Heat Unit Model for Predicting Bloom Dates in *Rubus*

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Abstract. ‘Navaho’ and ‘Apache’ blackberry plants were maintained at 10, 15, 20, 25, 30, or 35 °C in growth chambers to determine optimum temperature for budbreak and flowering (fewest days to flowering). In a separate experiment, bloom dates were observed for a collection of 117 *Rubus* genotypes over four seasons. Using these phenological data, predictive linear and curvilinear models were tested using a range of cardinal temperatures. The growth chamber experiment indicated optimum temperatures for bloom were 25.6 °C for ‘Apache’ and 29.2 °C for ‘Navaho’. For the field observations, time to bloom was best defined by a linear model with base and optimum temperatures of 6 and 25 °C and a curvilinear model defined by base and optimum temperatures of 4 and 27 °C, respectively. Based on the linear growing degree hour (GDH) model, heat units to bloom varied among cultivars in the collection from 9,200 GDH for ‘Chickasaw’ to 18,900 GDH for ‘Merton Thornless’.

Some caneberry (*Rubus* L.) production regions experience dramatic seasonal variation in bloom date and fruit ripening time. Phenology and biology of flowering in both cultivated and wild raspberries (*Rubus idaeus* L.) and blackberries have been studied under diverse environmental conditions in Scotland (Robertson, 1957) and throughout the United States, including in Maryland (Waldo, 1933), Missouri (Warmund and George, 1990; Warmund and Krumme, 2005), Oregon (Takeda et al., 2002; Waldo, 1933), and

West Virginia (Takeda et al., 2002; Takeda and Wisniewski, 1989). Hoover et al. (1989) reported that when primocane-fruiting raspberry cultivars were grown at a range of sites across North America, temperature emerged as the critical factor for cane growth because it was correlated with heat unit accumulation (base 5 °C) throughout the season. Under temperate-zone growing conditions, floricanes-fruiting blackberries have a clearly defined seasonal pattern of dormancy, entering the endodormant phase as a result of a shortened photoperiod and low and moderate temperatures in fall, and exiting after sufficient winter chilling (Moore and Caldwell, 1985). In floricanes-fruiting blackberries, budbreak occurs from late March to early April in temperate regions of North America. Fruiting lateral shoots emerge from the axillary buds along the length of floricanes and their lateral branches. Over the next 4 to 5 weeks, the inflorescence develops distally on fruiting lateral shoots, and flower buds on the inflorescence open from mid-May to mid-June. Jennings (1979) compared bloom dates and fruit ripening times in eight blackberry cultivars of diverse genetic origin over three seasons and concluded that accumulated heat units (the accumulated temperatures above 6 °C) successfully quantified fruit ripening time (time from flowering to ripe fruit) but

were not useful in predicting bloom date. However, no details were provided as to how these accumulated heat units were calculated. In eastern West Virginia, flowering in semi-erect ‘Black Satin’, ‘Dirksen Thornless’, and ‘Hull Thornless’ blackberries occurred over a 5-week period and fruits with bloom dates of 7, 14, and 21 June needed 50, 55, and 61 d to reach maturity (Takeda, 1987). It appeared that bloom date affected the onset of fruit development as well as maturation rate, but that study did not use temperature recordings to account for seasonal variations in the onset of bloom in the spring and the fruit-ripening period in summer.

Models that reliably predict bloom and fruit ripening are useful in understanding the environmental constraints on crop development, which in turn is useful in matching genotypes to their environment for optimum cropping. An understanding of how environmental conditions affect plant development has also been used in an attempt to predict the potential impacts of global climate change (Hanninen, 1995). Furthermore, increased interest in producing blackberries in protected cultivation (Strik et al., 2007) requires a better understanding of the relationship between temperature and crop development. This is particularly important in managing greenhouses and high tunnels designed to advance fruiting (Heidenreich et al., 2008).

