Winter wheat phenological development model with a vernalization function using sigmoidal and exponential functions

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Abstract

Wheat is one of the world’s most important crops, and its phenological model is useful for scheduling agricultural practices such as fungicide or fertilizer application. Although various wheat phenological models have been developed throughout the world, a conventional model—mostly used for Japanese cultivars—is one wherein temperature and daylength responses are expressed as sigmoidal and exponential functions that do not have a vernalization function. Since a gradual rise in daily development rate is expressed as an increase in mean temperature in the conventional model, the model may potentially miscalculate the wheat development when used to predict the phenology of a cultivar with a strong vernalization requirement. In this study, we proposed a modified model that combines the conventional model and a vernalization function that expressed the daily vernalization rate using an inverse sigmoid function. Cultivation data for five winter wheat cultivars with relatively strong vernalization requirement were collected for several years (more than 4 years), and the model for flowering date prediction was calibrated based on the sowing date for each cultivar. Six-fold cross-validation was conducted to calibrate and validate the models. We found that the proposed model predicted the flowering date of the wheat cultivars more accurately in the median of root mean square error (RMSE: 1–2 days) than the conventional model (RMSE: 2–5 days). Although the accuracy of the model varies with the cultivar, our results indicated the advantage of using the proposed model compared with that of using the conventional model for describing winter wheat phenology. These findings can contribute to further studies on the crop models of winter wheat and would be an example of combining the vernalization function expressed by an inverse sigmoidal function with the crop model.

Key words: Crop development model, Crop phenology prediction, Model comparison, Triticum aestivum L., Vernalization requirement

1. Introduction

Wheat is one of the world’s most important crops and cultivated in various places in Japan. Agricultural practices associated with wheat cultivation, such as fertilizer or fungicide application, are usually based on wheat development stages such as stem elongation or flowering periods. Therefore, it is important for farmers to identify the development stages of wheat to manage their land well.

Thus, scheduling agricultural management practices based on the wheat development stage is important. Many researchers have developed tools for predicting or sensing conditions for wheat development. For predicting the growth stages of plants, numerical models that express daily crop development using daily meteorological data, such as temperature or photoperiod, have been developed around the world. For predicting the growth stage of wheat, various models have been developed; for example, the agricultural production systems simulator for wheat (APSIM-wheat) model (Wang et al., 2002; Keating et al., 2003), Wang and Engel model (Wang and Engel, 1998), and crop estimation through resource and environment synthesis (CERES)-wheat model (Ritchie and Otter, 1985). These models have been used in various places such as Australia, Europe, China, and the US.

In Japan, a number of researchers developed wheat phenology models for predicting the heading or flowering date of wheat (Maruyama et al., 2010; Nakazono et al., 2014; Kawakita et al., 2019). One popular model is the slightly modified rice phenological development model developed by Horie and Nakagawa (1990). This model expresses the responses to temperature and daylength as sigmoidal and exponential functions. So far, this model has been adapted for many Japanese wheat cultivars such as Chikugozumi, Norin61, Iwainodaichi, Kinuhime, Satonosora, Akitukko, and Kitahonami (Maruyama et al., 2010; Nakazono et al., 2014; Kawakita et al., 2019).

Although the wheat phenology models have been widely used in Japan, one of the problems of the conventional model is that it does not have a vernalization function (Kawakita et al., 2019). Vernalization is a physiologically important process for winter wheat, and it requires experiencing a certain period of cool conditions to accelerate flowering (Brooking and Jamieson, 2002). To achieve higher accuracy in predicting wheat phenology, it is necessary to develop wheat phenological models that consider the vernalization response of winter wheat (Fukushima, 2012; Nakazono et al., 2014). However, the phenological development model targeted for Japanese wheat...
cultivars is mostly the conventional sigmoidal and exponential based model. This is because the model can empirically predict phasic development stages, such as heading, flowering, or maturity of wheat, with relatively good accuracy, especially in spring wheat cultivars (Maruyama et al., 2010; Nakazono et al., 2014). To the best of our knowledge, this is the first study to combine a conventional sigmoidal and exponential based model with the vernalization function for winter wheat cultivars. To evaluate the advantage of the vernalization function, it is necessary to compare the predictive performance of the conventional model with and without the vernalization function.

