**Conyza bonariensis** growth and development according to thermal time accumulation and photoperiod

**Abstract** — The objective of this work was to characterize the growth and development of hairy fleabane (*Conyza bonariensis*) according to thermal accumulation and photoperiod, at different sowing times, and to propose a scale representing the main plant development stages. The experiment was carried out with ten replicates in the 2011/2012 growing season. The sowing dates were: 05/31/2011, 07/04/2011, 08/03/2011, 09/09/2011, and 11/07/2011. Plant height (cm) and phenology were evaluated weekly. The duration of the different stages (days) and thermal time accumulation (°C day) were determined. The linear regression analysis showed that plant height was related to thermal time accumulation. Regardless of the sowing date, the vegetative stage had a longer duration (in days and in °C day) than the reproductive stage. Sowing on 11/07/2011 promoted the shortening of the vegetative stage, and the rosette stage did not occur. Flowering was induced in the photoperiod between 12.5 and 13.5 hours of light, regardless of the sowing date. Slow growth was observed at lower temperature conditions, when plants accumulated 30.9 and 16.3 °C day per centimeter of height for the 05/31/2011 and 11/07/2011 sowing dates, respectively. The phenology scale adequately predicts the development stages of hairy fleabane.

**Index terms**: morphology, phenology, weed.

**Crescimento e desenvolvimento de Conyza bonariensis em razão do acúmulo térmico e fotoperíodo**

**Resumo** — O objetivo deste trabalho foi caracterizar o crescimento e o desenvolvimento da buva (*Conyza bonariensis*) em razão do acúmulo térmico e do fotoperíodo, em diferentes épocas de semeadura, e propor uma escala para representar os principais estádios de desenvolvimento das plantas. O experimento foi realizado com dez repetições, no período de cultivo 2011/2012. As datas de semeaduras foram: 31/05/2011, 04/07/2011, 03/08/2011, 09/09/2011 e 07/11/2011. A altura de planta (cm) e a fenologia foram avaliadas semanalmente. A duração dos diferentes estádios (dias) e a soma térmica acumulada (°C dia) foram determinadas. A regressão linear mostrou que a altura de plantas relacionou-se à soma térmica acumulada. Independeentemente da data de semeadura, a fase vegetativa teve maior duração (em dias e em °C dia) do que a fase reprodutiva. A semeadura em 07/11/2011 promoveu o encurtamento da fase vegetativa, e o estádio roseta não ocorreu. Houve indução do florescimento em fotoperíodo entre 12.5 e 13.5 horas de luz, independentemente da época de semeadura. Observou-se crescimento mais lento na condição de menor temperatura, em que as plantas acumularam 30.9 e 16.3 °C dia per centímetro de altura, nas semeaduras em 31/05/2011 e 07/11/2011, respectivamente. A escala fenológica prevê adequadamente as fases de desenvolvimento da buva.

**Termos para indexação**: morfologia, fenologia, planta daninha.
Introduction

Hairy fleabane [*Conyza bonariensis* (L.) Cronquist] is a weed of the *Asteraceae* family whose main characteristics are high competitiveness and prolificacy, producing more than 800 thousand seed per plant (Kaspary et al., 2017). Worldwide, hairy fleabane is one of the main weeds in wheat, soybean, and maize cultivations, causing significant drops of grain yield (Vargas et al., 2007; Agostinetto et al., 2017). Furthermore, there are recognized cases of this species resistance to several mechanisms of herbicidal action, the main of which is the resistance to glyphosate (Heap, 2019). Moreover, knowledge regarding bioecology, and the growth and development characteristics of hairy fleabane are essential for more adequate and sustainable management strategies (VanGessel et al., 2009; Moreira et al., 2010a), including the choice of timing, chemical, mechanical, and physical control of more sensitive plants. Frequently, farmers decide in favor of weed control based on days (Marques et al., 2014), number of leaves and/or plant stature, with the adoption of a phenology scale, including the effects of environmental conditions which can improve these practices (Paula & Streck, 2008).