For processes that are primarily temperature-driven, a measure of heat unit accumulation accounts for seasonal differences in development time. The basic concept in heat unit accumulation is that growth occurs when temperatures are above some minimum (base temperature) and that growth rate increases with temperature. Further refinements provide for optimum and critical temperatures (Richardson et al., 1975). The optimum temperature is the point at which there is no longer a continued increase in growth rate (plateau), whereas the critical temperature is the maximum temperature at which growth will continue. Historically, temperature data were often limited to daily maximum and minimum, in which growing degree day accumulation was based on averaging the daily maximum and minimum subtracting the base temperature and summing this value for each day (Arnold, 1960). A refinement on this method is according to Baskerville and Emin (1969) in which a sine curve is fitted to daily maximum and minimum temperatures to approximate diurnal fluctuations and thereby estimates the amount of time each day when temperatures exceed the base temperature for growth. With improvements in automated weather monitoring, it is now practical to calculate heat unit accumulation on an hourly basis and sum growing degree hours (GDH), eliminating the need to mathematically approximate diurnal fluctuations.

A linear model for accumulated heat units (Anderson and Seeley, 1992) can be defined by a basal, optimum, and critical temperature (Fig. 1). A further refinement of this model is the use of an asymmetric curvilinear relationship (ASYMCUR) between temperature and

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Fig. 1. Relative heat unit accumulation for the linear, ASYMCUR, and modified ASYMCUR models. ASYMCUR is according to Anderson et al. (1986). ASYMCUR modifications are by Roundy and Frisby (unpublished data). ASYMCUR = asymmetric curvilinear relationship.

growth (Anderson et al., 1986). The purpose of this work was to determine heat requirements for bloom in *Rubus*, primarily blackberry, under both controlled environment and field conditions.

Materials and Methods

Growth chamber study. Primocanes of 5- and 6-year-old 'Navaho' and 'Apache' blackberry plants were dug from the field at the USDA-ARS Appalachian Fruit Research Station in Kearneysville, WV, in early November of 2003 and 2004 and potted into 11-L nursery pots containing Fafard Mix No. 4 (Conrad Fafard, Inc., Agawam, MA). These plants were combined with tissue culture plants of 'Navaho' that had been established in 11-L pots in 2003. Plants were assigned to one of five blocks according to origin, transplant date, and size and moved to cold storage (6 °C) on 3 Dec. 2004. On 28 Dec. 2004, five plants from each block were removed from cold storage and pruned to a single floricanes that was cut back to 0.9 m height when necessary. Pruned plants were then placed in one of five randomly assigned growth chambers (Conviro E15, Winnipeg, Canada) programmed at 10, 15, 20, 25, 30, or 35 °C constant temperature and a 16-h photoperiod. Plants were observed at least twice weekly for 65 d to determine dates of bud-break and of first open flower. On 3 Mar., these plants were removed from the chambers and the experiment repeated with a second set of plants that had been maintained in cold storage at 5 °C. Air temperature near the base of the plant canopy and soil temperatures at 8- to 10-cm depth were recorded within the growth chamber environments using thermocouples attached to a data logger (CR-7; Campbell Scientific, Logan, UT). Data were analyzed in the PROC GLM procedure of SAS (SAS Institute, Cary, NC) using orthogonal contrast coefficients for

uniformly spaced treatments to determine the relationship between temperature and time to flowering.

Field study. A collection of 125 blackberry, red raspberry-blackberry hybrid, and black raspberry (*R. occidentalis* L.) genotypes, primarily of eastern North America origin, was established in 2000 at the Henry A. Wallace Beltsville Agricultural Research Center, Beltsville, MD. The majority of the numbered selections were from the USDA-ARS breeding program at Beltsville, MD. A lesser number were from the breeding programs at the University of Arkansas, North Carolina State University, and the University of Maryland. Two replicate plots were established for 53 of the genotypes with four plants per replicate. For the remaining genotypes, there was insufficient plant numbers to establish replicate plots, and a single plot was established with one to four plants per plot. Canes were trained to a vertical trellis, and a 1-m weed-free strip was maintained under the plants with the use of a woven plastic weed barrier. Supplemental irrigation was supplied through a drip line placed within each row. The soil at the site was a Croom-Downer complex consisting of a deep, well-drained gravelly sandy loam with 3% to 8% slope.