This study is aimed to develop a modified phenological development model with a vernalization function for Japanese winter wheat cultivars. To explain the effect of the vernalization function, we compare the accuracy of flowering prediction for the conventional model and the modified model with the vernalization function using five winter wheat cultivars.

2. Material and Methods

2.1 Data

We collected the sowing and flowering dates of the five winter wheat cultivars (Iwainodaichi, Kinuhime, Satonosora, Akitakko, and Kitahonami) from different places in Japan (Fig. 1). The winter habit, which expresses the degree of vernalization requirement from I to VII (Gotoh, 1979; Crofts, 1989), is all grade IV for Iwainodaichi, Kinuhime, and Satonosora, and those of Akitakko and Kitahonami are grades V and VI, respectively. The sowing years for the cultivation data are listed in Table 1. We used the data of the sowing time between October and December every year; we also used data from several previous research studies (Table 1). For Kinuhime, we added original data collected in Fukuyama and Higashihiroshima in the 2017 season, and the data in Higashihiroshima were obtained from a domestic farmland. Further, we added some data collected in Matsusaka for Satonosora, which were originally collected by Mie Prefecture Agricultural Research Institute as part of a performance test for recommendable varieties. Fertilizers were applied in all cultivars using common practices; the details of these practices are described in previous research (Fukushima et al., 2005; Nakazono et al., 2014; Kawakita et al., 2019). The average monthly temperatures between 2009 and 2018 are listed in Table 2. The daily mean temperature and photoperiod at the study site were obtained from the Agro-Meteorological Grid Square Data system (Ohno et al., 2016).

2.2 Models

In the models used in this study, we divided the development phases of winter wheat into two stages: (1) from sowing to emergence and (2) from emergence to flowering; we changed the method to calculate the daily development rate of wheat at each stage.

In the first stage, we used a simple thermal time model, in which the daily development was expressed as the daily mean temperature. In this model, we set the base temperature as 0 °C and determine that wheat starts emergence when the accumulation of the daily mean temperature becomes more than 110 °C · day after the sowing date, based on previous research (Nakazono et al., 2014; Zheng et al., 2014) and our preliminary tests.

In the second stage, we used two different growth models—without and with the vernalization function. For the model without the vernalization function, we adopted a model used in previous research for Japanese wheat cultivars (Maruyama et al., 2010; Nakazono et al., 2014; Kawakita et al., 2019). In this model, the daily developmental rate (DVR) of wheat was expressed as the product of the effect of the temperature and photoperiod factors (Eq. 1).

\[
DVR_i = \frac{1}{C_i} \times f(T_i) \times g(P_i)
\]  

(1)

Effects of the temperature and photoperiod function were expressed by logistic and exponential functions, respectively, as follows:

\[
f(T_i) = \frac{1}{1 + \exp \left\{-C_i(T_i - T_b)\right\}}
\]  

(2)

\[g(P_i) = 1 - \exp \left\{-C_p(P_i - P_b)\right\}
\]  

(3)

where \(C_i\), \(C_p\), and \(C_v\) are coefficients of the models. \(T_b\) and \(P_b\) are the base temperature and photoperiod, respectively. \(T_i\) and \(P_i\) are the daily mean temperature and photoperiod of day \(i\), respectively.

The exponential function for the photoperiod response was also used in the Wang and Engel model (Wang and Engel, 1998).

For the model with the vernalization function, we developed models that combined the conventional model with the vernalization function to compare the influence of the vernalization function on the prediction accuracy of the model. In this model, unlike the original model, not only the temperature and photoperiod function, but also the function describing the relative daily development rate of vernalization \(f_{ver}(T_i)\) (0–1), was multiplied to express the daily development of wheat (Eq. 4).

