

Effect of air temperature on each fruit growth and ripening stage of strawberry ‘Koiminori’

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Abstract. Strawberries are an economically valuable fruit in Japan; hence, their production must be maintained throughout the year. In this study, we investigated the effect of temperature on the number of days required for each fruit growth and ripening stage in order to obtain a basic knowledge for the highly accurate prediction and control of fruit harvest time. We planted the ‘Koiminori’ variety in artificial climate chambers, and then the effect of the average air temperature on the number of days required for each stage was analysed in four stages. The results showed that the correlation between temperature and the number of days required for fruit maturity was high at the white stage, moderate at the flowering and turning stages, and weak at the green stage. In comparing our proposed method which estimates the entire maturation period of the strawberries by totalling the predicted number of days required for each stage with the conventional method of estimating the entire maturation period at once, our proposed method significantly reduced the mean absolute error. However, the difference was slight at 0.18 days. This result suggests that the number of days required for each stage should be optimized for prediction by adding parameters other than air temperature as independent variables.

Keywords: harvest date prediction, regression analysis, fruit growth and ripening stage, accumulated temperature, strawberries

1. INTRODUCTION

There is a large market for strawberries (*Fragaria × ananassa* Duch.) in Japan because strawberries can be used for various purposes; for example, they can be eaten fresh or used as an ingredient for confectionery processing. Unlike other fruits and vegetables such as tomatoes and cucumbers, the price of and demand for strawberries fluctuates constantly (Onishi and Morie, 2016). Therefore, if the growth and ripening period of strawberry fruit could be adjusted, then the date and yield of the harvest could be controlled and tailored, respectively, in order to meet the current demand for strawberries. To date, various technologies designed to promote flower bud differentiation and control flowering time have been developed and are widely used in Japan (Kumakura and Shishido, 1994; Yoshida *et al.*, 2012). However, techniques for controlling fruit harvest time after flowering have not been fully developed as yet.

In order to predict and control the fruit harvest date, the number of days required from flowering to harvestable maturity (*i.e.*, days to maturity) should be estimated. Methods for predicting the harvest dates of some fruits



and vegetables have been developed. For example, Bonora *et al.* (2014) predicted the harvest date of nectarines 2–3 weeks in advance using non-destructive visible light/near-infrared radiation absorbance differences. More recently, the harvest dates of tomatoes (Minagawa and Kim, 2022), peppers (Lin and Hill, 2007), and strawberries (Yang *et al.*, 2019; Corvino *et al.*, 2023) have been forecasted based on fruit colour information provided by their images. However, these colour-based techniques only indicate the harvest date to within a few days; hence, they are inappropriate for harvest time control.

As fruit growth rate is influenced by temperature, the ‘accumulated temperature’ is generally referred to as it predicts the number of days to harvestable maturity; for example, Léchaudel *et al.* (2010) proposed a harvest date prediction method based on accumulated temperature for tropical fruits. In addition, the relationship between the number of days to maturity and the average air temperature was investigated for several Japanese strawberry varieties (‘Toyonoka’ and ‘Nyoho’ by Matsuzoe *et al.*, 2006; ‘Amaou’ by Sato and Kitajima, 2007; ‘Sagahonoka’ by Tagawa *et al.*, 2021 and Tagawa *et al.*, 2022).

It is worth noting that differences in susceptibility according to temperature ranges as well as differences in fruit growth and ripening stages should be considered in predicting the number of days to maturity using accumulated temperatures. In the studies reported to date, predictions have generally been made for the entire fruit maturation period. However, strawberries undergo several fruit growth and ripening stages—from flowering to fruit enlargement and colour development—during maturation. For example, an investigation into the relationship between temperature and fruit growth and the ripening stage of tomatoes revealed that the accelerating effect of temperature on fruit maturation varies with each stage (de Koning, 2000). Boechel *et al.* (2022) also argued that predicting the harvest date of apples using a linear model with accumulated temperature as a variable is highly unreliable at specific stages and cannot adequately represent the phenomenon. Similar to tomatoes and apples, strawberries have different temperature sensitivities to maturity depending on the fruit growth and ripening stage; however, this has not been fully elucidated in previous studies.

