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ORIGINAL PAPER

Impact of warmer winters on the flowering display of Tokyo cherry (*Cerasus ×yedoensis* 'Somei-yoshino') at its southern range

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Abstract

With a warming climate, many temperate plants may not meet their winter chilling requirements and may not flower normally in spring. This effect may represent a particular problem for the culturally important Tokyo cherry (*Cerasus ×yedoensis* 'Somei-yoshino') at the southern limits of its range in Japan. We investigated the flowering period and dormant bud development of Tokyo cherry at study sites at the southern limits of the plant's range in Kagoshima Prefecture, Japan and at sites in cooler parts of the plant's range in Kumamoto Prefecture, Japan. We analyzed long-term observations collected at two sites during the years 1965–2024, and more detailed observations collected at 14 sites during the years 2021–2024. Cumulative chill units (cCU), a measure of winter chilling, showed strong negative correlations with full bloom date and flowering intensity, with milder winters associated with delayed spring flowering and lower proportions of flowers open at peak flowering. Trees experiencing mild winters with cCU values of less than 1,500 tended to exhibit development disorders for flowers and leaf buds. These effects were particularly pronounced in very mild winters with cCU values of less than 1,000. This study highlights how the lack of sufficient winter chilling threatens the flowering display of this culturally important tree at the southern edge of its range. Such threats will become more frequent and widespread as the climate continues to change. Managers need to consider alternative strategies to maintain flower displays during cherry blossom festivals, such as planting species with lower winter chilling requirements.

Keywords Bud dormancy · Climate change · Flower phenology · 'Somei-yoshino' · Winter chilling

Introduction

Warmer spring weather associated with climate change is causing many temperate plant species to flower and leaf out earlier in the spring (Primack et al. 2009a). Most plants in temperate regions must experience a certain period of cold weather before they are able to respond to spring weather; this is termed endodormancy and is controlled by a winter chilling requirement (Lang et al. 1987). This winter chilling requirement is a key aspect of plant phenology to ensure that plants do not end their winter dormancy too early and experience cold damage to swelling flower and leaf buds (Campoy et al. 2011). With a warming climate, many temperate plants may no longer be exposed to sufficient winter chilling, which could lead to delays in spring flowering and leafing out or could simply counteract earlier flowering associated with warmer springs (Ibáñez et al. 2010; Beil et al. 2021; Hsu et al. 2023).

Insufficient winter chilling may also lead to poor bud development and flower formation (Luedeling et al. 2013; Man et al. 2017). This is a particular concern for cultivated temperate fruit trees and wild plants because many of them need strong flowering synchrony to ensure adequate pollination and subsequent fruit development (Guo et al. 2015; Acarsoy and Misirli 2018; Bartolini et al. 2019; Fadón et al.

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2020; Dinu et al. 2021; Fernandez et al. 2023; Osorio-Marín et al. 2024). Landscape architects also sometimes rely on spring-flowering ornamental plants that display high densities of flowers all at once, creating visually striking landscape features. If plants are unable to adapt to future climate change, fruit production for human consumption could decrease, ornamental displays could diminish, and ecosystem services provided by flowers (e.g., provision of nectar and fruit) could suffer (Alburquerque et al. 2008; Fadón et al. 2020, 2021, 2023; Ibáñez et al. 2010; Luedeling et al. 2013).

One ornamental plant of special concern is Tokyo cherry (*Cerasus* ×*yedoensis* 'Somei-yoshino'), a clonally-propagated hybrid between *C. itosakura* and *C. speciosa*, (Kuitert 1999; Chung et al. 2011; Katsuki and Iketani 2016). The cultivar is also known as 'Somei-yoshino' and Yoshino cherry and is sometimes included in the genus *Prunus* (with plums, peaches, apricots, and almonds). The generic classification of cherries is still under investigation. In this paper we consider cherries in a stand-alone genus *Cerasus*, as is common in Japan, where our study takes place (Ohba 2001; Katsuki and Iketani 2016). This cultivar is extensively grown throughout Japan, especially in urban areas, and its flowering is celebrated as a major festival known in Japan as the Hanami festival and known elsewhere as the Cherry Blossom festival (Kuitert 1999; Primack et al. 2009b; Sakurai et al. 2011; Nagai et al. 2019). The annual viewing of flowering cherries (though not the Tokyo cherry) has been recorded in court records over the past 1,000 years in Japan, with additional standardized observations of Tokyo cherry made throughout Japan since 1953 by the Japan Meteorological Agency (JMA) (https://www.data.jma.go.jp/sakura/data/, Omoto and Aono 1989; Aono and Omoto 1990; Aono and Moriya 2003; Maruoka and Itoh 2009; Primack et al. 2009a; Asakura et al. 2010; Ibáñez et al. 2010; Aono 2015; Aono and Nishitani 2022). Extensive studies using these records generally show earlier flowering of Tokyo cherry with rising spring temperatures, particularly at higher latitudes (over 35°N) (Miller-Rushing et al. 2007; Chung et al. 2011; Allen et al. 2014).