In this model, vernalization was supposed to start from emergence and finish when experiencing a certain duration/days of low temperature (Weir et al., 1984; Ritchie, 1991; Wang and Engel, 1998). The daily vernalization rate was expressed as an inverse sigmoidal curve (Eq. 5), and it was used for calculating \(f_{ver}(T_i)\). As suggested in a previous research approach (Wang and Engel,
Table 1. Sowing year and size of data of each cultivation data used in this study.

| Place        | Cultivars           | Sowing year | Size of data |
|--------------|---------------------|-------------|--------------|
| Tsukuba **   | Iwainodaichi        | 2008–10 (12) | *           |
| Matsusaka    | Kinuhime            | 2008–17 (10) |              |
| Fukuyama *** | Satonosora          | 2016–17 (9)  |              |
| Higashihiroshima *** | Akitakko | 2016–17 (36) |              |
| Yamaguchi ***| Kitahonami          | 2012–15 (22)|              |
| Chikugo ****|                    | 1998–2002 (15)|             |

*The number of parenthesis indicates the size of data.
**The data from Tsukuba was obtained from Nakazono et al. (2014).
***The data was obtained from Kawakita et al. (2019).
****The data from Chikugo was obtained from Fukushima et al. (2005).

Table 2. Average monthly temperature and altitude of the study sites.

| Place       | Altitude (m) | Oct     | Nov     | Dec      | Jan     | Feb     | Mar     | Apr     | May     | Jun     |
|-------------|--------------|---------|---------|----------|---------|---------|---------|---------|---------|---------|
| Tsukuba     | 24           | 17.13   | 10.97   | 5.59     | 3.20    | 4.30    | 8.14    | 13.16   | 18.26   | 21.20   |
| Matsusaka   | 7            | 18.17   | 12.49   | 7.21     | 4.84    | 5.68    | 8.99    | 14.01   | 18.71   | 22.04   |
| Fukuyama    | 1            | 18.09   | 11.87   | 6.35     | 4.00    | 5.01    | 8.36    | 13.61   | 18.90   | 22.79   |
| Higashihiroshima | 270–300 | 15.49   | 9.78    | 4.10     | 1.97    | 3.06    | 6.63    | 11.94   | 16.81   | 20.27   |
| Yamaguchi   | 20           | 17.57   | 11.83   | 6.14     | 3.87    | 5.55    | 9.00    | 14.15   | 18.80   | 22.29   |
| Chikugo     | 11           | 19.15   | 13.06   | 7.23     | 4.97    | 6.71    | 10.21   | 15.12   | 20.11   | 23.32   |

1998), we calculated the \( f_{orr}(T) \) only after the accumulation of the DVR became higher than the base vernalization days (\( VD_{base} \)); we stopped calculating when the accumulation became higher than the physiological full vernalization requirement days (\( VD_{full} \)) (Eq. 6), which is described as follows:

\[
DVR = \frac{1}{C} \times f(T) \times g(P) \times f_{orr}(T)
\]

\[
h(T) = \frac{1}{1 + \exp \left\{ C_1 \left( T - T_n \right) \right\}}
\]

\[
f_{orr}(T) = \min \left\{ 1, \max \left\{ 0, \sum_{i=1}^{n} \left( \frac{h(T) - VD_{base}}{VD_{full} - VD_{base}} \right) \right\} \right\}
\]

where \( C_i \) is the coefficient of the model, \( T_n \) is the base temperature for vernalization, and \( T_\infty \) is the inflection point of the inverse sigmoidal curve; based on the preliminary research, we set it as 13°C, 11°C, 11°C, 9°C, and 8°C for Iwainodaichi, Kinuhime, Satonosora, Akitakko, and Kitahonami, respectively. We set \( VD_{full} \) and \( VD_{base} \) as 43 and 8, respectively, based on previous (Wang and Engel., 1998; Streck et al., 2003) and preliminary research. Once the vernalization requirement is satisfied, the value of \( f_{orr}(T) \) is set to 1, which indicates that the calculated DVR is equal to that of the conventional model (Eq. 2). The vernalization function was applied until vernalization finished so that two different temperature response curves exist in the proposed model (Fig. 2).

In both models (conventional and proposed), we calculated the DVR from the emergence stage and determined the wheat start flowering stage when the accumulation of the DVR became \( \geq 1 \).

2.3 Calibration and evaluation of the models

Root mean square error (RMSE) was used to evaluate the accuracy of the model (Eq. 7), and its calculation was as follows:

\[
RMSE = \sqrt{\frac{1}{n} \sum_{i=1}^{n} (S_i - O_i)^2}
\]

where \( i \) indicates the sample number, \( S_i \) is the simulated flowering date of sample \( i \), \( O_i \) is the observed flowering date of sample \( i \), and \( n \) is the sample size.

