Applying Thermal Time Scales to Sunflower Development

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Abstract

Knowledge of sunflower (*Helianthus annuus* L.) development can support integrated pest management and cultural practices to enhance crop yield potential while reducing production costs. The objective of this research was to evaluate the suitability of thermal time to provide a continuous scale of vegetative leaf appearance and of reproductive development in sunflower. Empirical models were fit to leaf appearance and reproductive growth stage observed for an oilseed hybrid over nine planting periods; two analogous sets of coefficients corresponded to simple or weighted average calculations of thermal time. The resulting models were tested for predictive value using similar observations for another oilseed and a confection hybrid. The leaf appearance model accounted for > 80% of observed variation; predictive accuracy exceeded 80% as well. The reproductive growth stage model accounted for 95% of variation in observed growth stage (RMSE < 0.35) and had predictive accuracy exceeding 94% (RMSE $\leq$ 0.51). The development model is consistent with recent reports of sunflower development and is suitable for forecasting sunflower growth stages where late-vegetative photoperiod exceeds 14 h. Further observations are required to evaluate effects of photoperiod < 14 h on reproductive development.

Introduction

Sunflower crop growth requirements and susceptibility to environmental hazards change with crop development. Water requirements coincide with canopy formation—typically maximized at flowering (Hattendorf et al., 1988). Population surges of insect pests can be avoided by selective planting dates (Rogers et al, 1983; Sunderman et al., 1997) or mitigated by timely pesticide applications (Aiken and Charlet, 2003). Freeze damage of late-planted or double-cropped sunflower may be avoided by prudent cultivar selection. Knowledge of sunflower development can support integrated pest management and cultural practices to enhance crop yield potential while reducing production costs.

The concepts of thermal time, photoperiod and growth stage are relevant to the problem of forecasting sunflower development. Thermal time (Ritchie and NeSmith, 1991), which can be calculated as growing degree days (GDD, ^{o}Cd), corresponds to leaf appearance (phyllochron, thermal time required for a new leaf to emerge) and duration of reproductive growth stages (Villalobos et al., 1996; Robinson et al., 1967; Goyne et al, 1989). Villalobos et al. (1996) reviewed photoperiod sensitivity, identified as the period separating juvenile growth stage and floral initiation; citing evidence that photoperiod response differed among cultivars. Thermal requirements also appear to be a heritable trait (Goyne et al., 1990). Thermal time and photoperiod sensitivity appear to be suitable scaling factors for forecasts of sunflower development.

Prior studies of sunflower development give emphasis to topics relevant to breeding techniques, e.g. timing of anthesis (Goyne et al., 1990), and to specific developmental processes, i.e., photoperiod sensitivity, achene growth, and oil yield formation (Villalobos et al., 1996). Applications for crop management practices are less common. Robinson et al. (1967) and

Villalobos et al. (1996) reported durations of sequential growth stages, which could be used to provide a piecewise linear function describing development. However, the utility of such functions, under field conditions, is limited by the cost of extensive sampling required to establish duration of specific growth stages when emergence is non-uniform. The objective of this research was to evaluate the suitability of thermal time to provide a continuous scale of vegetative leaf appearance and for reproductive development in sunflower.

Methods and Materials

We evaluated thermal time as a scaling factor for sunflower development using weekly growth stage observations from three studies involving two oilseed hybrids and a single confection hybrid. An empirical model was fit to leaf appearance and reproductive growth stage observed for one of the oilseed hybrids that is frequently used as a maturity check in performance trials. Regressing predicted growth stage on observations of development for the other oilseed hybrid and the confection hybrid tested the resulting model. This model development and evaluation procedure was implemented using two alternative algorithms for calculating degree days. Details of cultural practices and evaluation procedures follow.

A planting date study (Aiken and Stockton, 2003a) utilized SF 187 (conventional oleic oilseed) and S 954 (confection) for four planting dates in 2000 and 2001. A supplemental water study (Aiken and Stockton, 2003b) utilized SF 187 for five water application treatments in 2000 and 2001. A pest management study (Aiken and Charlet, 2003) utilized TR 652 (mid-oleic oilseed) for three planting dates under irrigation in 2001 and 2002. All studies were conducted on a Keith silt loam soil (fine silty, mixed, mesic Aridic Argiustoll) at the Northwest Research—Extension Center, Colby, KS (39.4^o N, 101.0^o W)

All sunflower seed was planted (0.76 m rows) into disked and harrowed soil using a fluted coulter and double-disk opener. Planting rates were 58,045 seeds ha^{-1} for irrigated studies and 44,460 and 34,580 seeds ha^{-1} for oilseed and confection cultivars, respectively, under rain-fed conditions. Supplemental soil fertility included 11.2 kg N ha^{-1} and 33.6 kg P_2O_5 ha^{-1} banded adjacent and below the seed furrow at planting. Irrigated studies also received 101 kg N ha^{-1} applied as urea using injector nozzles, while 90 kg N ha^{-1} were similarly applied for studies under rain-fed conditions. Glyphosate (Roundup, 280 g a.i. ha^{-1}), sulfentrazone (Spartan, 158 g a.i. ha^{-1}) and pendimethalin (Prowl, 87 g a.i. ha^{-1}) were applied within three days following planting.

Date of emergence (80% of final stand with cotyledons emerged from soil) was noted by daily qualitative emergence ratings. In 10 of 24 cases, emergence was not directly observed, but calculated from leaf appearance observations (see below). Growth stage observations included leaf appearance (LN, number of true leaves greater than 4 cm in length) prior to floral bud appearance (R1), and of reproductive stages (RS) thereafter, following the definitions of Schneiter and Miller (1981). Observations were noted weekly for each replicate plot. In 2001, leaf number was noted at R3 growth stage for the cultivar TR 652, prior to completion of leaf appearance. Observations represent a qualitative assessment of median growth stage for a given plot.

