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Method for the Evaluation of Thermal Requirements for Development Based on Phenological Observations

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Abstract—A new method for the evaluation of threshold temperature of development involving phenological observations and based on hyperbolic imaging of dependence between the day of development and temperature values close to the threshold was proposed. The rare species *Clematis integrifolia* was used as an example to evaluate thermal requirements for six stages of its development. The method proposed in this study was also compared with some common methods for the estimation of threshold temperature basing on phenological data.

Keywords: phenological dates, thermal requirements, threshold temperature, base temperature, sum of effective temperatures, degree-days, development rate, plants, ecology

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Temperature is one of the most important factors that determine the development of poikilothermic organisms, since it activates various physiological processes and regulates their rate. The interaction of temperature and developmental processes was noted long ago [1]. It was found that there are some temperature values below which no development is possible. This value is called threshold temperature [2, 3], zero temperature point [4], base temperature, or biological zero. Environmental temperature that lies above this threshold value is called effective temperature. It was found that a poikilothermic organism needs a certain amount of heat for its development. This amount can be calculated using the following equation: [2, 5]:

$$\sum T_{\text{eff}} = (T_a - C)D = T_{\text{eff}} D,$$

where $\sum T_{\text{eff}}$ is thermal constant or the sum of effective temperatures that the organisms needs for certain stage of development, C is threshold temperature, and D is the number of days of development at environmental temperature T_a or effective temperature T_{eff} (i.e., the number of days during which T_a exceeds C). The threshold temperature and date when the developmental process begins can be determined in controlled conditions, e.g., in a climatic chamber. Based on these, temperature and date, T_{eff}, D and, consequently, $\sum T_{\text{eff}}$ can be calculated. For this purpose, an organism needs to be adapted to some constant T_{eff}.

In natural conditions, T_{eff} is never constant. The determination of threshold temperature is also a problem, since the date when the developmental process starts is unknown. At the same time, a great amount of data of phenological observations, e.g., collected in nature reserves, requires a tool for the estimation of thermal requirements needed for the development of organisms.

In the articles of Russian authors, the sum of effective temperatures is often replaced by simply the sum of temperatures $\sum T$ (e.g., [6–8]). This value is not constant; threshold temperatures are usually considered to be 0, 5, or 10°C, which is not physiologically correct.

As an alternative tool in the studies of European authors and some enthomological Russian studies, linear regression models of dependence between the developmental rate and temperature have been used [9–19]. However, they are most often used for organisms kept under controlled conditions. When using the data of phenological observations in such models, the determination of threshold temperature is still a problem. A number of approaches have been proposed to solve this problem [13, 14, 18, 20–22, etc.]; some approaches provide the detection of precise date of development [23]. However, these methods have some drawbacks. Some of such drawbacks are described in [19]. We suppose that the measurement of starting time point of development in a changing environment is impossible, since the developmental processes can vary widely. Thus, only the statistical date can be determined.

We propose a new method for the determination of threshold temperature and evaluation of other thermal requirements in poikilothermic organisms; this method is based on data obtained in natural conditions. We used *Clematis integrifolia* L., which is a rare species in the studied region [24] and inhabits the Galich'ya Gora Nature Reserve (Lipetsk oblast, Russia). The purposes of this study are to estimate the thermal requirements of development in *Clematis integrifolia* based on the data of phenological observations and using our new method and to compare its effectiveness with that of other common methods.

MATERIALS AND METHODS

The Galich'ya Gora Nature Reserve is situated in the center of Lipetsk oblast in an agricultural landscape. The reserve consists of slopes, upland areas, and floodplains and has a cluster structure with six small sections with a total area of 231 ha. Plant communities include mountain oak forests, smaller pine forests, and herbal and subshrub steppificated and meadow communities.