Observations of the date when the first flower opened and the first fruit was fully colored were made twice weekly during the 2002 to 2005 seasons. Weather data, including hourly temperature and photosynthetic photon flux, were collected using an automated weather station located within 160 m of all points of the planting. The program WinTree (Rojas-Martinez et al., 1999) was used to calculate GDH based on linear and curvilinear heat unit models using a range of cardinal temperatures. The curvilinear models included ASYMCUR (Anderson et al., 1986) and a modified ASYMCUR (Roundy and Frisby, unpublished data). The difference

between the two ASYMCUR models is in how temperatures between optimum and maximum are treated. A comparison of these models is shown in Figure 1. Each model was optimized for cardinal temperatures and compared by multiple regression analysis to maximize the coefficient of regression.

Results and Discussion

Growth chamber study. All of the plants held at 10 °C flowered within 76 d, indicating a base temperature below 10 °C. All of the 'Apache' plants and approximately half of the 'Navaho' plants held at 35 °C either died or failed to flower after 76 d. For the second run of the experiment, the plants flowered $\approx$ 5 d later than for the first run, but the trend across temperatures was identical and data for the two runs were averaged. The optimum temperature to achieve the shortest time to flowering was between 25 and 30 °C for both cultivars. Fitted curves predicted that the temperature optimum was 25.6 °C for 'Apache' and 29.2 °C for 'Navaho' (Fig. 2).

Field study. Date of first bloom varied from season to season. Averaged over all genotypes, first bloom ranged from 1 May in 2002 to 17 May in 2005 with average first bloom in 2003 and 2004 occurring on 16 May and 10 May, respectively. Some plant loss occurred over the course of the experiment and diseased or dying plants were excluded from the calculations with 117 of the original 125 genotypes included in the final calculations.

A range of base and optimum temperatures were compared in each model by selecting those that provided the maximum regression coefficient. For the field study, there were relatively few days before bloom in which temperatures were above 30 °C, making it difficult to define a critical temperature for either the linear or curvilinear model. The growth chamber study indicated critical temperatures for blackberry near 35 °C. However, it should be noted that the potted plants in the growth chamber study also experienced elevated soil temperatures that likely would not be achieved under field conditions. Although it was previously shown that soil temperature had no effect on time to anthesis (Hammond and Seeley, 1978), the soil temperatures experienced by a potted plant held in a growth chamber at a constant 35 °C would be dramatically higher than in the field. For calculating the models, 37 °C was used as a critical temperature in all models.

The best fit models were a linear model defined by base and optimum temperatures of 6 and 25 °C and a modified ASYMCUR model defined by base and optimum temperatures of 4 and 27 °C, respectively ($R^2 > 0.85$, Table 1). By contrast, calendar date showed an $R^2 = 0.602$. Multiple regression analysis indicated that the linear and curvilinear models adequately accounted for seasonal variations in bloom date when cardinal temperatures were optimized for each model. The best fit linear and curvilinear models produced different optimum and critical temperatures that can be explained by the

Fig. 2. Time to flowering of 'Navaho' and 'Apache' blackberry at five temperatures. Values are the means $\pm$ SE of five replicate plants and two repeat experiments.

Table 1. Optimized cardinal temperatures for linear, ASYMCUR, and modified ASYMCUR models for predicting date of anthesis in a collection of *Rubus* selections and cultivars.

Model type	Temperature (°C)		R^2
	Base	Optimized	
Linear	6	25	0.8515
ASYMCUR	4	28	0.8508
Modified ASYMCUR	4	27	0.8514

ASYMCUR = asymmetric curvilinear relationship.

inherent differences in these models. Base temperature was higher in the linear model than in the two curvilinear models, which can be explained by the characteristic lag in a sigmoid curve (Fig. 1). Likewise, the optimum temperature differed among the models in relation to how each model treated temperatures between optimum and critical.