We conducted a six-fold cross-validation to calibrate and validate the models. We divided the cultivation data obtained from different places into six sub-datasets for each cultivar, among which five datasets were used for calibrating the models, and the rest were used for validating the model. Since a six-fold cross-validation was conducted for different validation datasets, we can calculate the RMSE of each result of fitting.
We determined the parameters of the model by minimizing the difference between the actual and predicted flowering dates of each wheat cultivar. The augmented Lagrange multiplier method (Rockafellar, 1976) or Lagrange multiplier method was used for parameterization (five parameters for the conventional model and six for the proposed model) as suggested in a previous study (Kawakita et al., 2019). Here, we set the parameter constraints for the conventional and proposed models as \(0.1 < C_t, C_v < 1; 0 < T_b < 15; 0.1 < C_p < 1; 8 < P_b < 11; 0.1 < C_e < 1; 0 < C < 100\) based on previous research (Kawakita et al., 2019). R-3.2.5. (R Core Team, 2018) and Microsoft Excel were used for analysis and data arrangement. The “Rsolnp” package (Ye, 1987; Ghalanos and Theussl, 2012) was used to determine the parameters using the augmented Lagrange multiplier method.

3. Results

The median of the RMSE obtained from the proposed model was smaller than that of the conventional model for all cultivars (Fig. 3). The median of the RMSE obtained from the proposed model ranged from around 1 to 2 days, whereas that of the conventional model ranged from around 2 to 5 days, depending on the cultivar. Although the difference in the median between the RMSE of both models is small in Satonosora (< 1 day), the results for other cultivars such as Iwainodaichi, Kinuhime, and Kitahonami showed more than 2 day differences between the models. Figure 4 shows the RMSE of each place for Iwainodaichi, Kinuhime, and Satonosora; the figure demonstrates that the accuracy of the models varies in different regions, especially for the conventional model in Kinuhime. The relationship between the timing of sowing and the model error for each cultivar was shown in Figure 5 with quadratic curve fitting each model. Most errors were within 3 days for the proposed model, whereas they were greater than 5 days in some cases for the conventional model, especially for Iwainodaichi and Kinuhime. In these cultivars, the flowering date estimated by the conventional model was earlier than the observed date for early and late sowing times (early October and December). When the sowing time was between the middle of October and late November, the flowering date estimated by the conventional model was later than the observed date. The results of both Akitakko and Kitahonami indicated that the conventional model tended to make larger errors in the late sowing time (December). Regarding parameters, the parameter values of each model are shown in Table 3. The mean of parameter \(C_t, C_v,\) and \(T_b\) was used for describing the temperature responses of each cultivar (Fig. 6), which showed clear differences between the models for the responses of the development rate to the temperature. The proposed model before vernalization finished was bell-curve shaped and reached the maximum value between 7°C to 11°C each cultivar. The both conventional model and proposed model after vernalization finished had logistic curves but the former had steeper slope than the later.
The parameter values of the conventional and proposed models (mean ± SD)*.

| Model  | Parameter | Cultivars |
|--------|-----------|-----------|
|        |           | Iwainodaichi | Kinuhime | SATOSORO | AKITAKKO | KITAHONAMI |
| Conventional | $C_1$ | 0.82 ± 0.21 | 0.28 ± 0.18 | 0.75 ± 0.18 | 0.22 ± 0.08 | 0.42 ± 0.12 |
|          | $T_x$ | 7.92 ± 0.92 | 6.02 ± 0.92 | 7.82 ± 0.76 | 9.21 ± 1.19 | 11.01 ± 1.24 |
|          | $C_2$ | 0.29 ± 0.23 | 0.31 ± 0.23 | 0.37 ± 0.18 | 0.38 ± 0.21 | 0.39 ± 0.33 |
|          | $P_b$ | 9.95 ± 0.48 | 9.6 ± 0.27 | 10.22 ± 0.34 | 10.69 ± 0.09 | 10.71 ± 0.23 |
|          | $C$   | 19.5 ± 14.18 | 28.45 ± 10.53 | 35.11 ± 9.54 | 18.13 ± 6.60 | 19.5 ± 10.32 |
| Proposed | $C_1$ | 0.22 ± 0.07 | 0.25 ± 0.09 | 0.42 ± 0.11 | 0.24 ± 0.07 | 0.23 ± 0.05 |
|          | $T_x$ | 11.59 ± 1.23 | 10.20 ± 2.92 | 6.88 ± 0.94 | 11.25 ± 1.65 | 11.75 ± 1.72 |
|          | $C_2$ | 0.67 ± 0.24 | 0.53 ± 0.23 | 0.76 ± 0.11 | 0.61 ± 0.27 | 0.70 ± 0.18 |
|          | $P_b$ | 8.22 ± 0.15 | 8.52 ± 0.23 | 8.49 ± 0.31 | 8.81 ± 0.57 | 8.40 ± 0.28 |
|          | $C$   | 0.50 ± 0.24 | 0.56 ± 0.24 | 0.77 ± 0.12 | 0.54 ± 0.33 | 0.42 ± 0.26 |
|          | $C$   | 33.02 ± 4.31 | 33.47 ± 5.75 | 55.95 ± 6.00 | 33.41 ± 5.67 | 39.50 ± 7.11 |