In this study, the effect of air temperature during each growth and ripening stage of strawberry fruit and the overall effect on the number of days taken to reach maturity was analysed. The period from flowering to maturity was divided into four stages based on changes in fruit appearance, and the effect of the average air temperature on the number of days required for each stage was determined. Then, an equation was formulated to predict the number of days required for each stage based on the average air temperature, and the accuracy of this equation was compared with that of the conventional methods that use a single formula to predict the entire fruit maturity period for a strawberry

variety ‘Koiminori’. The results of this study will provide the fundamental knowledge required to control harvest schedules and maintain the production of strawberries to meet the fluctuating demand for strawberries in different seasons.

2. MATERIAL AND METHODS

2.1. Growing conditions

The experiment was conducted in medium-sized artificial climate chambers (Emu-3HS; ESPEC MIC, Osaka, Japan) in an incubation laboratory. The internal dimensions of the artificial climate chambers were 1720 mm (width) x 1720 mm (depth) x 1865 mm (height). The experiment was conducted twice: from 28 April 2022 (planting) to 28 July 2022 (final fruit harvest) and from 11 November 2022 (planting) to 24 January 2023 (last fruit harvest). Fourteen strawberry specimens per chamber were planted and tested in double-staggered rows. In the first trial, all of the specimens planted were ‘Koiminori’; in the second trial, the seven plants on one side of the double-staggered rows were ‘Koiminori’. The experiment covered the harvesting period of apical fruit bunches, with seven fruit per bunch, and the eighth and succeeding flowers were thinned out. The number of leaves was maintained at six. After flower bud differentiation, the seedlings were planted in 12 cm black pots. The planting spacing was 150 mm, and liquid fertilizer (OAT Agrio, Tokyo, Japan) with an electrical conductivity of 0.8 dS m⁻¹ was applied at a water supply rate of 300 mL/plant/day. Pollination was performed manually to promote fertilization.

2.2. Setting the air temperature of the artificial climate chambers

Based on the assumption that the effect of temperature acceleration on fruit maturation varies with each fruit growth and ripening stage, the air temperature in the artificial climate chambers was manipulated during the growth period. In order to promote flower bud development and leaf unfolding during the pre-flowering stage, the daily average air temperature was maintained at 19.0°C until more than half of the plants had flowered. After flowering, the plants were exposed to daily average air temperatures ranging from 6.5 to 21.4°C in the experiment. During the first trial, the temperature was maintained in the following range for the heating treatment: (0.0 to 3.1°C) or in the following range for the cooling treatment: (2.4 to 0.0°C) based on the average daily temperature (which varied from 8.7 to 18.2°C) in a greenhouse at Kurume (Japan) from November 2019 to January 2020. Two treatments were set up in the second trial: a treatment simulating the daily average temperature at the abovementioned Plant Factory, and a treatment with controlled heating (0.0 to 4.9 °C). Mean temperatures and standard deviations for the cooling period, a simulation of greenhouse conditions, and heating

treatments during the control period were $13.3 \pm 3.12^\circ\text{C}$, $14.6 \pm 2.23^\circ\text{C}$, and $15.4 \pm 2.46^\circ\text{C}$, respectively. Multiple comparisons with the Tukey-Kramer test revealed a significant difference ($p < 0.01$) between the heating and cooling treatments.

Relative humidity and CO_2 concentration were maintained at 70% and 400 ppm, respectively. The light source was a plant growth LED device HS180W/BGR001 (ESPEC MIC, Osaka, Japan) with 16 lamps per room; the LED device was developed specifically for plant growth applications, with purple and far-red regions added to approximate sunlight and metal halide lamps. The wavelength peak characteristics included peaks at 399, 447, 575, 669, and 747 nm with relative power ratios of 33.7, 100, 67.6, 73.5, and 14.1%, respectively. The plants were grown at a day-length of 12 h and at a light intensity of $500 \mu\text{mol s}^{-1} \text{m}^{-2}$. In all trials, the values of the environmental conditions in the artificial climate chambers were recorded at 5 min intervals on the cloud server of an environmental monitoring device, Agrilog (ITKobo-Z, Aichi, Japan), installed inside the chambers.