Heat requirements to bloom can also be influenced by the amount of dormant chilling that a plant receives. Inadequate chilling may delay response to warm temperatures and result in asynchronous budbreak (Seeley, 1996). Chilling in excess of plant requirements has been shown to reduce the amount of heat necessary for budbreak in several tree fruit species (Couvillon and Erez, 1985). Optimum chilling for 'Navaho' is reported to be between 800 and 900 h at 3 °C (Drake and Clark, 2000). Warmund and Krumme (2005) reported that 'Apache' had a relatively longer chilling requirement than 'Navaho' and several other Arkansas cultivars (although the exact number of chill hours was not given and a different model was used). Some Arkansas blackberry cultivars typically have chilling requirements less than 700 h and may be as little as 200 h

Fig. 3. Heat units ($GDH_{6,25,36}$) to flowering in 117 *Rubus* genotypes. Vertical lines represent SD as an indicator of seasonal variation. Genotypes are plotted by ranked GDH to flowering. The ranks corresponding to each genotype are shown in Tables 2 through 6. Heat units are calculated using a linear model with 6, 25, and 36 °C as base, optimum, and maximum temperatures, respectively. GDH = growing degree hours.

Table 2. Mean heat units to first flowering for *Rubus* cultivars and selections from the USDA-ARS breeding programs at Beltsville, MD, and Carbondale, IL.

Cultivar/selection	$GDH_{(6,25,36)}$		Replication ^x
	Mean ^z	Rank ^y	
Black Satin	11,100	60	Yes
Chester Thornless	14,430	99	Yes
Hull Thornless	9,980	31	Yes
Smoothstem	18,090	115	Yes
Thornfree	16,280	111	Yes
Triple Crown	14,050	95	Yes
B2-4	10,360	42	No (1)
B5-4	10,390	44	No (3)
US1637	8,780	1	No (4)
US1670	9,750	22	No (1)
US1688	15,080	106	No (1)
US1705	12,690	82	No (3)
US1713	10,470	46	No (3)
US1721	11,930	75	No (4)
US1729	15,370	107	No (2)
US1730	12,530	80	No (4)
US1732	11,080	59	No (2)
US1733	12,390	78	No (1)
US1736	10,270	40	No (1)
US1749	11,440	69	No (2)
US1754	14,950	105	No (3)
US1762	13,490	90	No (3)
US1765	21,710	117	No (4)
US1766	11,700	72	No (1)
US1767	10,610	48	No (4)
US1769	12,730	83	No (1)
US1773	10,780	53	No (1)
US1774	12,000	77	No (1)
US1777	13,510	91	No (2)
US1779	10,740	51	No (1)
US1780	9,830	27	No (1)
US1794	11,800	73	No (3)
US1797	9,400	12	Yes
US1798	10,750	52	No (1)
US1799	10,140	37	No (1)
US1811	13,710	92	No (1)
US1818	9,760	23	No (1)
US1821	10,200	38	Yes
US1824	16,060	110	No (1)
US1839	13,340	89	No (1)
US1842	12,760	84	No (2)
US1844	15,900	108	No (1)
US1846	14,040	94	No (1)
US1849	9,280	10	No (1)
US1861	12,460	79	No (2)
US1865	14,590	101	No (1)
US1866	14,440	100	No (3)
US1872	14,290	98	No (1)
US1873	14,860	104	No (1)
US1874	13,940	93	No (1)
US1875	14,080	96	No (1)
US1876	10,070	35	No (2)
US1877	14,720	102	No (1)
US1878	18,030	114	No (1)
US1880	11,070	58	No (1)
US1882	14,240	97	No (3)
US1888	13,080	86	No (2)
US1962	13,270	88	No (1)
Black raspberries			
US1775	10,460	45	No (1)
US1782	11,390	68	No (1)
US1789	9,290	11	No (1)
US1795	13,040	85	No (1)
US1803	18,020	113	No (1)
US1804	9,450	13	No (2)
US1805	16,350	112	No (1)

^zHeat units calculated as growing degree hours (GDH) using a linear model with 6, 25, and 36 °C as base, optimum, and maximum temperatures, respectively.

^yRelative earliness ranked for each genotype, in which the lowest numbers represent the fewest heat units to bloom.

^xThere were not sufficient numbers to establish replicated plots for some selections, and a single plot was established for each. The number of plants in nonreplicated plots is shown in parentheses.