Weather data were obtained from the Cooperative Observer Site (Colby 1SW), associated with the National Weather Service (NWS), which was maintained by the Northwest Research—Extension Service. Daily evaporation from a Class A Pan was determined from April 1 through September 30 at this site. Degree days were calculated by two methods: simple or weighted averages of daily thermal extremes. The simple average method was derived from Robinson (1971), calculating degree day by subtracting a base temperature (T_{b1}) of 7.2 ^{o}C from the simple average of daily temperature extremes; this method was modified by limiting daily extremes to lower (T_{b1}) and upper (T_{ul}, 40 ^{o}C) values. The weighted average method involved a more complex algorithm following Jones et al. (1986). This algorithm provided a weighted average of daily temperature extremes, considering an optimal temperature (T_{opt}), as well as base temperature (T_{b2}) and upper limit (T_{ul}).

The weighted average algorithm considers two exclusive conditions for daily temperature extremes i) $T_{mn} > T_{b2}$ and $T_{mx} < T_{opt}$, then GDD = DTT where

$$DTT = \frac{T_{mx} + T_{mn}}{2} - T_{b2} \quad [1]$$

ii) Otherwise, $GDD = \frac{1}{8} \cdot \sum_{i=1}^{8} \left(TT_i\right)$, where

$$TT_i = T_{mn} - T_{b2} + TF_i \cdot (T_{mx} - T_{mn});\ i = 1 \text{ to } 8 \quad [2]$$

and $TF_i = 0.931 + 0.114 \cdot i - 0.0703 \cdot i^2 + 0.0053 \cdot i^3$; when $T_{opt} < (TT_i + T_{b2}) < T_{ul}$ then

$$TT_i = \left(T_{opt} - T_{b2}\right) \cdot \left[1 - \left(TT'_i - T_{opt}\right) \div \left(T_{ul} - T_{opt}\right)\right] \quad [3]$$

where TT'_I is the value computed from [2]; when $T_{ul} < TT_i < T_{b2}$ then $TT_i = 0$. This algorithm is identical to the simple average method for daily temperatures within T_{b2} and T_{opt}. When temperatures were beyond these limits, the day was partitioned into eight three-hour intervals with subsequent weightings (TF_i) and limits applied. Following Villalobos et al. (1996) T_{b2} = 4 ^{o}C, T_{opt} = 28 ^{o}C and T_{ul} = 40 ^{o}C. Cumulative thermal time was computed from emergence for both degree day calculation methods.

Where emergence was not directly observed, apparent emergence dates were calculated from planting date, the earliest observation of leaf appearance, cumulative degree days, and the rate of leaf appearance under favorable moisture conditions:

$$cGDD_{P-E} = cGDD_{P(j)} - j \cdot P_E \quad [4]$$

where $cGDD_{P-E}$ is cumulative growing degree days (^{o}Cd) from planting to emergence, $cGDD_{P(j)}$ is cumulative growing degree days (^{o}Cd) from planting until emergence of leaf ‘j’, and P_E is the rate of leaf appearance (^{o}Cd leaf^{-1}) under favorable moisture conditions for emergence and vegetative growth. Cumulative growing degree days from emergence ($cGDD_E$) was calculated from cumulative growing degree days from planting ($cGDD_P$) by subtracting $cGDD_{P\text{-}E}$

$$cGDD_E = cGDD_P - cGDD_{P-E} \qquad [5]$$

The value for P_E used to calculate apparent plant emergence was determined under water sufficiency from observation of leaf appearance in the supplemental irrigation study, where initial soil water supply did not limit leaf appearance; P_E was determined by the slope of leaf appearance (through 14 leaves) regressed on observed $cGDD_E$, with the intercept forced to zero. Parallel analyses were completed for $cGDD_E$ calculated either by simple or weighted average.

Photoperiod sensitivity to day length was hypothesized for development from floral initiation to visible appearance of the floral bud (Villalobos et al., 1996). Day length (DL) was calculated from solar declination (Rosenberg et al., 1983), day of year and latitude (DeCoursey, 1992). We assumed floral initiation (end of juvenile development) and the initial visible appearance of the floral bud (R1) define the duration of photoperiod sensitivity. Floral initiation was assumed to occur 295 ^{o}Cd (calculated by weighted averages) following emergence, corresponding to the value reported by Villalobos et al. (1996) for a full-season cultivar. Day length during photoperiod sensitivity (DL_{PS}) was calculated as the average of day lengths at 295 ^{o}Cd $cGDD_E$ and at R1.

Sunflower development was hypothesized to scale with $cGDD_E$, as modified by photoperiod sensitivity. This hypothesis was tested by fitting an empirical model to observations of the cultivar SF187 and testing the predictive accuracy of this model against observations of the cultivars TR 652 and S 954. Evaluation criteria include coefficient of determination, residual mean square error and predictive bias.

In the case of leaf appearance (phyllochron) a linear model was used. Leaf appearance was regressed on DL_{PS} and $cGDD_E$.

$$LN = \alpha_{LN} \cdot DL_{PS} + P^{-1} \cdot cGDD_E + e \qquad [6]$$

The coefficient α_{LN} represents photoperiod sensitivity of leaf number and P^{-1} represents the inverse of phyllochron. In the case of reproductive development, a quadratic model was used. The numeric values corresponding to reproductive growth stages (R1 to R9) were regressed on $cGDD_E$, $cGDD_E^2$ and DL_{PS}.

$$RS = \alpha_{RS} \cdot DL_{PS} + \beta \cdot cGDD_E + \gamma \cdot cGDD_E^2 + e \qquad [7]$$

The coefficient α_{RS} represents photoperiod sensitivity of reproductive development; and β and γ represent linear and quadratic effects of thermal time. As variability among replicates was minimal, observations averaged among replicates are taken as representative of an experimental treatment. Parallel analyses were completed using both methods of calculating $cGDD_E$.