2.3. Methods for determining the number of days required for each fruit growth and maturity stage

Studies on fruit maturity have been conducted to determine the number of days required for each fruit growth and ripening stage, which is the period from flowering to harvest and may be further divided into four stages (flowering, green, white, and turning stages). An overview of the fruit growth and ripening stages used in this study is shown in Fig. 1. The stages were determined once a day based on the visual appearance of the plants, as described by the following criteria:

- The flowering stage (FL) starts when the petals are fully open and ends when the petals are fully detached.
- The green stage (GR) commences at the end of the FL stage and continues until the fruit is enlarged and the same area is occupied by seeds (achenes) and fruit skin.
- The white stage (WH) is the period from green ripening until the fruit skin becomes white, and then the initial red colour change is confirmed.

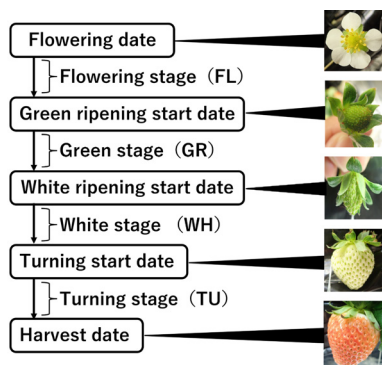


Fig. 1. Diagram of the stage classification rules referred to in this study.

- The turning stage (TU) is the period between the onset and spreading of a red hue throughout the fruit skin.

The flowers were tagged on the day of flowering. The dates of flowering, onset of each stage, and the harvest date were recorded on the tags. The number of days required for each stage was calculated after the fruit were harvested. In order to assess the differences between the treatments with regard to the number of days required for each stage, a Tukey-Kramer post-hoc test was conducted after a one-way ANOVA. It proved to be suitable for unequal sample sizes, thereby allowing for the identification of significant differences between treatments. P-values < 0.01 were considered significant.

2.4. Regression analysis between the number of days to maturity and daily average air temperature

A single regression analysis was conducted in order to predict the number of days required to reach maturity for each growth and ripening stage. The number of days recorded in the previous section was used as a dependent variable, and the daily average temperature was used as an independent variable.

The first regression analysis (Analysis I) was conducted to determine the number of days required for the entire maturity period without distinguishing between the stages. An inversely proportional relationship was observed between the number of days to reach maturity and the daily average temperature, therefore Eq. (1) was applied to the regression:

$$ND_{all} = \frac{CT_{all}}{AT_{all}}, \quad (1)$$

where: ND_{all} is the number of days required to reach maturity (*i.e.*, from flowering to harvest), CT_{all} is the accumulated temperature required from flowering to harvest, and AT_{all} is the daily average temperature during the maturation period.

After Analysis I, another regression analysis (Analysis II) was conducted to determine the number of days required for each growth and ripening stage. Since the stages differ in terms of their temperature sensitivities, the regression equations were individually fitted. Eq. (2) was the regression equation used for the fitting:

$$ND_i = \frac{CT_i}{a_i \times AT_i + b_i}, \quad (2)$$

where: ND_i is the number of days required in stage i , CT_i is the accumulated temperature required for stage i , and AT_i is the daily average temperature in stage i . a_i is a stage i -specific coefficient which indicates the contribution of the daily average temperature to the number of days required for a certain stage. In addition, b_i is a constant which is specific to stage i and determines the number of days required in the stages where a_i is small.

Equation (2) was also compared to the linear regression equation shown in Eq. (3). The linear regression equation is defined as follows:

$$ND_i = c_i AT_i + d_i, \quad (3)$$

where: c_i , d_i , are stage i -specific parameters. These are coefficients and constants that may be used to estimate the number of days required for a certain stage i .

In the regression analyses, the parameters of the approximate curves and lines were determined using a least-squares fitting. The statistical and regression analyses were performed using the Scikit-learn function (version 1.0.2) using Python software (version 3.7.12). Of the 188 fruit harvested in the experiment, only 157 normally developed fruit (40 fruit in cooling, 40 in simulating, and 77 in heating treatments) were included in the analyses.