(Drake and Clark, 2000; Yazzetti and Clark, 2001). Two replicate runs of the growth chamber experiment were carried out over the course of one winter. Plants used for the first run received 600 h of chilling in cold storage in addition to any chilling received in the field before transplanting. Plants used in the second run received 1400 h more chilling than those in the first run. Chilling temper-

Table 3. Heat units to first flowering for *Rubus* cultivars and selections from the breeding program at the University of Arkansas.

Cultivar/ selection	GDH _(6,25,36)		Replication ^x
	Mean ^z	Rank ^y	
Apache	10,040	33	Yes
Arapaho	10,500	47	Yes
Cherokee	10,260	39	Yes
Cheyenne	9,670	18	Yes
Chickasaw	9,200	7	Yes
Navaho	10,800	54	Yes
Ouachita	11,140	62	Yes
Shawnee	9,620	17	Yes
A 1631	9,500	14	Yes
A 1689T	11,170	63	Yes
A 1713	9,700	21	Yes
A 1811	9,520	15	Yes
A 1817T	9,760	24	Yes
A 1818T	9,680	19	Yes
A 1844	9,950	30	Yes
A 1854	9,070	5	Yes
A 1857T	9,830	26	Yes
A 1942T	10,930	55	Yes
A 1959T	11,230	65	No (3)
A 1963T	13,220	87	Yes
A 2005T	9,220	8	Yes
A 2049T	9,270	9	Yes

^zHeat units calculated as growing degree hours (GDH) using a linear model with 6, 25, and 36 °C as base, optimum, and maximum temperatures, respectively.

^yRelative earliness ranked for each genotype, in which the lowest numbers represent the fewest heat units to bloom.

^xWhere only one plot of a genotype existed, the number of plants in the plot is shown in parentheses.

Table 4. Heat units to first flowering for *Rubus* selections from the breeding program at the North Carolina State University.

Cultivar/ selection	GDH _(6,25,36)		Replication ^x
	Mean ^z	Rank ^y	
NC 95-2-1	11,630	70	No (4)
NC 378	11,240	66	No (4)
NC 383	8,920	2	Yes
NC 385	12,000	76	Yes
NC 387	11,000	57	Yes
NC 388	10,120	36	No (4)
NC 392	11,370	67	Yes
NC 395	10,930	56	Yes
NC 408	9,010	4	No (2)
NC 415	8,950	3	No (3)
NC 430	10,380	43	Yes

^zHeat units calculated as growing degree hours (GDH) using a linear model with 6, 25, and 36 °C as base, optimum, and maximum temperatures, respectively.

^yRelative earliness ranked for each genotype, in which the lowest numbers represent the fewest heat units to bloom.

^xWhere only one plot of a genotype existed, the number of plants in the plot is shown in parentheses.

Table 5. Heat units to first flowering and fruit ripening time for *Rubus* cultivars and selections from the breeding program at the University of Maryland.

Cultivar/ selection	GDH _(6,25,36)		Replication ^x
	Mean ^z	Rank ^y	
Chesapeake	10,720	50	Yes
Raven	9,560	16	Yes
OAL-W3	11,680	71	Yes
OAL-W6	11,830	74	No (4)
QCU-1	9,870	28	Yes
QDB-1	10,020	32	Yes
QDB-2	11,190	64	No (3)
QDB-b1	10,300	41	Yes
QDE-1	9,880	29	Yes
QDE-2	9,160	6	Yes
QDE-3	11,100	61	Yes
QEZ-1	14,790	103	Yes

^zHeat units calculated as growing degree hours (GDH) using a linear model with 6, 25, and 36 °C as base, optimum, and maximum temperatures, respectively.

^yRelative earliness ranked for each genotype, in which the lowest numbers represent the fewest heat units to bloom.

^xWhere only one plot of a genotype existed, the number of plants in the plot is shown in parentheses.

atures in excess of plant requirements did not significantly reduce heat unit requirements, but rather heat unit requirements were slightly greater in the second run.

The best heat unit model for the genotypes included in this study did not account for all variation in bloom. Aside from temperature and chilling, other factors that may influence budbreak and anthesis include plant age and vigor, bud position on the cane (Takeda, 1987; Takeda et al., 2002), cold injury, and genetics. Considering genetic variation, it would likely be possible to determine specific cardinal temperatures for each genotype. However, a more applicable model would be one that reasonably predicts bloom across a number of genotypes.