Recent findings show that the sowing date influences the phenological development of hairy fleabane (Soares et al., 2017). Seed of this plant that emerged under decreasing temperature and photoperiod conditions show an increase of dry matter production and reduced flowering induction, whereas under increasing temperature and photoperiod conditions there is less accumulation of dry matter and more flowering induction (Soares et al., 2017). Therefore, based on the climatic conditions, it is possible to predict this species development and, then, make recommendations for control at the appropriate time. For instance, in subtropical environments, such as southern Brazil and Argentina, the emergence flow of hairy fleabane seed occurs with a greater intensity from late fall to spring, extending the cycle through summer (Sansom et al., 2013; Bajwa et al., 2016). However, it is possible to see a wide variation of hairy fleabane plant growth, which requires a careful description of development, and a phenological scale can contribute to this.

Growth and development stages of weeds are best defined by environmental conditions (Marques et al., 2014). The stem elongation in a hairy fleabane plant begins around four weeks after emergence, in the subtropical environment (Kaspary et al., 2017), which can happen with changes according to temperature and photoperiod conditions (Soares et al., 2017). There is no information on the environmental factors that control this behavior, mainly those related to thermal time accumulation. It is important to know the hairy fleabane development in response to environmental conditions, for the species management programs to be constructed based on the interaction between genotype and environment, to minimize the damage caused by competing weeds with crops and reduce its environmental impact.

The objective of this work was to characterize the growth and development of hairy fleabane according to thermal accumulation and photoperiod, at different sowing times, and to propose a scale representing the main plant development stages.

Materials and Methods

The experiment was carried out in the 2011/2012 growing season, in field conditions, in the experimental area of the Plant Science Department of Universidade Federal de Santa Maria, in the municipality of Santa Maria, in the state of Rio Grande do Sul (RS), Brazil (29°43’S, 53°43’W, at 95 m altitude), in a completely randomized design, with 10 replicates (pots). According to the Köppen-Geiger’s climatic classification, the local climate is Cfa, subtropical humid without a defined dry season, and hot summers (Köppen, 1948). Seed used in the experiment were from spontaneous hairy fleabane plants in soybean fields in the municipality of Cruz Alta, RS (28°32’25.2”S, 53°34’11.6”W). Before each sowing date, seed dormancy was broken by immersion in water and conditioning for 72 hours at 7°C for imbibition.

A total of 100 to 150 seed were sown on the soil surface at different sowing dates, representing the entire period of hairy fleabane plant growth, such as 05/31/2011 (autumn), 07/04/2011 (beginning of winter), 08/03/2011 (mid-winter), 09/09/2011 (end of winter) and 11/07/2011 (spring). The experimental units were composed of plastic pots with 12 L capacity, filled with 6.3 kg of commercial substrate (MEC PLANT, Telêmaco Borba, PR, Brazil), class “A” (CTC 200 mmol kg⁻¹ and 60% water saturation),
whose fertility was adjusted by the pre-sowing addition of 500 kg ha\textsuperscript{-1} of N-P\textsubscript{2}O\textsubscript{5}-K\textsubscript{2}O fertilizer with the formulation 5-20-20, respectively, plus 200 kg ha\textsuperscript{-1} of urea (45-00-00), to avoid nutritional deficiency. The pots were perforated, spaced at 1.0 m x 0.85 m, and were buried to represent the soil temperature and humidity of the site.

In each experimental unit, three plants were kept, and the date of emergence (EM) was considered when 50% of the hairy fleabane seedlings were visible above the substrate. From that moment on, the plants were evaluated weekly, and the variables measured were height (cm), vegetative and reproductive plant growth, and morphology related to number of leaves, flowering, and capitula appearance. The date when these characteristics occurred was recorded. The phenology scale was proposed based on the study of the morphology of hairy fleabane plants (Kissmann & Groth, 1999; Weaver, 2001), as well as on plants of the family Asteraceae, based on specialized literature whose observations followed nondestructive methods (Bleiholder et al., 1991; Hess et al., 1997; Lazaroto et al., 2008; Shrestha et al., 2010). The duration of each stage was measured in days and thermal time accumulation (TTa, °C day).