The subject of our study was *Clematis integrifolia* L. (family Ranunculaceae). Its range includes the Caucasus, southern regions of Western and Eastern Siberia, Central and Eastern Europe, the Mediterranean region (the Balkans), Central Asia, and Asia Minor [25]. In Russia, this species can be found in the southern regions of its European part, in Siberia, and in the Pre-Caucasian region. In the midlands, it sometimes can be found in all areas of the Central Black Earth Region. In the Galich'ya Gora Nature Reserve, *Clematis integrifolia* inhabits motley grass-grasses and subshrub communities on calciferous slopes and plateaus near valleys as well as oak forest edges.

Phenological observations of *Clematis integrifolia* were performed by conventional methods [26–28]: the starting point of vegetation was the date when the shoots began growing from buds formed during the previous season at the base of reproductive shoots; the starting point of flower-bud formation was the date when flower buds were hardly seen and green; the starting point of the flowering period was the date when the first flowers were open; massive flowering started when flowers were found on at least half of the plants; the starting point of fruit ripening was the date when green fruits turned brownish (light-brown color); massive ripening started when the fruits turned brown (the color of ripe fruits). We used the data of phenological observations in the Galich'ya Gora Nature Reserve performed from 1990 until 2014 (Table 1) as well as the values of mean daily air temperature obtained on the weather station of reserve during this period.

A number of common methods for the determination of threshold temperature are based on the assumption that the variation of developmental rate is minimal for "true constant." For example, the least standard deviation in growing degree-days (i.e., of the sum of temperatures) method [20, 22] is based on the assumption that real temperature among the values is the one with the minimal value of SD_{gdd}. In this case, SD_{gdd} is the standard deviation of the sum of temperatures $\sum T = TD$, where $T = T_m - C$, T_m is mean air temperature of the studied period D, C is the studied constant.

The least standard deviation in days method [13] derived from the previous method:

$$SD_D = \frac{SD_{gdd}}{T_m - C}. \quad (1)$$

An alternative variant is the coefficient of variation in days method [21]:

$$CV_D = \frac{SD_D}{D} 100\%. \quad (2)$$

Other approaches are focused on the regression of developmental parameters and studied temperature values. For example, another common method, the regression coefficient method [18], is focused on the dependence between developmental rate (expressed as the sum of temperatures) and the temperature of development:

$$\sum T = a + bT_m, \quad (3)$$

hereinafter a and b are universal symbols of coefficients for regression equations.

A temperature value is considered as a threshold when $b \approx 0$.

Our approach also requires the calculation of the regression function. Its important feature is the analysis of dependence of $\sum T$ on D. At the same time, we assume that there is an artifact of positive linear correlation between arbitrary sum of temperatures and corresponding number of days of development:

$$\sum T = a + bD. \quad (4)$$

This linear dependence does not cover the area of "real" threshold temperature due to a hyperbolic pattern of interrelation, which corresponds with the Blunk equation [2] and linear dependence of $\sum T$ and T. Moreover, regression coefficient b can have negative values at the same time. In order to determine the threshold temperature, significance graphs are plotted for p of the regression coefficient and the regression coefficient itself. Constant C can be detected by the minimal values of b among the maximal values of p. A temperature range from –5°C to 20°C at a pitch of 1°C was chosen for examination.

Table 1. Phenodates of developmental stages of *Clematis integrifolia* in the Galich'ya Gora Nature Reserve