Genotypic differences. The heat units required to promote flowering varied dramatically by genotype with more than a twofold difference in GDH to bloom among genotypes, indicating significant genetic variation (Fig. 3). Among cultivars in the collection, GDH to bloom varied from 9,200 GDH for ‘Chickasaw’ to 18,900 GDH for ‘Merton

Thornless’ based on a linear model with cardinal temperatures of 6, 25, and 36 °C. In general, the semierect types from the USDA programs tended to be among the latest flowering (Table 2). Although pedigrees are not available for all of these, it is interesting to note that ‘Merton Thornless’ was the source of thornlessness used in the USDA program and ‘Merton Thornless’ was among the latest to flower. Conversely, the genotypes from Arkansas (Table 3) tended to be among the earliest to flower, ranking in the lower half of the genotypes included. Selections from North Carolina tended to be intermediate in heat units to flower (Table 4). NC 408 and NC 415 were ranked 3 and 4 lowest for GDH. Although both are from the North Carolina State University breeding program, they have quite different backgrounds. NC 408 has NC 194, the source of primocane fruiting in tetraploid blackberries, as a grandparent, whereas NC 415 has ‘Floradagrand’, a cultivar largely derived from *R. trivialis* Michx. from Florida and Texas (Clark et al., 2007). Although NC 383 was ranked second lowest for GDH, its siblings NC 387 and NC 378 were in the middle of all genotypes for GDH to bloom. The University of Maryland material varied widely in GDH to bloom, but this was not surprising because this material has a mixture of western trailing cultivars, eastern erect cultivars, and selections of *R. caesius* L., *R. cuneifolius* Pursh, *R. idaeus* L., *R. lasiostylus* Focke, and *R. sachalinensis* H. Lev. in their pedigrees (Table 5). ‘Aurora’ was the only western trailing blackberry included in the study, and not surprisingly, based on work by Takeda et al. (2002), it was in the lowest 20% for GDH to bloom (Table 6). Several black raspberries were included in this study and although they all were originally from North Carolina sources, they ranged from having among the lowest to among the highest GDH (Table 2). It is interesting to note that ‘Apache’ and ‘Navaho’ bloomed at 10,000 to 10,800 GDH (Table 3) in the field and at ≈10,100 GDH in the 20 and 25 °C growth chambers, indicating similar heat requirements under very different growing conditions.

We also tested heat unit models for predicting fruit development rate, but none of the models showed good correlation with actual developmental rates. With total light

Table 6. Heat units to first flowering and fruit ripening time for blackberry cultivars from various sources.

Cultivar/selection	GDH _(6,25,36)		Replication ^x	Source
	Mean ^z	Rank ^y		
Aurora	9,690	20	Yes	USDA–Oregon
Bailey	10,720	49	Yes	New York
Ebano	12,550	81	Yes	Brazil
Illini Hardy	10,050	34	Yes	U. Illinois
Lucretia	9,800	25	No (3)	West Virginia
Merton Thornless	18,940	116	Yes	UK John Innes Inst.
Perron’s Black	16,010	109	Yes	Quebec

^zHeat units calculated as growing degree hours (GDH) using a linear model with 6, 25, and 36 °C as base, optimum, and maximum temperatures, respectively.

^yRelative earliness ranked for each genotype, in which the lowest numbers represent the fewest heat units to bloom.

^xWhere only one plot of a genotype existed, the number of plants in the plot is shown in parentheses.

integral added to the model, the predictive value was increased. However, for the seasons observed, these models were not significantly better than simply counting calendar days (data not shown). This suggests that influences of environmental conditions on fruit development are clearly more complex than a simple temperature relationship. A more refined model that integrates temperature, light, and photosynthesis limitations may need to be developed to account for seasonal differences in fruit ripening time. Our findings directly contradict those of Jennings (1979) who reported that their undefined heat units predicted fruit development (time from flowering to ripe fruit) but did not work well for predicting bloom date. This contradiction may be the result of the increased number of genotypes in the present study and improved methods for determining heat accumulation, including the use of optimal and critical temperatures and summing heat units on an hourly basis.

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