Daily minimum and maximum air-temperature data throughout the experimental period were collected at an automatic meteorological station, which belongs to the 8th Meteorology Department of the Instituto Nacional de Meteorologia (DISME / INMET), located 100 m from the experimental area, in the municipality of Santa Maria. The growing degree day (GDD, °C day) was calculated according to the following equation (Arnold, 1960):

\[ \text{GDD} = (T_{\text{avg}} - T_b) \times 1 \text{ day}, \] (1)

In which \( T_{\text{avg}} \) is the mean air temperature (°C) calculated by the arithmetic mean of the minimum and maximum daily air temperatures; and \( T_b \) is the base temperature (°C) which was used at 8.4°C (Soares et al., 2017). The thermal time accumulation (TTa, °C day) was obtained through the sum from GDD:

\[ \text{TTa} = \Sigma \text{GDD} \] (2)

The statistical analysis of the data was performed using the R software (R Core Team, 2017). Mixed models, combining fixed and random sources of variation were constructed using the “lme4” package (Bates et al., 2015), for the duration of phenological stages at sowing dates measured (in days and °C day). The duration of the stages in days or in thermal time was transformed by the equation \( y = \log x \) for the residues, to meet the assumptions of the analysis of variance, at 5% probability. The significance was obtained by comparing the means, by the Tukey’s test, at 5% probability, in days and °C day for the plant stages. For plant height, the linear regression analysis was performed between the height of plants and the thermal time accumulation.

**Results and Discussion**

The proposed phenological scale divided the hairy fleabane development into the three following stages: seedling, which goes the emergence (EM) to the formation of rosette (RS); vegetative, emergence to visible floral bud (EM to Vn,); and reproductive, flowering to senescence (R1 to R6) (Table 1). The environmental conditions during the experiment are described in Figure 1.

The hairy fleabane seedling and vegetative stages began when the cotyledon leaves were visible on the soil surface, described as EM to Vn stages (Table 1, Figure 2). During the seedling stage, the first true leaf appeared, and then the other leaves appeared successively, which were sessile and alternate at the base of the rosette-shaped plant stage (RS), characterized by very short or imperceptible hypocotyl and epicotyl. Plants overwinter at the rosette stage (Sansom et al., 2013), but the existence or not of RS stages depends on the plant emergency stage (Lazaroto et al., 2008). The main stem appears from the center of the RS, presenting a height of 0.5 to 2 m (Sansom et al., 2013). The beginning of the stem elongation stage (EL) was considered when the distance from the apex of the plant growth to the soil surface was greater than or equal to 3 cm (Table 1, Figure 2). Leaves can be present throughout the extension of the stems (Kissmann & Groth, 1999), and should be counted to determine the number of vegetative stages (V), in which each new leaf represents V-stage advances. The RS and EL stages are important determinants for the management strategies of hairy fleabane because the chemical control is more efficient in these development stages.
Table 1. Developmental scale for hairy fleabane plants (*Conyza bonariensis*) with code and description of the events used in the study.

| Stage | Name                                    | Description                                                                 |
|-------|-----------------------------------------|-----------------------------------------------------------------------------|
| EM    | Emergency                               | Visible seedling cotyledon leaves.                                          |
| RS    | Rosette                                 | Vegetative growth of plant, with several leaves arranged in a rosette shape. |
| EL    | Main stem elongation                    | Distance from the apex to the soil surface $\geq$ 3 cm.                    |
| Vn    | Visible floral bud                      | Differentiation of the apical meristem.                                    |
| R1    | Beginning of flowering (main stem)      | View of the unisexual flowers, located around the central disc of hermaphrodite flowers. |
| R2    | Filarasis senescence of main stem capitula | Pale chlorotic coloration of filarasis.                                  |
| R3    | First open capitula on main stem        | Pappus externalized, making globular capitula.                            |
| R4    | Last open capitula on main stem         | When all main stem capitula have already externalized the pappus.         |
| R5    | Last open capitula in the plant         | When all capitula of plants have already externalized the pappus.         |
| R6    | Dead plant                              | No green tissues                                                           |

Figure 1. Average air temperature (°C), daily photoperiod (hours), date of occurrence of solstices and equinoxes, and vegetative growth of hairy fleabane plants (*Conyza bonariensis*) in relation to sowing date.
Conyza bonariensis growth and development

(Vargas et al., 2007). In general, failures to control hairy fleabane plants were mostly associated with herbicide applications on plants at an advanced stage, at the stage of EL, and on plants with high stature (VanGessel et al., 2009; Moreira et al., 2010b).

The reproductive stage starts with Vn that also represents the end of the vegetative stage, when there is no more appearance of new leaves on the main stem, followed by R1, R3, R5, and R6. It is important to know the reproductive biology of hairy fleabane because the species is characterized by high-seed production, as well as by dispersion over long distances (Dauer et al., 2006). The identification of the reproductive stages is important for the adoption of practices that prevent seed production, to avoid “soil-seed rain”.