2.5. Assessment of the accuracy of the harvest time prediction equation

The number of days required to reach maturity was predicted and assessed for accuracy based on the equations obtained from the regression analyses described in the previous section.

The number of days required to reach maturity was predicted using Eq. (1) in Analysis I and Eq. (4), wherein the number of days required for each stage i was predicted using Eqs (2) and (3) and totalled:

$$ND_{stage} = \sum_{i=1}^4 ND_i, \quad (4)$$

where: ND_{stage} is the predicted number of days required to reach maturity and ND_i represents the number of days required for stage i , as predicted by Eqs (2) and (3).

In order to verify the accuracy of the prediction equation, the mean absolute error (MAE), mean absolute percentage error ($MAPE$), and coefficient of determination (R^2) were used in the following equations:

$$MAE = \frac{1}{n} \sum_{i=1}^n |y_{obs,i} - y_{pred,i}|, \quad (5)$$

$$MAPE = \frac{100}{n} \sum_{i=1}^n \left| \frac{y_{obs,i} - y_{pred,i}}{y_{obs,i}} \right|, \quad (6)$$

where: y_{obs} is the actual measured value and y_{pred} denotes the estimated value. Each indicator was calculated using the leave-one-out cross-validation method.

The Diebold-Mariano test (<https://github.com/johntwk/Diebold-Mariano-Test>) was performed in order to compare the prediction performance of the conventional method, and the total maturation period prediction Eq. (1), with the proposed prediction equation based on stage-specific predictions Eq. (4).

3. RESULTS

3.1. Differences in daily average temperature by stage

In order to illustrate the differences in the daily average temperatures at each stage, the percentage of fruit in each temperature range is shown in Fig. 2. The proportion of fruit in the lower-temperature range increased as the maturity process progressed, this was probably due to the lower daily average temperatures during the second half of the maturation period, as the temperature settings were mainly greenhouse temperatures from November to January. Despite the temperature range bias identified above, a certain percentage of the fruit was obtained in each temperature range in all of the experiments. A data set of the fruit was obtained with variation in the daily average temperatures at each stage.

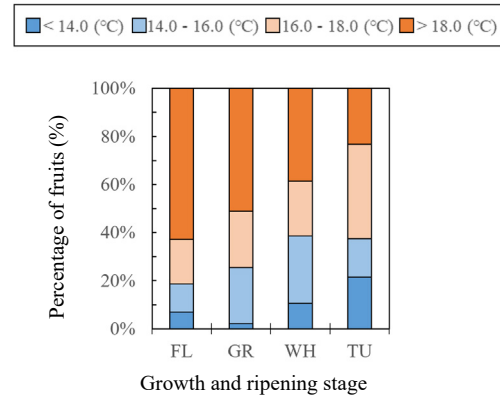


Fig. 2. Percentage of fruit at each fruit development stage subjected to varying temperatures.

3.2. Differences in the number of days required by stage

Table 1 shows the differences in the total number of days required to reach maturity and the number of days required for each stage by treatment. The differences in the alphabetic symbols indicate significant differences among the treatments ($p < 0.01$). The total number of days was found to be significantly shorter in the heating treatment, and this was also true for WH, which required a relatively longer number of days. On the other hand, there were no significant differences found between treatments in FL and GR. TU was significantly longer in cooling than other treatments.

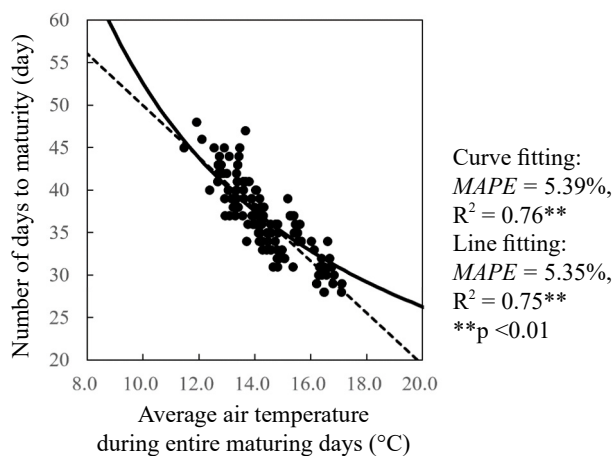
3.3. Analysis I: Relationship between the number of days to maturity and the daily average temperature over the entire fruit maturation period