* The values were calculated from six models obtained from six-fold cross-validation.

4. Discussion

Our study was aimed to develop a modified sigmoidal and exponential based winter wheat phenological model with a vernalization function and to evaluate the performance of the proposed model with the conventional model, which is conventionally used as the wheat development model especially in Japan. Although the proposed model expresses the daylength response as an exponential function, similar to that in the Wang and Engel (Wang and Engel, 1998) model, it expresses the temperature response as a sigmoid (logistic) curve, which is different from the other major wheat development models such as APSIM-wheat, Wang and Engel, and CERES-wheat models. For example, in the APSIM-wheat and the Wang and Engel models, the temperature response is expressed as a three-stage linear function (Wang et al., 2002; Keating et al., 2003) and a $\beta$ function shape (Wang and Engel, 1998), respectively. The logistic curve has advantages in that it can express the wheat response to normal temperature (<30°C) more naturally and continuously compared with that expressed by the combination of the linear functions. Further, the $\beta$ function type shows an upward convex smooth curve in temperature growth. However, it has a disadvantage in that it requires three cardinal temperatures (base minimum, optimum, and maximum temperature) of the wheat cultivars (Wang and Engel, 1998) to be described before model calibration, whereas there is only one cardinal temperature in the logistic temperature response curve (Maruyama et al., 2010; Nakazono et al., 2014; Kawakita et al., 2019). Although the $\beta$ function type is useful since it can express the negative effect on higher temperature on wheat development, we omitted considering that situation since the average temperature hardly increased beyond 25°C in our study site between the emergence and flowering seasons (from October to May) (Table 2). We believe that expressing the temperature response using a logistic curve is practical for describing the various stages of wheat development, especially in the condition that higher temperature (e.g., >25°C) rarely happen until flowering.

Our results indicate that the proposed model improves the accuracy of predicting the flowering time of Japanese winter wheat cultivars compared with that when using the conventional...
Our results suggest that the conventional model is fairly accurate in predicting winter wheat development when using certain sowing times (DOY: around 300-330), and it is possible to use it for practical purpose, especially for central and western Japan where the optimal sowing time of winter wheat is around November. However, it should be noted that the conventional model can potentially miscalculate the development rate of winter wheat. Normally, winter wheat with a strong vernalization requirement does not grow faster as the temperature increases when the vernalization requirement is not satisfied. However, in the conventional model, the response function for temperature is expressed as a single sigmoidal growth curve, which monotonically increases with an increase in temperature, and thus, this model is likely to miscalculate the development of wheat, especially during a warm winter. Figure 6 demonstrates the example of the response curves of both models against the daily mean temperature. The single response curve for temperature was expressed in the conventional model, whereas two different response curves can be expressed based on whether the vernalization was finished in the proposed model. In this model, the response curve before the vernalization finished shows the negative effect on the development rate for the higher temperature (Fig. 6). Brooking and Jamieson (2002) reported that winter wheat with a strong vernalization requirement showed the highest vernalization saturation at 8°C, and other research showed that vernalization occurred between around \(-5°C\) and 15°C (McMaster et al., 2008). The temperature response varies depending on the cultivar, and the optimal temperature for vernalization remains unknown (Brooking and Jamieson, 2002); however, several research studies showed that a higher temperature can delay vernalization saturation (Chujo, 1966; Porter and Gawith, 1999), which suggests that it is preferable to have a vernalization function in winter wheat phenological models considering the natural development process of winter wheat.

