, T_{opt}, and T_{max} of 7.8, 30.2, and 40.8 °C, respectively. To our knowledge, there are no reported cardinal temperatures for root development.

Dry matter accumulation is a good indicator of the ability of a plant to turn sunlight into a carbon source and then partition the source to various sinks throughout the plant. Although the cardinal temperatures differed between LDW, StDW, and RDW, calculation of the overall cardinal temperatures for total dry matter (TDW) accumulation provides insight into the plant's overall ability to produce photosynthates that responds to temperature. TDW accumulation was best described by a T_{min}, T_{opt}, and T_{max} of 13.5 °C, 30.5 °C, and 38 °C, respectively.

The biomass fraction present in various plant structures relative to the entire plant's total biomass is not fixed and may vary across time and environmental conditions. However, biomass allocation is considered a strong driver of a plant's capacity to produce carbon and uptake water and nutrients. It, therefore, is an indicator of which of these functions a plant is prioritizing or of deficiencies the plant may be compensating for [35]. In this study, we found that plants partitioned more dry weight to the root systems under sub-optimal temperatures. At supra-optimal temperatures, plants partitioned more dry weight to the leaves. The greatest dry weight partitioning to the plant stem occurred when temperatures were closest to T_{opt}. High partitioning to the plant stem around T_{opt} could be a result of the plant maximizing photosynthesis and producing more photosynthates than is required to meet the demands of root and leaf growth. Our results agree with those reviewed by Porter et al. [35], who suggested that plants often decrease the fraction of biomass allocation to stems and leaves while increasing the allocation percentage to roots under low temperatures. This change in allocation could be an attempt to compensate for reduced water uptake rates often observed under low temperatures. Greater partitioning to the root system at lower temperatures could also be due to lower demand for photosynthates from above-ground parts experiencing lower growth rates [5]. Following the methods outlined in Section 2.5.3, cardinal temperatures generated from each sampling period were utilized as individual replicates and tested for differences among shoot growth, shoot development, root growth, and root development categories. No differences were found among the individual parameters within each category. Normalized values were fit to a simplified beta function representing the relative response to the temperature of these four growth and development categories: shoot growth, and development and root growth and development (Figure 8).

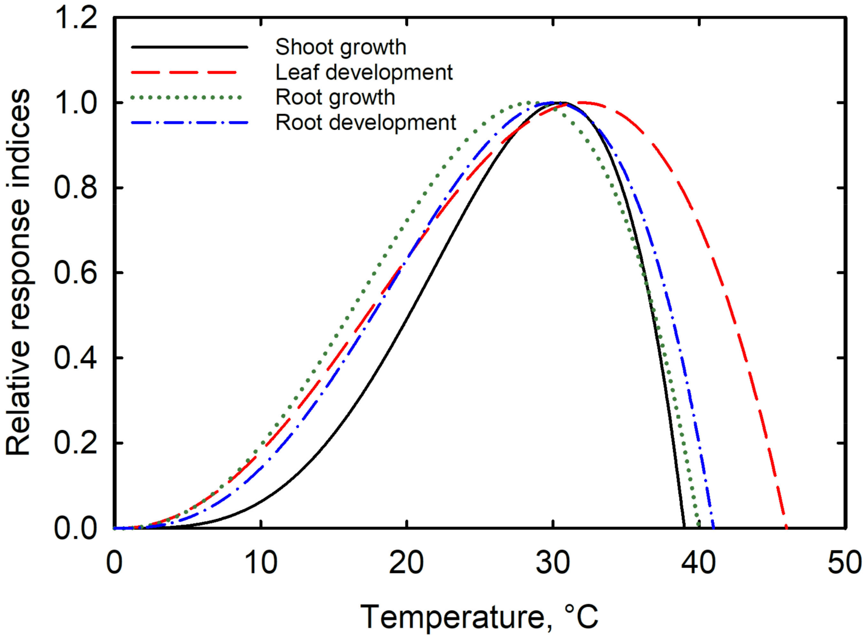

Figure 8. A simplified modified beta function best described the mean response of shoot growth, shoot development, root growth, and root development to temperature.

Estimated minimum shoot and root development temperatures were the lowest among the four groups, with an average T_{min} of 5.5 and 3.7 °C, respectively, with shoot growth having the highest T_{min} of 12.5 °C. Optimal temperatures also were significantly different. Shoot development was estimated to have the highest T_{opt} at 32.6 °C, and root growth was estimated to have the lowest T_{opt} at 28.3 °C. Maximum temperatures were the lowest for both shoot and root growth at 38.9 °C and the highest for shoot development at 46.0 °C.

Understanding potential growth and development under optimal conditions is useful when optimizing crop simulation models [36] and when creating simple models for field application [37,38]. The potential growth and development values for each parameter in this study were derived from the modified beta functions fit to the data at each harvest shown in Figures 4–6. These values varied among each parameter and increased over time (Figure 9). Functional algorithms were fitted to each parameter to describe its potential behavior over time (Table 4). Corn mainstem leaves, root tips, root length, and root surface area increased linearly (Figure 9). In contrast, plant height, leaf area development, root forks, and root volume increased exponentially over time (Figure 9, Table 4). The functional algorithms could estimate potential corn shoot and root growth parameters at any given location for any given sowing dates. Additionally, the algorithms could improve the existing corn models [36–40] in enhancing their functionality. Both simple and complex crop simulation models will have potential utilization in emerging precision agriculture technology [41].