Figure 3 shows the relationship between the number of days to maturity and the daily average temperature over the entire fruit maturation period based on the experiment. The curve in Fig. 3 represents the regression equation obtained by fitting Eq. (1). The line was obtained by fitting Eq. (3). The data generally followed the curve and line ($R^2 = 0.55-0.59$).

Table 1. Differences in the average number of days for each stage between treatments

Treatment	all		FL		GR		WH		TU	
	ND_{all}	S.D.	ND_1	S.D.	S.D.	ND_2	S.D.	ND_3	S.D.	
Cooling	38.93	4.30 a	4.78	0.88 a	8.40	1.70 a	20.53	3.97 a	5.23	1.74 a
Simulating	38.40	3.49 a	5.03	1.15 a	8.93	2.08 a	20.78	3.25 a	3.68	0.96 b
Heating	33.91	3.67 b	4.99	1.13 a	8.38	1.82 a	16.78	3.34 b	3.77	1.26 b

FL – flowering, GR – green, WH – white, TU – turning stages, ND_{all} – the total number of days required for maturity, ND_i – the number of days required in stage i .

**Fig. 3.** Relationship between the average air temperature and the number of days required to reach maturity.

The coefficient of the determination values were approximately equivalent between the linear and the curvilinear regressions.

3.4. Analysis II: Relationship between the daily average temperature and the number of days required for each stage

The correlation between the daily average temperature and the number of days required for each stage is shown in Fig. 4. The approximate curves and lines obtained using Eqs (2) and (3) from the regression analysis are also shown in the figure. The analysis results show that the correlations are all significant, with R^2 in the WH stage being the highest among the stages (0.55-0.59), moderate in the FL (0.41-0.43) and TU (0.29-0.35) stages, and weak in the GR stage (0.11-0.15). The coefficient of determination was slightly higher for the curvilinear regression than for the linear regression. However, the difference was limited as in Analysis I. When compared to Analysis I, the coefficients of R^2 for all stages were lower than those for the results of Analysis I, and the model was not optimized at each stage.

3.5. Assessment of the accuracy of the days to maturity prediction equation

Figure 5 shows the results of a comparison between the prediction accuracy of the prediction equations used in this study. In Fig. 5, ‘all’ indicates the accuracy of the conventional method which is used to predict the numbers

of days required for the entire fruit maturation period at once. By contrast, ‘stage’ indicates the prediction accuracy of the stage-by-stage method proposed in this study. The *MAE* of the two prediction equations were compared as an indicator of prediction accuracy. The results showed that the proposed formula significantly reduced the *MAE*, but the difference was as small as 0.18.

4. DISCUSSION

The effect of the daily average temperature on the number of days required to reach maturity was the highest at the WH stage, moderate at the FL and TU stages, and lowest at the GR stage.

During the FL period, the petals gradually open until the fully open state (maximum opening) is reached; then, they detach from the sepals. The rate of petal unfolding is reportedly affected by temperature (Uematsu, 1998), this finding is consistent with the results of this study. The results showed that temperature had a moderate effect on the number of days required for flowering. The lower coefficient of determination of the FL stage as opposed to the WH stage may be due to the effects of light quality (Garello *et al.*, 1995), and also the differences in jasmonic acid hormones and ethylene production, which regulate the timing of petal detachment (Kim, 2014) and individual differences in morphological characteristics (van Doorn and Schröder, 1995); however, it was difficult to draw conclusions from these results.