Year	Stage of development											
	Starting point of vegetation		Starting point of flower-bud formation		Starting point of flowering period		Massive flowering		Starting point of fruit ripening		Massive fruit ripening	
	date	no.*	date	no.	date	no.	date	no.	date	no.	date	no.
1990			7.V	127	25.V	145	10.VI	161	7.VIII	219	15.VIII	227
1991	17.IV	107	20.V	140	28.V	148	5.VI	156	20.VI	171		
1992	1.V	122	17.V	138	9.VI	161	13.VI	165	10.VIII	223	18.VIII	231
1993	11.IV	101	11.V	131	29.V	149	7.VI	158	5.VIII	217	17.VIII	229
1994	20.IV	110	17.V	137	6.VI	157	15.VI	166	15.VIII	227	28.VIII	240
1995	13.IV	103	8.V	128	23.V	143	1.VI	152	24.VII	205	17.VIII	229
1996	2.V	123	12.V	133	27.V	148	6.VI	158	22.VII	204	12.VIII	225
1997	2.V	122	12.V	132	6.VI	157	15.VI	166	6.VIII	218	30.VIII	242
1998	17.IV	107	15.V	135	31.V	151	12.VI	163	28.VII	209	21.VIII	233
1999	6.IV	96	5.V	125	2.VI	153	7.VI	158	29.VII	210	8.VIII	220
2000												
2001	15.IV	105	10.V	130	29.V	149	10.VI	161	15.VII	196	5.VIII	217
2002	5.IV	95	5.V	125	17.V	137	30.V	150	20.VI	171	5.VII	186
2003	5.V	125	24.V	144	27.V	147	5.VI	156	1.VII	182	10.VII	191
2004	13.IV	104	15.V	136	26.V	147	5.VI	157	25.VI	177	18.VII	200
2005	18.IV	108	20.V	140	26.V	146	28.V	148	20.VI	171	17.VIII	219
2006	26.IV	116	20.V	140	27.V	147	5.VI	156	27.VI	178	23.VIII	235
2007	22.IV	112	15.V	135	26.V	146	1.VI	152	1.VII	182	10.VIII	222
2008	3.IV	94	7.V	125	18.V	139	24.V	145	20.VI	172	15.VIII	228
2009	1.V	121	18.V	138	26.V	146	1.VI	152	11.VII	195	1.VIII	213
2010	15.IV	105	9.V	129	18.V	138	29.V	149	14.VI	165	31.VII	212
2011	26.IV	116	16.V	136	21.V	141	24.V	144	15.VI	166	30.VI	181
2012	18.IV	109	13.V	134	16.V	137	21.V	142	20.VI	172	19.VII	201
2013	28.IV	118	11.V	131	17.V	137	23.V	143	13.VI	164	20.VIII	232
2014	18.IV	108	9.V	129	18.V	138	23.V	143	12.VI	163	1.VIII	213

* no. is the number of days from the beginning of the year.

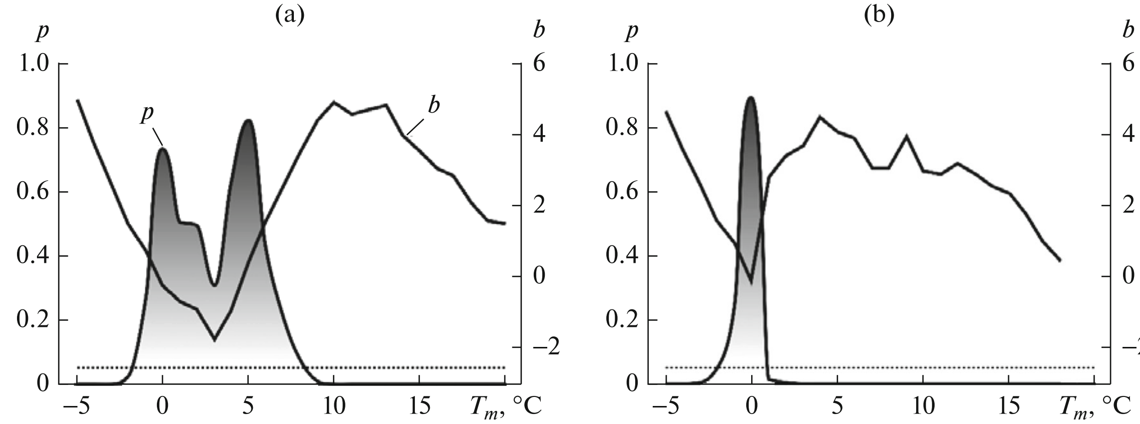

Fig. 1. Plots of functions of regression coefficient *b* and its significance level *p* in the temperature range from −5°C to 20°C for the (a) stages of flower-bud formation and (b) vegetation of *C. integrifolia*. Dashed line designates a 5% significance threshold for regression coefficient.