The analysis of variance for duration (days and °C day) indicated the interaction of sowing dates and development stages (Tables 2 and 3). The plant height in relation to sowing date was fitted by linear regression with R² coefficient equal or greater than 0.80 (Table 3 and Figure 4). The sowing dates allowed of the development of hairy fleabane plants under different temperature and photoperiod conditions, which made it possible to identify variations in the stages (in days or °C day). Regardless of the sowing dates, the vegetative stage (EM to Vn stages) showed the longest duration (in days and in °C day) than the other stages. In this sense, changes in the vegetative growth and development of plants are related to emergency timing, and the decision for post-emergence control based on days, or according to plant height, may not represent the period of greatest weed sensitivity to hairy fleabane. Thus, an important weed management practice is the application of pre-emergent herbicides (Nunes et al., 2018) that can reduce infestation by retarding emergence.

Table 2. Duration (days) of each hairy fleabane development stage of Conyza bonariensis in relation to sowing date(1).

| Sowing date       | RS(2) | EL    | Vn    | R1    | R2    | R3    |
|-------------------|-------|-------|-------|-------|-------|-------|
| 05/31/2011        | 109.1aA | 16.9bB | 12.4bA | 13.2bA | 1.6dAB | 8.5cBC |
| 07/04/2011        | 77.0aBC | 11.8bC | 13.7bA | 12.0bAB | 2.0dA | 6.1cD |
| 08/03/2011        | 60.6aC | 16.2bB | 15.5bA | 10.8eABC | 1.8eA | 6.9dCD |
| 09/09/2011        | 85.0aAB | 57.5bA | 14.1cA | 8.6dC | 1.7eA | 11.8cDA |
| 11/07/2011        | -     | 63.3aA | 14.5bA | 8.7eBC | 1.1dB | 10.7eAB |
| Average           | 81.61 | 31.84 | 13.59 | 10.30 | 1.48 | 7.75 |
| Coefficient of variation (%) | 5.44 | 21.92 | 3.64 | 8.42 | 19.83 | 13.36 |

(2)Means followed by equal letters, lowercases in the lines and uppcercases in the rows, do not differ by the Tukey’s test, at 5% probability. (2)RS, rosette; EL, main stem elongation; Vn, visible floral bud; R1, beginning of flowering (main stem); R2, filariasis senescence (main stem capitula); R3, first open capitula (main stem).

Figure 2. Main stages of development of hairy fleabane plants (Conyza bonariensis) during the developmental cycle. RS, rosette; EL, main stem elongation; Vn, visible floral bud; R1, beginning of flowering (main stem); R2, filariasis senescence (main stem capitula); R3, first open capitula (main stem).
The sowing dates between 05/31/2011 and 08/03/2011 resulted in a vegetative growth stage (up to Vn) from 92 to 138 days (Table 2). Similarly to these results, a hairy fleabane biotype required 93 days to reach the Vn stage, in the spring/summer period, and 171 days in the fall/winter period (Kaspary et al., 2017). In the first sowing date (05/31/2011), the cycle of plants was around 109 days in the RS stage, which was lower only for the sowing date 09/09/2011 (Table 2). This characteristic was due to the fact that, during the winter time, the lower-temperature conditions promoted a slower development of the vegetative stage and a longer duration of the RS stage.

Table 3. Thermal time accumulation (°C day) of each Conyza bonariensis development stage in relation to sowing date(1).

| Sowing date   | RS(2)    | EL | Vn | R1    | R2    | R3  |
|---------------|----------|----|----|-------|-------|-----|
| 05/31/2011    | 659.0aB  | 184.9bB | 136.5bcC | 155.3bA | 17.2dC | 107.6cB |
| 07/04/2011    | 534.8aB  | 131.3bC | 156.7bcB | 148.2bA | 27.2dAB | 78.7cB  |
| 08/03/2011    | 486.8aB  | 189.1bB | 196.4bB | 147.4bA | 27.2dAB | 102.8cB |
| 09/09/2011    | 1082.0aA | 970.5aA | 242.8bA | 140.5cA | 26.4dAB | 165.6cA |
| 11/07/2011    | -        | 991.1aA | 254.7bA | 153.6cA | 17.3dBC | 191.3bcA |
| Average       | 674.1    | 477.8 | 189.6 | 144.0 | 20.5 | 115.3 |
| Coefficient of variation (%) | 5.4    | 15.7 | 4.9 | 1.2 | 7.0 | 6.3 |