Photoperiod sensitivity was also analyzed separately by evaluating thermal time required from emergence to initial visible appearance of the floral bud (R1). Thermal time to R1 was regressed on DL_{PS}. This analysis was completed using the weighted average method of calculating $cGDD_E$, to permit direct comparison with photoperiod sensitivity parameters reported in Villalobos et al. (1996).

Adequacy of the development model was evaluated against observations of the oilseed cultivar TR 652 and the confection cultivar S 952. Growth stages (LN and RS) calculated from the empirical model derived from SF 187 observations were regressed on the independent observations of growth stages for cultivars TR 652 and S 952. Predictive bias was identified by significant deviation of intercept from 0 and of slope from 1; precision was determined by R^2 and by RMSE.

Results

Cumulative annual precipitation and growing season (April 1 to September 30) evaporation from a Class A pan for the experimental site are presented in Fig. 1. Cumulative monthly normals representing the 30-year interval 1971-2000 are included for reference. Growing season pan evaporation exceeded normal in 2000, 2001 and 2002 by 17%, 6% and 20%, respectively. Precipitation was less than normal by 22%, 9% and 31% during 2000, 2001 and 2002, respectively. The annual precipitation normal constitutes 35% of the growing season pan evaporation normal in this semi-arid environment.

The two methods for computing degree days were highly correlated, with the poorest correlation ($r = 0.9986$) occurring in 2001 (Fig 2). The magnitude of cGDD from the April 1 to September 30 growing season was similar as well. The weighted average method resulted in fewer cGDD than the simple average method. The differences between these methods ranged from 20.1 to 81.3 GDD (0.9% to 3.7% of cGDD). Values calculated by weighted average were higher than those calculated by simple average in early summer. The lower base temperature resulted in greater GDD accumulation for the weighted average. In late summer, values calculated by weighted average were lower than those calculated by simple average. During this period, temperatures exceeding T_{opt}, led to the weighting adjustments, which reduced GDD accumulation.

Day of planting, emergence, bloom and maturity observed for experimental treatments are presented in Table 1. Drought conditions in 2000 resulted in delayed emergence for PD 2 and PD 3 for rain fed studies of cultivars SF 187 and S 954. Leaf appearance was not determined for PD 1, thus emergence could not be evaluated and subsequent observations were not included in the analysis. Average thermal time from planting to emergence under water sufficient conditions was 129 ^{o}Cd and 157 ^{o}Cd computed by simple and weighted averages, respectively.

A linear relation between leaf appearance (to V14) and $cGDD_E$ supports the phyllochron concept in sunflower (Fig 3d-f, Table 2). Including DL_{PS} as a regressor did not improve R^2 and the coefficient for DL_{PS} was not significantly different from zero. Values for phyllochron (36.1 $\pm$ 1.2 and 31.1 $\pm$ 1.1 ^{o}Cd leaf^{-1}; simple and weighted averages, respectively) were significantly greater ($p > t = 0.001$) than that obtained under water sufficient conditions (31.8 $\pm$ 1.0 and 26.4 $\pm$ 0.7 ^{o}Cd leaf^{-1}; simple and weighted averages, respectively).

Reproductive development stages were related to $cGDD_E$ by a quadratic function, modified by a function of DL_{PS} (Fig. 3a-c, Table 2). When the DL_{PS} term was included as a regressor term, a coefficient for intercept did not significantly differ from zero, and was, therefore, excluded from the model. The precision of this model was similar for both methods of calculating $cGDD_E$ (Table 2).

No bias was detected in predicted leaf appearance or for reproductive development for either hybrid (Table 3). Precision was similar for values derived from either simple or weighted average methods of calculating $cGDD_E$.

The limited data available support the photoperiod sensitivity hypothesis for hybrid SF 187prior to R1 (Fig 4). Thermal requirements to reach R1 growth stage increased with a positive difference in day length from 15 h.

Discussion

The simple average calculations of ^{o}Cd are more convenient than the weighted average algorithm. However, physiological interpretations of super-optimal and limiting temperatures support the weighted average algorithm. The two methods are similar in predictive accuracy, analogous to the result that air and soil temperature provided similar predictive accuracy for a wheat developmental model (McMaster and Wilhelm, 1998). Users applying one form or the other should take care to utilize the corresponding coefficient (Table 2) in ^{o}Cd calculations. Imposing limits on T_{mx} and T_{mn} restricts accumulation under extreme conditions, and avoids the conceptual difficulty of decrements in cGDD, which can occur when T_{b1} exceeds the average of daily temperature extremes.

The method of calculating a single phyllochron during vegetative development is a simplification of differential leaf appearance rates before and after V7 (Villalobos and Ritchie, 1992). The phyllochron calculated by the weighted average method (31.1 ^{o}Cd leaf^{-1}) was 6% lower than the **average** of values reported by Villalobos et al. (1996) for the first six leaves (43 ^{o}Cd leaf^{-1}) and subsequent leaves (23 ^{o}Cd leaf^{-1}). This is a reasonable comparison because phyllochron, in this study was determined by regression on observation of leaf appearance up to V14 growth stage. Observations of leaf number at R1 and R3 growth stages prior to final leaf appearance in 2001 for the TR 652 hybrid indicate a phyllochron of 18 $\pm$ 2.8 ^{o}Cd leaf^{-1} (N = 3) for leaves emerging after V12. These limited data support inference of differential phyllochron during early and later leaf appearance. Utilizing a single linear function for leaf appearance, prior to reproductive growth stages, offers the advantage of simplicity.