When C was determined, temperature T used for evaluation was taken as T_{eff}. The sum of effective temperatures was calculated by the approximation of dependence between D and T_{eff} according to the hyperbolic Blunk equation [2]:

$$D = \frac{\sum T_{\text{eff}}}{T_m - C} = \frac{\sum T_{\text{eff}}}{T_{\text{eff}}}. \quad (5)$$

Then, the developmental rate G can be described by the following equation [11, 15]:

$$G = \frac{1}{D} = bT_{\text{eff}} = a + bT_m, \quad (6)$$

where $b = 1/\sum T_{\text{eff}}$ is the coefficient of thermolability, $a = -bC$. The coefficient of thermolability is equal to the tangent of an angle between the line of regression of developmental rate on temperature and X-axis. This coefficient reflects the dependence of developmental rate on temperature: if T_{eff} is used, the line of regression crosses the origin of coordinates; if T_m is used, the line crosses the X-axis in the point of C. This is another way to determine the thermal constant (e.g. [10, 11, 16, etc]). The values of G and T_m obtained during field studies are approximated by linear regression. The threshold temperature can be calculated by the following equation: $C = -a/b$. However, the starting date of development is needed for this equation.

As mentioned above, hyperbolic dependence of the sum of temperatures and the number of days is only characteristic of the area of real temperature threshold:

$$\sum T = a + bT_{\text{eff}} = a + b\frac{\sum T_{\text{eff}}}{D}.$$

All the calculations were performed with the use of MS Office Excel 2003, StatSoft Statistica 6.0 and MathCAD 2001 packages.

RESULTS AND DISCUSSION

We will now describe our method in detail using the first stage of flower-bud formation of *C. integrifolia* as an example. During the last 25 years of observations, this stage occurred between the May 5 and 24 (Table 1). For each of the dates, we calculated $\sum T$ and D for each examined C in the range from −5°C to 20°C at a pitch of 1°C. Then linear regression was calculated for each of examined threshold temperatures (equation 4). We planned to calculate the regression coefficient b and its significance level p, which form two functions when bound to the examined C. Their graphical presentation (Fig. 1a) helped to determine the threshold temperature of 3°C with a prespecified degree of accuracy. A line parallel to the X-axis represents a 5% threshold and separates significant regression coefficients, which reflect the linear pattern of studied dependence, from insignificant ones, which reflect the hyperbolic interrelation between $\sum T$ and D. An increase in the level of significance b in the area of 3°C is caused by its inversion to negative values ($b = -1.74$.) Figure 1b shows the plots of functions for the first stage of vegetation; the plots indicate that the threshold temperature at this stage is 0°C. At the same time, the regression coefficient is close to 0 ($b = -0.11$.)

Now, when the threshold temperature is obtained, $\sum T$ and D, as well as $T = T_{\text{eff}}$, are known for each year of observations. Constant $\sum T_{\text{eff}}$ is estimated by the approximation of dependence of D on T_{eff} using the Blunk hyperbole (equation 5). The estimated value of $\sum T_{\text{eff}}$ for the first stage of flower-bud formation is 304.01°C (Fig. 2). Estimated parameters result in the equation of developmental rate included in Fig. 2:

$$G = 0.0033T_{\text{eff}} = -0.0099 + 0.0033T_m.$$

However, the equations of developmental rate constructed with the use of observed values were found to be underestimating C. For example, when regression was adjusted to the shape of a point cloud of observed values (crosses in Fig. 2), the equation $G(3°C) = 0.0099 + 0.0013T_m(3°C)$ determined $C(3°C) = -7.89°C$. If nonnegative values of T_m are used, the equation $G(0°C) = 0.0032 + 0.0016T_m(0°C)$ determines $C(0°C) = -2.05°C$. Moreover, the estimate of C depends greatly on measured values of G and T_m. Therefore, a precise starting date of development needs to be determined for using the equation of developmental rate.