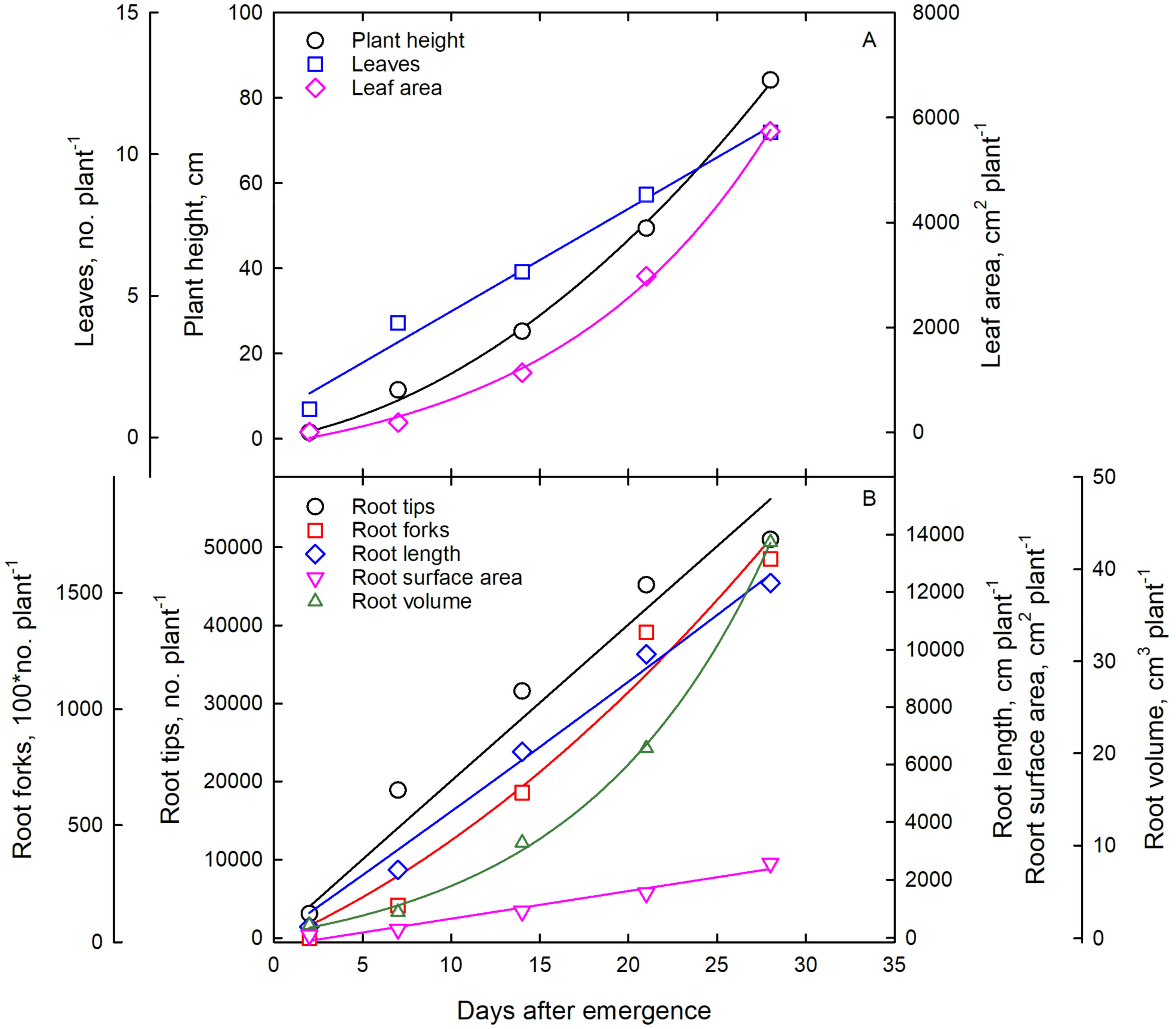

Figure 9. Estimated potential corn growth and developmental parameters from the fitted modified beta functions model as temperature at various harvests.

Table 4. Regression parameters and coefficients of corn estimated maximum growth values over time at optimum temperature for all shoot and root morphological parameters of corn (Y = a + bx for linear; Y = a + bx + cx^2 for quadratic), where Y is the plant parameter and x is days after sowing.

Parameters	Regression Parameters			Regression Coefficients
	a	b	c	R^2
Plant height, cm	-	0.7255	0.0805	0.99
Mainstem leaves, no. plant^{-1}	0.8313	0.3625	-	0.98
Leaf area, cm^2 plant^{-1}	88.51	−51.483	9.0394	0.99
Root tips, no. plant^{-1}	0	2006.3	-	0.98
Root forks, no. plant^{-1}	0	33.31	1.0205	0.99
Root length, cm plant^{-1}	429.60	0.7432	-	0.99
Root surface area, cm^2 plant^{-1}	−293.25	95.39	-	0.97
Root volume, cm^3 plant^{-1}	2.548	−0.4813	0.0678	0.99

The potential root and shoot growth and developmental parameters under optimum temperature conditions (Figure 9 and Table 4) and the relative response indices (Figure 8) under a wide range of temperatures under sun-lit conditions similar to field environments should be helpful to develop new subroutines or improve corn simulation models [37,39,40] for field applications and in policy areas [42]. In addition, the influence of other environmental stress actors, such as ultraviolet-b radiation [43], soil waterlogging [44], nutrients [45], and water stress [46] on corn growth and developmental processes are required to decrease the corn growth under field conditions further. Future research should also address reproductive yield and grain quality as a function of temperature under optimum water and nutrient conditions.

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Abbreviations

DAS, days after sowing, DAT, days after treatment; GDD, growing degree day; LA, leaf area; LDW, leaf dry weight; LN, leaf number; PH, Plant height; PVC, polyvinyl chloride; RDW, root dry weight; RF, root forks; RSA, root surface area; RT, root tips; RV, root volume; RS, root to shoot ratio; StDW, stem dry weight; TDW, total dry weight; TR, total root length; VPD, vapor pressure deficit.

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