Environmental effects—including soil water sufficiency—may contribute to variation in phyllochron. The value derived for water sufficient conditions (26.4 ^{o}Cd leaf^{-1}, weighted average) was 15% lower relative to that obtained from all growing conditions in these studies. Soil water deficits, which limit turgor pressure for cell expansion could account for this variability in leaf appearance—which is defined by leaves attaining a threshold size.

Photoperiod sensitivity of sunflower floral development is defined here as occurring during the interval between floral initiation (assumed 295 ^{o}Cd following emergence) and the visible appearance of floral bud, R1, (Villalobos et al., 1996). The limited data depicted for SF 187 in Fig 4 indicates development to R1 is delayed by 14.1 days for each hour the average photoperiod in this interval is less than 15. This calculation takes into consideration an average daily thermal accumulation of 15.7 ^{o}Cd from floral initiation to floral appearance in 2001 and 2002 at this site. This value for photoperiod sensitivity is 15% higher than the upper value (3.74 to 12.32 da h^{-1}) reported by Villalobos et al. (1996). Robinson (1971) found no significant effects of day length on time from emergence to R1 when day length exceeded 15 h during these vegetative developmental stages. However Robinson et al. (1967) reported that thermal time (simple average) required for an average of eight sunflower cultivars planted on May 14 to reach the R5 growth stage increased from 875 $\pm$ 37.6 ^{o}Cd at four upper-latitude sites (> 44 ^{o}N; day length > 15 h) to 996 $\pm$ 25.8 ^{o}Cd at three mid-latitude sites (< 40 ^{o}N; day length < 15 h). Goyne et al. (1989) concluded temperature was sufficient to predict sunflower development to R5 provided photoperiod was limited to the 14.5 to 16.2 h range; but photoperiod effects should be considered for conditions outside this range. These results support inference of photoperiod extending vegetative development when day length is less then 15 h.

The positive coefficient fit for α_{RS} in the RS model indicates reproductive development was slightly accelerated by photoperiod effect. Robinson (1971) reported that days required for sunflower hybrids to develop from R6 to R9 decreased from 33 to 29 in plantings from April 24 to June 28 at Rosemount, MN (44.7 ^{o}N). Corresponding thermal time (simple average) decreased, significantly, from 444 ^{o}Cd to 251 ^{o}Cd. Average day length duration from emergence to R5 decreased from 15.2 h to 14.5 h during this planting interval; and continued to decrease to crop maturity. These observations suggest day lengths < 15 h accelerated reproductive development for the six sunflower cultivars observed. The effects of photoperiod on extended duration of vegetative growth and on accelerated reproductive development may lead to lower yield potential for late-planted sunflower. This apparent effect may be significant for double cropping sunflower following wheat—particularly at latitudes less than 40^{o}.

Thermal time requirements from emergence to reproductive growth stages (RS) can be computed from the model developed here by solving for the quadratic roots of Eq [7], using coefficients from Table 2 which correspond to the appropriate $cGDD_E$ calculation method. Robinson et al. (1967) reported 1003 ^{o}Cd (simple average) were required for eight sunflower cultivars to reach R5 following a May 14 planting in Manhattan KS (39^{o} N). The corresponding value for the model presented here is 1125 ^{o}Cd (130 ^{o}Cd from planting to emergence and 995 ^{o}Cd from emergence to R5)—a value 12% greater than that of Robinson et al. (1967). The discrepancy is attributable to heritable differences among cultivars as three closely related inbreds observed by Robinson et al (1967) had 17% greater thermal requirements than the overall average. Robinson (1971) reported that 512 ^{o}Cd were required for six sunflower varieties, planted May 12 at Rosemount, MN (44.7^{o} N) to develop from R5 to R9. The corresponding value for the model presented here is 760 ^{o}Cd, a value that is 48% greater. The difference could result from heritable, day length and environmental effects.

Comparisons of thermal requirements for development with that of recent reports are closer than those cited in earlier literature—particularly with respect to seed fill duration.

Villalobos et al. (1996) reported thermal requirements (weighted average) from emergence to R1, R5 and R9 were 422 ^{o}Cd, 1002 ^{o}Cd and1602 ^{o}Cd, respectively, for Sungro 380, a full-season cultivar. Corresponding values for SF 187 were 471 ^{o}Cd, 844 ^{o}Cd and 1541 ^{o}Cd, respectively, all calculated for 14.5 h photoperiod. The model derived here for SF 187 gives results within variability expressed among genotypes (Robinson et al., 1967) for thermal requirements to R5 growth stage. Effects of genotype, photoperiod and abiotic stress factors on duration of seed fill (R6 to R9) are of particular interest for late-planted sunflower at latitudes less than 40^{o} and warrant further investigation.

The method of periodic qualitative observation of median growth stage has advantages and limitations. Rapid observation is a principle advantage, permitting relatively frequent observations for multiple experimental treatments. The method benefits from the principle of central tendency as observation errors diminish with replication and temporal sampling frequency. Also, the method does not require daily observation and avoids ambiguity of transitional growth stages as intermediate numeric values can be assigned to a given observation. This method may not substitute for detailed and repeated observations of individual plants required to clarify specific growth and development processes.

The growth stage model can be used to forecast sunflower development in environments similar to the experimental site. These forecasts can be useful to schedule crop scouting for pest management, irrigation requirements, and planting or harvesting equipment. Forecasts may also help anticipate canopy closure, which can affect the relative growth of weedy plants. The forecast can guide planting dates to avoid population surges of insect pests such as stem weevil (Armstrong and Koch, 1997; Barker and Charlet, 1993). Application beyond experimental conditions (central High Plains, early May to mid-June planting) should be supported by further evaluation at a range of latitudes and growing conditions.