Thermal requirements for each stage of development of *C. integrifolia* are presented in Table 2. As can be seen, the developmental processes start when mean air temperature exceeds 0°C; the "consumption" of approximately 150°C is needed for the appearance of first signs of vegetation. In the Galich'ya Gora Nature Reserve, it usually takes from 1 to 2.5 months. The formation of flower buds starts when mean air temperature exceeds 3°C. One or two months later, the flower buds can be visually seen; this stage of formation requires approximately 300°C. For the induction of flowering process, mean air temperature needs to exceed 9°C. The first stage of flowering starts 26–50 days later, when the consumed temperature reaches 180°C. The stage of fruit ripening has a threshold temperature of 0°C. This means that this stage does not require temperature-induced initiation. Obviously, more important factors are the general state of a plant and the volume of somatic resources accumulated during the growing season, since reproduction processes lead to the consumption of energy resources [29]. Before fruit ripening can start, a plant needs to consume approximately 1390°C of heat. In the Galich'ya Gora Nature Reserve, the duration of this stage is 4.5 to 6 months.

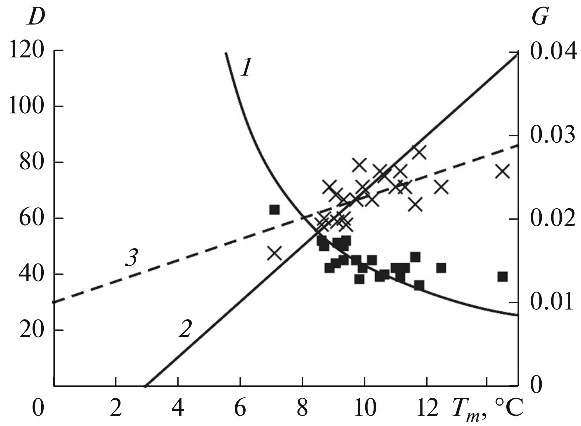

Fig. 2. Hyperbolic approximation of $D = 304.01/(T_m - 3)$ (1) for the stage of flower-bud formation and linear regression of developmental rate obtained by (2) approximation $G = -0.0099 + 0.0033T_m$ and (3) linear regression $G(3°C) = 0.0099 + 0.0013T_m(3°C)$ based of obtained values: D is the number of days of development, G is the rate of development, T_m is mean air temperature, °C. Symbols correspond with different observed values.

The threshold temperature is an important constant that determines the development of various stages in ontogeny and, on the other hand, helps to estimate another constant of developmental processes, namely the sum of effective temperatures. Therefore, the methods for its calculations are still actively studied [30–33, etc].

Figure 3 shows the results of different approaches for the investigation of phenological data on six developmental stages of *C. integrifolia*. In the first approach, the method of SD_{gdd}, the values do not reach their minimum along all the range of examined temperatures (Fig. 3a). The second approach, the method of SD_D (equation 1), provides the estimation

Table 2. Thermal requirements and other parameters of development of *C. integrifolia* calculated based on the data of phenological observations in the Galich'ya Gora Nature Reserve

Stage of development	C, °C	$\sum T_{\text{eff}}$, °C	b	D (min–max)	$\sum T$, °C (min–max)
Starting point of vegetation	0	149.05	0.067	36–88	85.0–279.4
Starting point of flower-bud formation	3	304.01	0.0033	36–63	248.5–448.9
Starting point of flowering period	9	184.93	0.0054	26–50	122.0–289.1
Massive flowering	9	258.54	0.0039	32–62	188.1–379.7
Starting point of fruit ripening	0	1391.45	0.0007	138–189	1056.0–2052.0
Massive fruit ripening	0	1995.44	0.0005	153–204	1345.0–2567.0

C is the threshold temperature, $\sum T_{\text{eff}}$ is the sum of effective temperatures, b is the coefficient of thermolability, D is the number of days of development, $\sum T$ is the sum of temperatures.