(1)Means followed by equal letters, lowercases in the lines and uppercases in the rows, do not differ, by Tukey’s test, at 5% probability. (2)RS, rosette; EL, main stem elongation; Vn, visible floral bud; R1, beginning of flowering (main stem); R2, filariasis senescence (main stem capitula); R3, first open capitula (main stem).

Figure 3. Days after emergence in days (A), and in growing degree-days (°C days) (B) of hairy fleabane developmental stages (Conyza bonariensis) in different sowing dates. Phenological stages: RS, rosette; EL, main stem elongation; Vn, visible floral bud; R1, beginning of flowering (main stem); R2, filariasis senescence (main stem capitula); R3, first open capitula (main stem).
The plants that emerge in the spring rarely show the RS stage, as occurs with those plants that emerge in autumn, which results in less time and energy invested in the seedling stage (Buhler & Owen, 1997; Tozzi & Van Acker, 2014). This fact is important because it can reduce the window of sensitivity for some post-emergence herbicides. The RS stage is essential for plant survival during the winter period, since it allows of carbon fixation and accumulation of energy at low temperatures (Lazaroto et al., 2008). Thus, the hypothesis of this observation is that the increase of air temperature shortened the vegetative stage of hairy fleabane sown in the spring (11/07/2011), the rosette stage (RS) was not verified, and the Vn stage occurred at around 75 days (Figure 3 A).

Some studies suggest that the horseweed EL stage does not respond to the photoperiod (Nandula et al., 2006). This response may be due to increasing average air temperature. In the present study, the treatments were sown when an increase of the mean air temperature occurred (09/09/2011 and 11/07/2011) during the experiment, and the EL stage showed a longer duration than the other treatments (Table 2).

Another study evaluating hairy fleabane, that was sown in spring under subtropical environment conditions, showed a floral induction faster than plants with a sowing date in winter and fall, in which the difference to reach the flowering stage between seasons was greater than 30 days (Soares et al., 2017), confirming the results of the present study (Table 2). This was attributed to the elevation of the average air temperature. However, the duration in days for reproductive stages from R1 to R3 had a small variation comparing sowing dates, without differences from 05/31/2011 to 08/03/2011 (Table 2).

The thermal time accumulation for the vegetative stage of hairy fleabane plants varied between 822 and 980°C day, for sowing dates between 05/31/2011 and 08/03/2011 (Table 3). However, for the sowing dates 09/09/2011 and 11/07/2011, higher values were found, which ranged from 2295 to 1246°C, respectively, and differed from stages previously described. In low-temperature conditions, like those observed in autumn, hairy fleabane maintained the mass accumulation of dry matter, but without floral induction (Soares et al., 2017). For the thermal time accumulation of the reproductive stage, in the different growing seasons, a lower variation was observed, in which the thermal time accumulation of the measured stages ranged from 254 to 362°C day (Figure 3 B), except for the R1 stage that showed no significant difference between sowing dates (Table 3). These results may indicate that air temperature has an impact on the vegetative growth of hairy fleabane, with little influence on the reproductive development. Thus, it is necessary to understand the effect of the photoperiod on the reproductive development of this weed species.

A previous study of hairy fleabane showed that there is a strong influence on flowering induction by day length and light intensity (Tozzi & Van Acker, 2014). In this sense, for the sowing date 09/09/2011, carried out at the end of winter, plants emerged when the temperatures were low (the average air temperature was 20°C), and showed a slower development of the vegetative stage with longer duration than the other stages (Figure 1). Therefore, it is suggested that the floral induction of hairy fleabane plants respond more to the photoperiod than to the thermal time accumulation, as observed in earlier flowering with longer days (Kaspary et al., 2017). For this reason, we can infer that climatic characteristics influence the development of hairy fleabane and, in practical terms, they allow of a decision-making on the management preferentially before seed dispersal.