Conclusions

An empirical model of sunflower development utilizes the concepts of thermal time, photoperiod sensitivity and growth stage to quantify sunflower development. The coefficients fit to an oilseed sunflower (SF 187), commonly used as a maturity check in yield trials, accounted for 80% of variation in leaf appearance and 95% of variation in reproductive development observed over nine planting periods. The resulting model effectively forecast vegetative and reproductive development of full-season oilseed and confection hybrids with no bias and precision exceeding 80% (vegetative, RMSE $\leq$ 2.50) and 94% (reproductive, RMSE $\leq$ 0.51). Coefficients for models using ^{o}Cd calculated by simple or weighted averages of daily temperature extremes gave similar results. The development model is consistent with recent reports of sunflower development and is suitable for providing forecasts of sunflower growth stages under rain fed and irrigated semi-arid growing conditions at mid-latitudes and late vegetative photoperiods exceeding 14 h. Further observations are required to extend the model to reflect effects of shorter photoperiod on reproductive development.

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Table 1 Day of year for planting, emergence (VE), bloom (R5) and maturity (R9)

	Year 1				Year 2			
Trt	Planted	Emerged	Bloom	Maturity†	Planted	Emerged	Bloom	Maturity
SF 187								
PD1	126	NA	196	230	131	140‡	199	257
PD2	140	174‡	230	NA	144	156	207	257
PD3	153	171	230	NA	159	168‡	219	264
PD4	167	180	235	NA	173	179	231	290
WU	161	174‡	225	NA	162	172	222	268
S 954								
PD1	126	NA	196	NA	131	140‡	193	257
PD2	140	174‡	234	NA	144	156	204	257
PD3	153	171	230	NA	159	168‡	215	264
PD4	167	180	235	NA	173	179	231	290
TR 652								
PD1	131	140‡	200	249	130	148	201	273
PD2	156	165	214	264	148	154	212	276
PD3	173	179	229	NA	157	168	218	281

†The final observation either preceded maturity or followed the probable maturity date in year 1, therefore day of maturity is noted only in limited cases.

‡Emergence dates were calculated from leaf appearance rates under water sufficient conditions and from initial vegetative growth stage observations (ref Eq. [4]).

Table 2 Coefficients for Sunflower Growth Stage Dependence on Thermal Time for SF 187

	Leaf Number†			Reproductive Growth Stage‡				
Method	P^{-1}	R^2	RMSE	α_{RS}	β	γ	R^2	RMSE
Simple average	0.0277 (9.95E-4)	0.808	2.33	-0.394 (0.0328)	0.0142 (9.07 E-4)	-3.25E-6 (4.01E-7)	0.957	0.324
Weighted average	0.0322 1.15E-3)	0.810	2.30	-0.409 (0.0323)	0.0169 (9.90E-4)	-4.68E-6 (4.83E-7)	0.954	0.347

†The inverse of phyllochron (P, degree days required for leaf appearance) was found by regressing leaf number on cumulative degree days from emergence ($cGDD_E$). Values for P correspond to degree days calculated using either simple or weighted averages of daily temperature extremes.

‡Coefficients relate reproductive growth stage to a quadratic function of $cGDD_E$, which also includes photoperiod effects. Values for coefficients correspond to either simple or weighted average calculations of degree days.

Table 3 Predictive Accuracy† of Sunflower Growth Stage Model

		Simple Average				Weighted Average			
	N	a_o	a_1	R^2	RMSE	a_o	a_1	R^2	RMSE
TR 652									
LN	19	1.12 (0.689	0.874 (0.089)	0.850	2.05	1.285 (0.649)	0.876 (0.084)	0.865	1.97
RS	64	-0.378 (0.199)	1.049 (0.032)	0.947	0.467	-0.409 (0.206)	1.043 (0.033)	0.943	0.510
S 954									
LN	20	0.815 (0.905)	0.897 (0.104)	0.804	2.50	0.724 (0.883)	0.916 (0.102)	0.818	2.34
RS	77	0.103 (0.156)	0.976 (0.024)	0.955	0.338	0.182 (0.170)	0.962 (0.026)	0.946	0.407

†Predictive accuracy of growth stage model developed for SF 187 was evaluated with observations from cultivars TR 652 and S 954 by regressing predicted growth stage on observations. Bias was evaluated by testing the hypotheses that intercept (a_0) was not different from 0 and slope (a_1) was not different from 1 at the 5% probability level.