Furthermore, a crop development model is not always used for simply predicting the developmental stage of the crop but also to predict or describe other factors of crop by combining other models or analyses. For example, Gao et al. (1992) combined the rice development model with the leaf age model to develop the total leaf number model, and they ultimately made crop organ development models by integrating various rice development models. Casadebaig et al. (2016) attempted to investigate the
potential effects of genotype, environment, and management conditions on the yield of Australian wheat combining the APSIM model and global sensitivity analysis. Since vernalization response is one of the important physiological process of wheat, combing this process with the wheat phenological model is fundamental for developing further applied models of wheat. As for the cultivar with lower vernalization requirement, although we did not test these cultivars, it is expected that there would be few differences between the conventional and proposed model. Since the $T_v$ is the base temperature for the daily vernalization genes to predict., 2006, 2007 loci and genes, which is important in regulating the phasic, is related to the photoperiod sensitivity, and therefore, it is likely that our model cannot study are mostly obtained from places that do not receive much from the temperature under the snow. The data we used in this study is miscalculated because the mean ambient temperature is different in the winter, it is likely that the daily development of wheat is changed drastically compared with flat lands, so winter wheat cultivars with relatively strong vernalization requirement are cultivated for preventing frost damages (Kamada et al., 2017). Considering the above, we believe it is informative for these cases to develop the wheat development model with the vernalization function for Japanese cultivars and to evaluate its performance. Vernalization is a common process in some plants, and therefore, the structure of the proposed model can potentially be used for other crops such as barley and some vegetables.

5. Conclusion

In this study, we proposed a new winter wheat development model that combined the sigmoidal and exponential based conventional model (the modified rice phenology model by Horie and Nakagawa (1990)) and the vernalization function. The result of six-fold cross-validation shows the advantage of using the proposed model with the vernalization function compared with the conventional model. Although the difference in the accuracy of the two models varied depending on the cultivar, a 1–2 days improvement of RMSE was found in four winter wheat cultivars (Iwainodaichi, Kinuhime, Akitakko, and Kitahonami). Certain biased errors can be made when using the conventional model, and thus it is preferable to use the proposed model with vernalization function for predicting winter wheat phenological development.

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References

Bloomfield MT, Hunt JR, Trevaskis B, Ramm K, Hyles J, 2018: Ability of alleles of PPDI and VRNI genes to predict flowering time in diverse Australian wheat (Triticum aestivum) cultivars in controlled environments. Crop and Pasture Science 69(1), 1061–1075.
Brooking IR, Jamieson PD. 2002: Temperature and photoperiod response of vernalization in near-isogenic lines of wheat. Field Crops Research 79(1), 21–38.
Casadebaig P, Zheng B, Chapman S, Huth N, Faivre R, Chen K. 2016: Assessment of the potential impacts of wheat plant traits across environments by combining crop modeling and global sensitivity analysis. PLoS One, 11(1), e0146385.
Chujo H. 1966: Difference in vernalization effect in wheat under various temperatures. *Japanese Journal of Crop Science* 35(3–4), 177–186. (in Japanese)

Crofts HJ. 1989: On defining a winter wheat. *Euphytica* 44(3); 225–234. doi: 10.1007/BF00037529.

Fukushima A, Kusuda O, Furuhasha M, Nakano H. 2005: Phenological development in relation to temperature of winter wheat Iwainadaiichi seeded early in southwestern Japan. *Plant Production Science* 8(2), 152–156.

Fukushima A, 2012: Effects of global warming on growth and yield of wheat in Japan: data analysis of field experiments. *Japanese Journal of Crop Science* 81(1), 83–88. (in Japanese)

Gao L, Jin Z, Huang Y, Zhang L. 1992: Rice clock model – a computer model to simulate rice development. *Agricultural and Forest Meteorology* 60(1–2), 1–16. doi: 10.1016/0168-1923(92)90071-B.

Ghalanos A, Theussl S, 2012: Rsolnp: general non-linear optimization using augmented Lagrange multiplier method. *R Package Version* 1.16.