Plants had the floral induction (Vn) in a photoperiod between 12.5 and 13.5 hours of light, regardless of the sowing date (Figure 1), indicating that the temperature condition was favorable for flowering during this photoperiod range. In autumn/winter, with decreasing temperatures and photoperiods, the dry matter accumulation is higher, but there is no floral induction, while when temperatures and photoperiods increase during spring/summer, hairy fleabane flowering induction occurs (Soares et al., 2017).

Moreover, there was an increase of the vegetative stage on the sowing date 09/09/2011 because the development of vegetative growth of plants occurred in a period distant from the critical photoperiod, that is, when the rate of photoperiodic induction was low (Figure 3 A, Figure 1). Hairy fleabane can be considered a day-neutral plant, since its flowering can occur in specific periods that depend on the internal regulation of the plant, as the days increase or decrease, allowing of the flowering at different
times depending on the environment (Sansom et al., 2013).

The results indicate that plants that emerge during the autumn or early winter begin their reproductive stages between October and November (Figure 1), coinciding with the sowing of summer crops. Therefore, due to the various cases of recorded herbicide resistant plants (Heap, 2019), the chemical management alternatives for the pre-sowing control may be inefficient because of the advanced development stage, such as after the EL stage (González-Torralva et al., 2010). However, plants that emerge in the late winter or early spring can be controlled easily with the application of contact herbicides, and the use of residual herbicides in the soil, due to the better control of smaller plants, or preventing the emergence of new plants. The application of 2,4-D, MCPA, fluroxypyr, and glufosinate herbicides, in a mixture with glyphosate, allowed of the control of resistant and susceptible biotypes in the seedling stage (Sansom et al., 2013). However, there is a restriction to the use of contact herbicides because the control efficiency is reduced in plants with ten leaves or more, during the EL stage (Moreira et al., 2010b). In general, it is necessary to emphasize that the best hairy fleabane management strategy is based on the planning of the life cycle and development stage of plants, in order to allow of the target plants to be more susceptible to control (Bajwa et al., 2016).

When the plant height of hairy fleabane was considered in relation to the thermal time accumulation, it was observed that, in general, there was a small variation in the final plant height, regardless of the sowing date; sowing on 11/07/2011 showed plants with a height approximately 20 cm higher than the others (Figure 4). It was also observed that, in the later sowing date, the linear coefficient was higher, indicating the increase in height for each °C day accumulated (Table 4). Proceeding to the calculation of the inverse of the linear coefficient, there is a growing degree-day accumulation of plants, such as 30.8 and 16.3°C day cm⁻¹, for the sowing dates 05/31/2011 and 11/07/2011, respectively, showing the slower growth under lower-temperature conditions. Results from the literature show that the hairy fleabane emerging in the spring or in the fall usually shows a higher stature (Tozzi & Van Acker, 2014). Plant stature characteristic is important, since there is a direct relationship between stature and the fecundity of plants (Dauer et al., 2006) due to the adaptations of the species to the great dispersion of propagules.

The results of the present study allowed of the understanding of thermal time accumulation as an important factor to evaluate the growth of hairy fleabane, besides observing a direct relation of photoperiod with the plant development. Further studies should be done regarding photoperiod evaluations and other control practices, besides herbicide use and its influence on the phenological scale.

Table 4. Linear equations and coefficient of determination (R²) related to the height of hairy fleabane (Conyza bonariensis) plants, as a function of thermal time accumulation in different sowing dates.

| Sowing date | Equation | R²  |
|-------------|----------|-----|
| 05/31/2011  | y = -7.7906 + 0.0324x | 0.80 |
| 07/04/2011  | y = -11.4700 + 0.0372x | 0.87 |
| 08/03/2011  | y = -4.4612 + 0.0342x | 0.86 |
| 09/09/2011  | y = -47.5873 + 0.0462x | 0.80 |
| 11/07/2011  | y = -38.6640 + 0.0613x | 0.89 |

Figure 4. Plant height and growing degree-days of hairy fleabane (Conyza bonariensis) in relation to different sowing date.

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Conclusions

1. The sowing date of hairy fleabane (Conyza bonariensis) in the autumn/winter increases the vegetative stage in comparison with sowing in late winter and spring.

2. The vegetative phase for the sowing date at the end of winter and spring shows a greater thermal accumulation than other dates.

3. The phenology scale adequately predicts the development stages of hairy fleabane divided into seedling, vegetative, and reproductive stages.

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