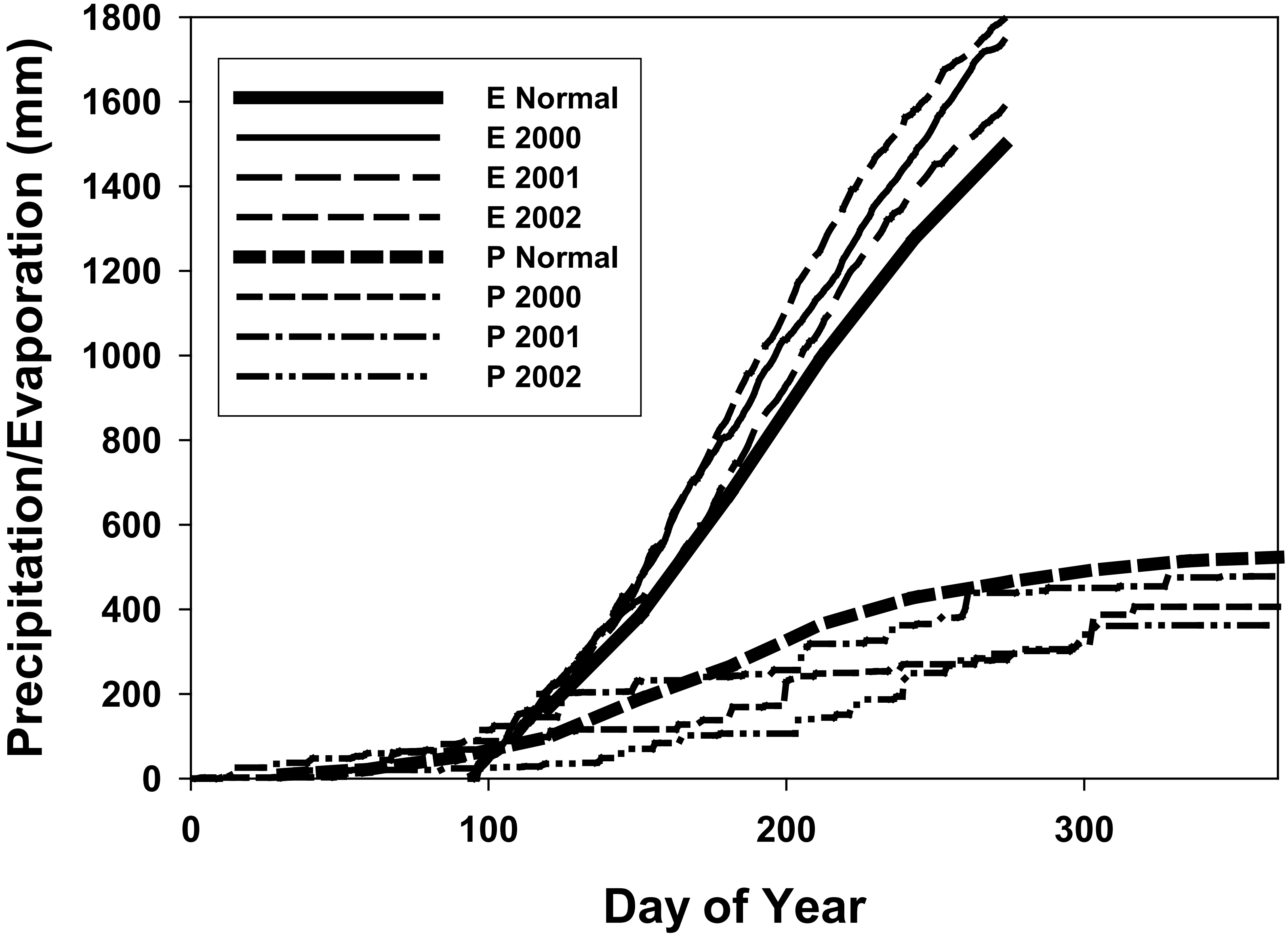
Figure captions

Figure 1. Cumulative annual precipitation (P) and growing season (April 1 to September 30) evaporation (E) from a Class A pan are depicted for 2000, 2001 and 2002; normals for the 1971-2000 period are shown as well.

Figure 2. Cumulative growing degree days for the 2001 growing season (May 1 to September 30) are calculated using simple or weighted averaging algorithms.

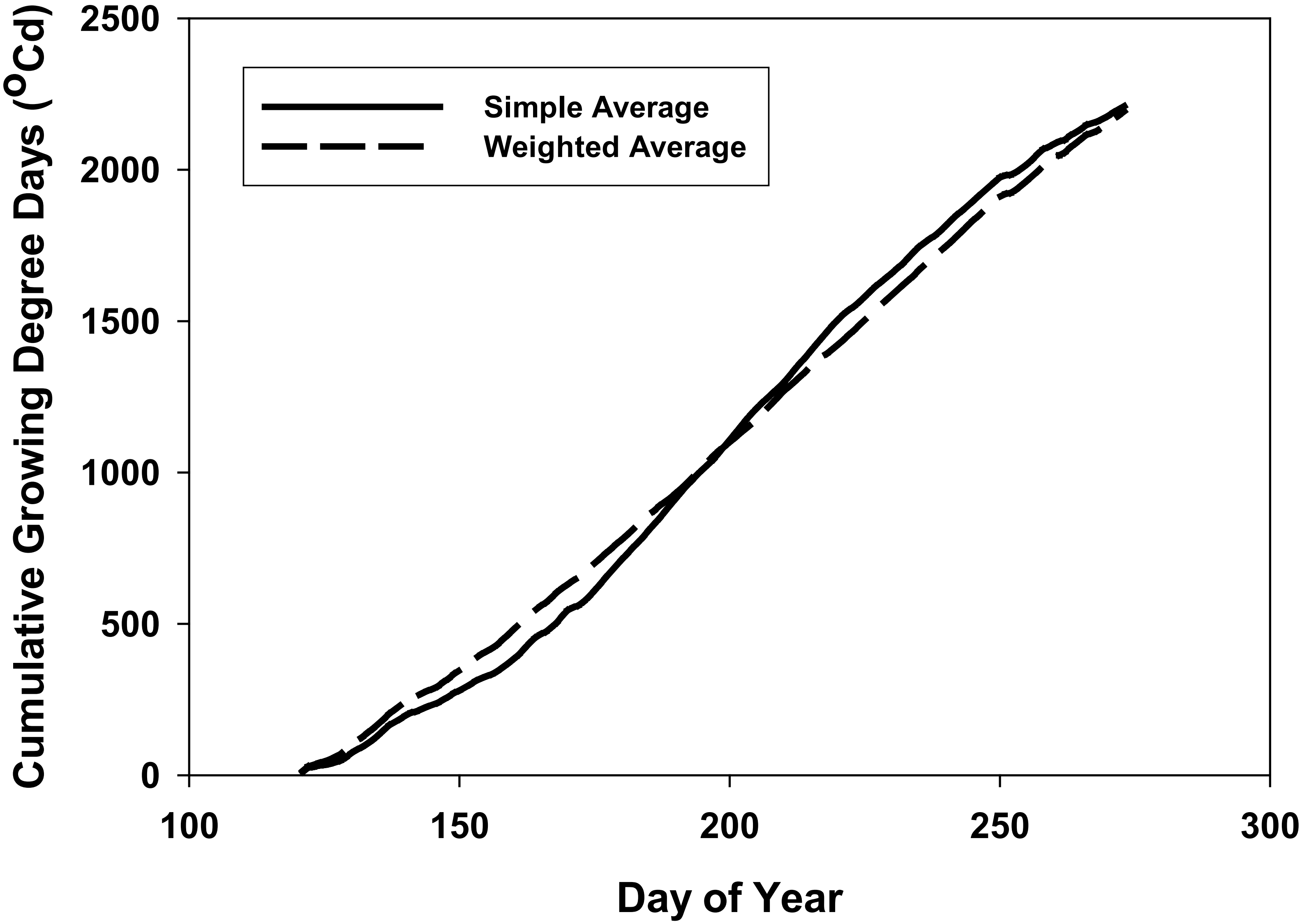
Figure 3. Sunflower development (leaf number, LN, and reproductive growth stage, RS) from 15 planting periods are shown, with respective to cumulative growing degree days (simple average algorithm) following emergence. Linear and quadratic relationships fitted to LN and RS for the hybrid SF 187 are reproduced for all three cultivars observed.