The GR and WH stages represent periods of progressive fruit enlargement. According to previous reports, strawberry fruit that have completed fertilization at flowering have two periods of progressive enlargement: achene growth after fertilization and cell enlargement due to the transport of assimilates (Miura *et al.*, 1990). The GR stage corresponds mainly to achene growth, while the WH stage corresponds to the enlargement of fruit cells. Even though the effect of temperature on the number of days required for the GR stage was observed, such an effect was smaller than that observed in the WH stage. This result is consistent with that of Yoshida *et al.* (1992), who compared fruit growth stages during low- (December) and high-temperature periods (March). No differences in fruit growth were observed during the FL stage; however, differences in fruit enlargement rates began to manifest during the GR stage, and significant differences in fruit size were highly noticeable

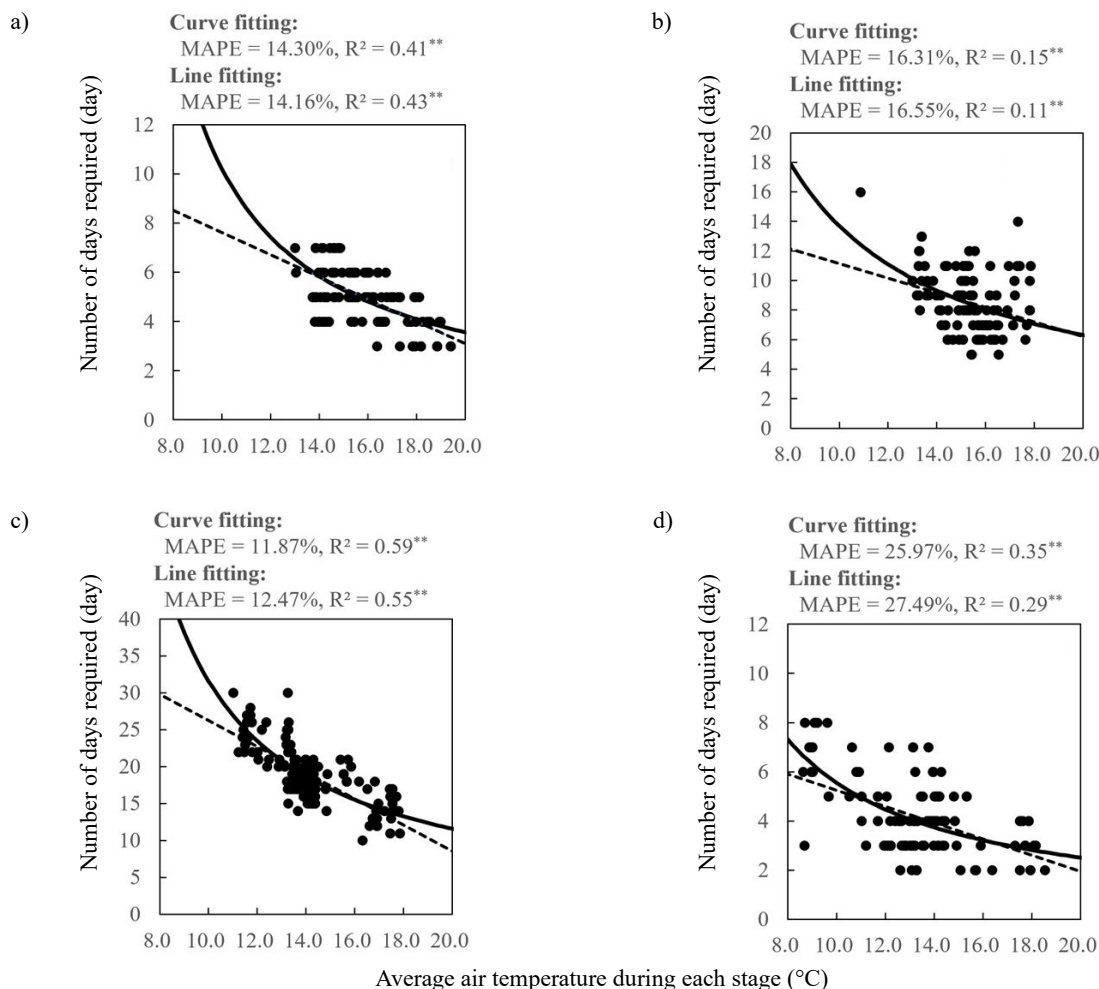


Fig. 4. Relationship between the average air temperature and the number of days required for each stage: a) flowering (FL), b) green (GR), c) white (WH), d) turning (TU) stages.

during the WH stage (Yoshida *et al.*, 1992). Therefore, the effect of temperature on the acceleration of fruit cell enlargement was more substantial than that of achene growth after fertilization, this explains why the WH stage was the most temperature-sensitive and exhibited the most accurate prediction among the stages studied.