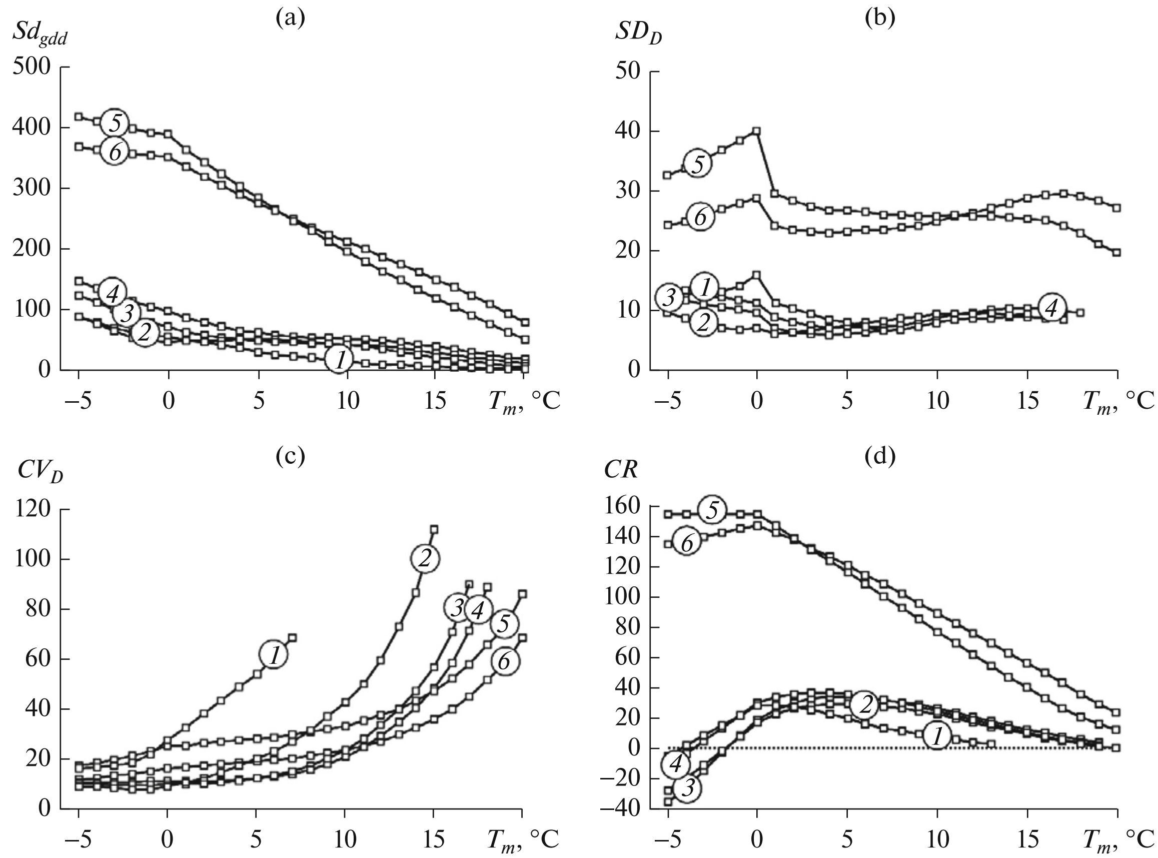

Fig. 3. Calculation of threshold temperature for the developmental stages of *C. integrifolia* by four common methods based on the data of phenological observations in the Galich'ya Gora Nature Reserve: (a) least standard deviation in growing degree-days method SD_{gdd}, (b) least standard deviation in days method SD_D, (c) coefficient of variation in days method CV_D, (d) regression coefficient method CR (dashed line designates zero value); T is examined temperature, °C; *1–6* are stages of development: *1*—starting point of vegetation; *2*—starting point of flower-bud formation; *3*—starting point of flowering period; *4*—massive flowering; *5*—starting point of fruit ripening; *6*—massive fruit ripening.