Figure 4. Cumulative growing degree days ($cGDD_{E-R1}$ weighted average algorithm) required for hybrid SF 187 to develop from emergence to visual appearance of the floral bud is shown in relation to a measure of day length. Day length for photoperiod sensitivity (DL_{PS}) was calculated as the average of day lengths at floral initiation and floral bud appearance. Day length is presented as the difference from 15 h, a possible threshold for photoperiod sensitivity.



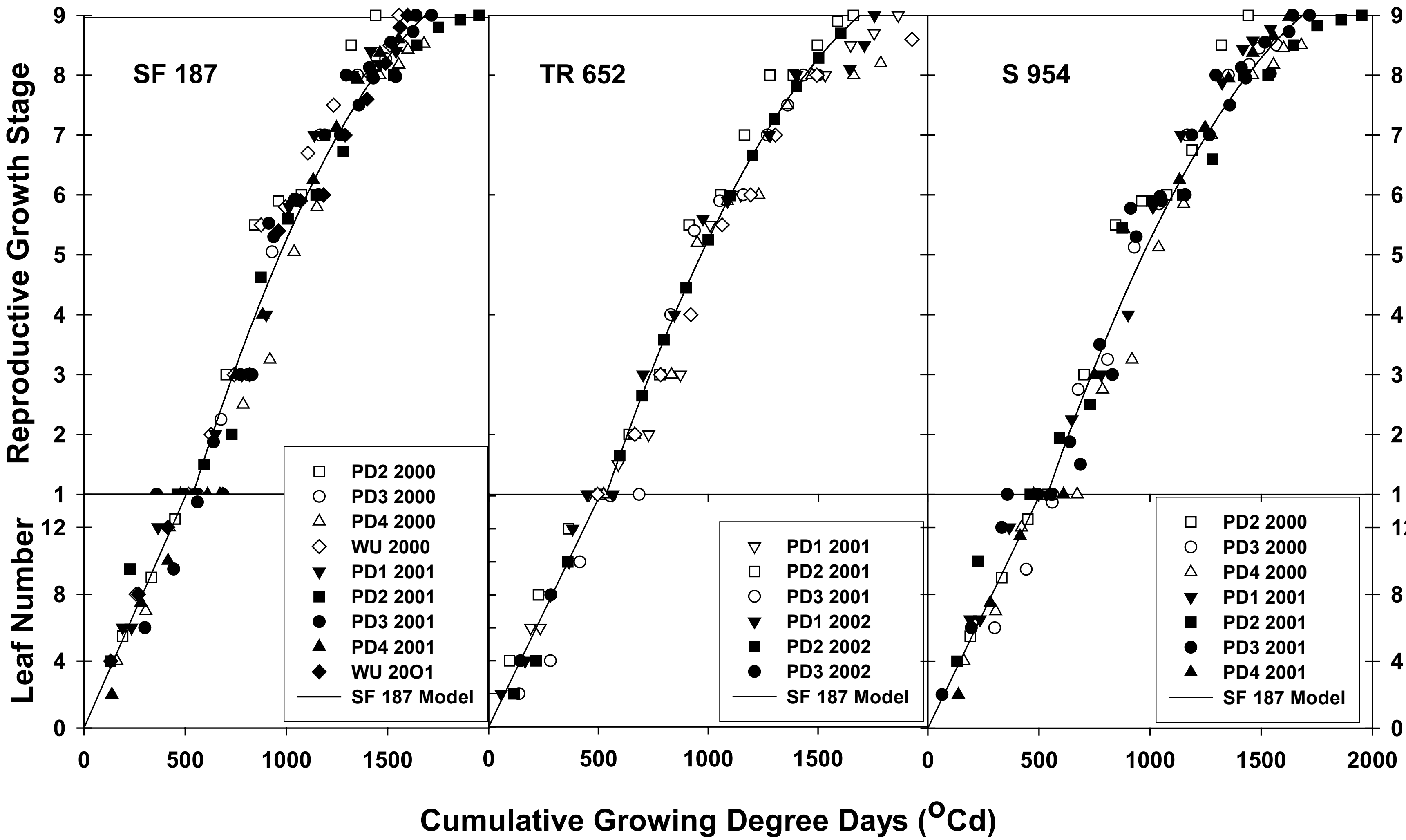
1800
1600
1400
1200
1000
800
600
400
200
0
0
100
200
300
Precipitation/Evaporation (mm)
Day of Year
E Normal
E 2000
E 2001
E 2002
P Normal
P 2000
P 2001
P 2002