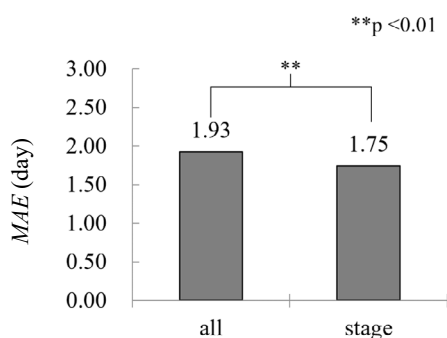


Fig. 5. Prediction accuracy of each method in predicting the number of days required to reach maturity.

The TU stage occurs when fruit pigments (anthocyanins) are produced, and the fruit are considered ready for harvest when the amount of anthocyanin increases and becomes distributed throughout the fruit. The results revealed that temperature had a moderate effect on the number of days required for the prodromal period. Previous studies have reported that the effect of temperature on strawberry coloration was largely influenced by light, mainly ultraviolet (UV) radiation (Yoshida and Yoshimoto, 2008). Moreover, the differences in the amount of light received by individual fruit due to shading by leaves and other fruit were assumed to cause differences in the number of days required for the TU stage. However, drawing conclusions based solely on differences in light sources could be challenging. In this study, fruit exposed to lower temperatures required significantly more days to complete ripening (Table 1).

A comparison between the two prediction formulas showed that the proposed stage-by-stage prediction method significantly improved the accuracy of the maturity prediction, but the difference was limited. This result suggests that when

the temperature is the only independent variable, as it is in this study, one equation like Eq. (1) is sufficient to predict the entire maturation period. At the same time, predicting the number of days required for each stage requires optimizing predictions using different approaches. The prediction accuracy for each stage may be further improved under certain conditions and by considering other factors. For example, both the inflorescence order (Kumakura and Shishido, 1994; Miura *et al.*, 1994) and stunted growth (Yoshida, 1991) influence the number of days required for fruit maturity. Although the factor of air temperature was used in this study, the prediction accuracy of the equations tested could be improved if the internal or surface temperature of the fruit was used directly. In tomato trials, it has been reported that predicting the growth rate based on fruit temperature, rather than on growing-facility temperature, may be more accurate in predicting the number of days required to reach maturity (Adams *et al.*, 2001). Prediction methods based on light intensity and quality must be considered, particularly during the TU stage, this was not accurately predicted in this study. It has been reported that UV intensity contributes significantly to colour promotion, and that intense red light is also adequate for some varieties (Yoshida and Yoshimoto, 2008). However, light irradiation also acts synergistically to increase fruit surface temperatures; increasing the amount of light received by fruit has been reported to increase fruit internal temperature and shorten the number of days required to reach maturity (Uto *et al.*, 2020). Hence, an experiment should be conducted in which the effects of light and temperature are determined separately in order to estimate the number of days required for the fruit to mature.

5. CONCLUSIONS

As a result of this study, the following findings were obtained.

1. The correlation between temperature and the number of days required for each stage was strong in the white stage, this stage represents a relatively long proportion of the total maturity period, the correlation was moderate in the flowering and turning stages, and weak in the green stage.

2. The correlation of the prediction equation for each stage was lower than that of the regression equation for the entire period.

3. The method of predicting each stage separately significantly improved the prediction accuracy of mean absolute error, but the difference was negligible at 0.18 days.

4. To improve the accuracy of predicting the harvest date further, it is necessary to improve the prediction models for the flowering, turning, and green stages by adding independent variables other than air temperature.

Conflicts of Interest: The authors declare no conflict of interest.

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