of threshold temperatures initiating flower-bud formation, flowering, massive flowering and massive fruit ripening (Fig. 3b). The method of CV_D provided poorer results (Fig. 3c). It only helped to estimate the threshold temperatures initiating flower-bud formation and flowering; the values for other stages do not reach their minimum along the whole range of examined temperatures. The fourth approach, the method of CR (equation 3), provides the estimation of threshold temperatures for the first four stages of development; the values were only close to zero for these stages (Fig. 3d).

The quality of estimates of threshold temperatures obtained by our method and other methods should be compared based on the experimental data collected in controlled conditions. Unfortunately, we have not obtained such experimental data. Literature data on *C. integrifolia* are also unavailable. Moreover, we found no such data on wild herbaceous plants in Russia. Therefore, we will compare the effectiveness of methods based on their ability to determine the threshold temperature and adequacy of obtained estimates.

The results of estimation of threshold temperature by different methods are presented in Table 3. It shows that our method and G(0°C) regression are the most effective for the estimation of C : they helped to obtain the value of threshold temperature for all six stages of development of *C. integrifolia*. The methods of SD_D and CR are also highly effective: they helped to obtain the target values for four stages. The methods of CV_D and SD_{gdd} were less effective: the former provided the values of temperature C for two methods, while the latter provided no estimates.

The methods of CV_D, CR, and G(0°C) provided consistent results for different stages of development. At the same time, all the estimates of C had negative values, which indicates that the values were underestimated. Moreover, the estimates of G(0°C) for the last two developmental stages were inadequate. Remark-

Table 3. Results and quality of calculation of threshold temperature for six developmental stages of *C. integrifolia* by different methods

Method	Estimate of threshold temperature, °C, for					
	starting point of vegetation	starting point of flower-bud formation	starting point of flowering period	massive flowering	starting point of fruit ripening	massive fruit ripening
Proposed method*	0	3	9	9	0	0
SD_{gdd}	–	–	–	–	–	–
SD_D	–	1	4	4	–	4
CV_D	–	–2	–2	–	–	–
CR	–4	–2	–2	–4	–	–
G(0°C)	–4	–2	–2	–4	–376	–81

* Method proposed by the authors; SD_{gdd} is least standard deviation in growing degree-days method; SD_D is least standard deviation in days method; CV_D is coefficient of variation in days method; CR is regression coefficient method; G(0°C) is equation of developmental rate for nonnegative mean air temperature values.

ably, nonnegative values of threshold temperature, which are more natural, especially during summer period, were only obtained by our method and the method of SD_D. Finally, our method was the only one that showed the dependence of fruit ripening on somatic resources accumulated by plants during the summer season.

CONCLUSIONS

Thermal requirements for plant development can be used for the evaluation of their adaptation rate and for the prognosis of a number of aspects in the protection of many rare species or in the practical use of common species. However, the determination of thermal requirements in changing environmental conditions is a big problem. The key task in the determination of temperature required for developmental processes is the measurement of threshold temperature values.

There are a number of common methods for the estimation of this constant. We proposed a new method for the estimation of threshold temperature based on the hyperbolic pattern of dependence between the number of days of development and temperature. We used this method to determine the normal temperature range of *C. integrifolia* based on the data of phenological observations in the Galich'ya Gora Nature Reserve. A formal comparison of common methods for the estimation of threshold temperature showed that the method proposed in this article is more effective. It provided the value of temperature constant for all the developmental stages of *C. integrifolia,* while other methods provided poorer data. Moreover, most of the methods gave negative values of threshold temperature even during the summer period.

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