Gotth T. 1979: Genetic studies on growth habit of some important spring wheat cultivars in Japan, with special reference to the identification of the spring genes involved. *Japanese Journal of Breeding* 29(2), 133–145. (in Japanese) doi: 10.1270/jbsbs1951.29.133.

Horie T, Nakagawa H, 1990: Modelling and prediction of developmental process in rice: I. Structure and method of parameter estimation of a model for simulating developmental process toward heading. *Japanese Journal of Crop Science* 59(4), 687–695. (in Japanese) doi: 10.1626/jcs.59.687.

Kamada E, Takahashi T, Inaba S, Araki H, Tanno K, 2017: Optimum sowing time of two wheat and two naked barley cultivars in the semi-mountainous area in Yamaguchi Prefecture determined from the yield characteristics. *Japanese Journal of Crop Science* 86(4), 375–381. (in Japanese) doi: 10.1626/jcs.86.375.

Kawakita S, Inaba S, Takahashi T, Kamada E, Ishikawa N, Takahashi H, Okuno R, 2019: Evaluation of non-linear wheat development models and optimization methods for their parameter determination. *Journal of Agricultural Meteorology* 75(2), 120–128.

Keating BA, Carberry PS, Hammer GL, Probert ME, Robertson MJ, Holzworth D, Huth NI, Hargreaves JNG, Meinke H, Hochman Z, Verbey K, Snow V, Dimes JP, Silburn M, Wang E, Brown S, Bristow KL, Asseng S, Chapman S, McCown RL, Freebairn DM, Smith CJ, McLean G, 2003: An overview of APSIM, a model designed for farming systems simulation. *European Journal of Agronomy* 18(1–2), 121–140.

Weir AH, Bragg PL, Porter JR, Rayner JH, 1984: A winter wheat Plant Production Science 10(2), 371–382. doi: 10.1016/S0168-1923(98)00028-6.

White JW, Herndl M, Hunt LA, Payne TS, Hoogenboom G, 2008: Simulation-based analysis of effects of Vrn and Ppd loci on flowering in wheat. *Crop Science* 48(2), 678–687. doi: 10.2135/cropsci2007.06.0318.

Ye Y, 1987: Interior algorithms for linear, quadratic, and linearly constrained non-linear programming. Department of EES, Stanford University, Stanford (CA), pp. 1–110. (Doctoral dissertation)

Zheng B, Biddulph B, Li D, Kuchel H, Chapman S, 2013: Influence of higher growing-season temperatures on yield components of winter wheat (*Triticum aestivum L.*). *Crop Science* 53(2), 621–628. doi: 10.2135/cropsci2012.05.0331.

Ohno H, Sasaki K, Ohara G, Nakazono K, 2016: Development of grid square air temperature and precipitation data compiled from observed, forecasted, and climatic normal data. *Climate in Biosphere* 16, 71–79. (in Japanese)

Porter JR, Gawith M, 1999: Temperatures and the growth and development of wheat: a review. *European Journal of Agronomy* 10(1), 23–36.

Ritchie JT, Otter S, 1985: Description and performance of CERES wheat: A user-oriented wheat yield model. *ARS wheat yield project*, 159–175.

Ritchie JT, 1991: Wheat phasic development. In: *Modelling Plant and Soil Systems* (ed. by Hanks RJ, Ritchie JT). American Society of Agronomy, Madison (WI), pp. 31–54.

Rockafellar RT, 1976: Augmented Lagrangians and applications of the proximal point algorithm in convex programming. *Mathematics of Operations Research* 1(2), 97–116. doi: 10.1287/moor.1.2.97.

Streck NA, Weiss A, Xue Q, Baenziger PS, 2003: Improving predictions of developmental stages in winter wheat: a modified Wang and Engel model. *Agricultural and Forest Meteorology* 115(3–4), 139–150. doi: 10.1016/S0168-1923(02)00228-9.

Team RC, 2018: R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. 2012. URL http://www.R-project.org. doi: 10.1108/ebo003648.

Wang E, Engel T, 1998: Simulation of phenological development of wheat crops. *Agricultural systems* 58(1), 1–24. doi: 10.1016/S0308-521X(98)00028-6.