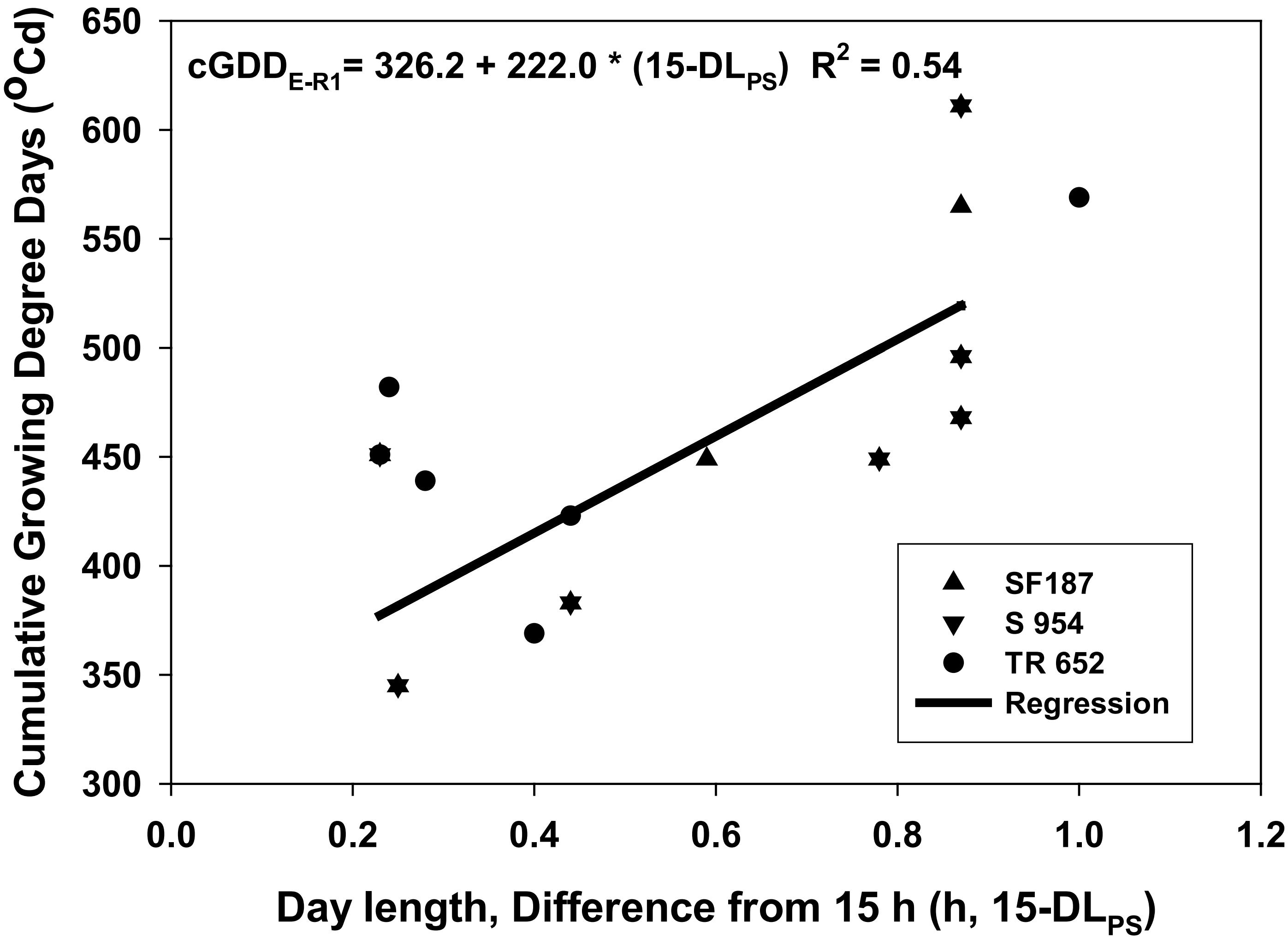
1


Cumulative Growing Degree Days (°Cd)
2500
2000
1500
1000
500
0
100
150
200
250
300
Day of Year
Simple Average
Weighted Average

1

1


SF 187
TR 652
S 954
Reproductive Growth Stage
Leaf Number
Cumulative Growing Degree Days (°Cd)
PD2 2000
PD3 2000
PD4 2000
WU 2000
PD1 2001
PD2 2001
PD3 2001
PD4 2001
WU 20O1
SF 187 Model
PD1 2001
PD2 2001
PD3 2001
PD1 2002
PD2 2002
PD3 2002
SF 187 Model
PD2 2000
PD3 2000
PD4 2000
PD1 2001
PD2 2001
PD3 2001
PD4 2001
SF 187 Model



cGDD$_{E\text{-}R1}$= 326.2 + 222.0 * (15-DL$_{PS}$) R^2 = 0.54
Cumulative Growing Degree Days (^{o}Cd)
650
600
550
500
450
400
350
300
0.0
0.2
0.4
0.6
0.8
1.0
1.2
Day length, Difference from 15 h (h, 15-DL$_{PS}$)
SF187
S 954
TR 652
Regression

1