Despite this general pattern of earlier flowering, some studies report that flowering of Tokyo cherry now occurs later at lower latitudes (under 32°N) near the southern limit of its range in Japan (Aono and Moriya 2003; Maruoka and Itoh 2009; Asakura et al. 2010; Matsumoto 2017; Hsu et al. 2023; Shin et al. 2025b). The reason for the flowering delay is thought to be insufficient winter chilling, as has been found in other cherry species (Alburquerque et al. 2008; Fadón et al. 2020, 2021, 2023; Shin et al. 2025b). In addition to the delays in flowering, there are also reports of weak flowering ("flowering without full bloom") at three of the most southern observation sites: Hachijojima and Tanegashima Weather Stations (Maruoka and Itoh 2009; Asakura et al. 2010) and Kagoshima Meteorological Office, currently the most southern observation site (Fig. 1) (Asakura et al. 2010). More recently, Katsuki et al. (2024) reported observations of flower buds dropping off or not opening at Kagoshima Prefecture following a mild winter, suggesting that warming climate conditions are negatively impacting flower development, not just delaying flowering.

Despite these studies to date, the quantitative relationships between insufficient winter chilling and flowering and bud development in Tokyo cherry remains understudied, particularly regarding delays in flowering times, the synchrony of flower buds opening, and flower and leaf bud development. An investigation of these relationships

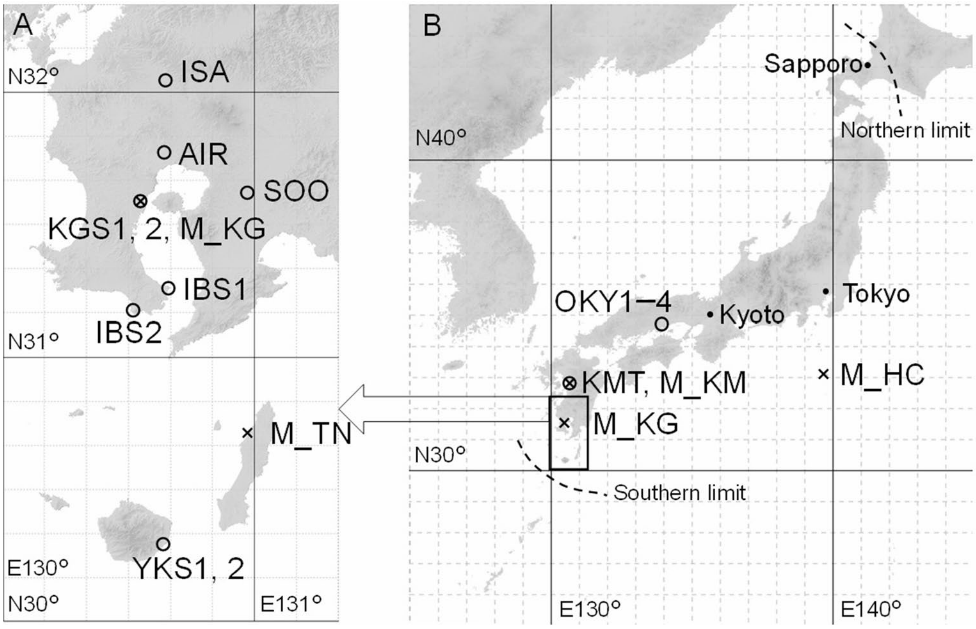

Fig. 1 Location of sites included in this study. **A** The nine study sites (circles) in Kagoshima Prefecture near the warmer southern edge of the range of Tokyo cherry **B** The five observation sites (circles) at cooler, more northerly locations. Dashed lines indicate northern and southern limits of Tokyo cherry range. Marked locations include: Aira City (AIR), Hachijojima Weather Station (M_HC), Ibusuki City (IBS1, 2), Isa City (ISA), Kagoshima City (KGS1, 2), Kagoshima Meteorological Office (M_KG), Kumamoto City (KMT), Kumamoto Meteorological Office (M_KM), Okayama City (OKY1–4), Soo City (SOO), Tanegashima Weather Station (M_TN), and Yakushima Town (YKS1, 2)

could lead to a better understanding of how climate change is affecting the flowering display of this iconic and culturally important ornamental species, and could also help to formulate strategies to manage for the future effects of climate change on Tokyo cherries and other ornamental plants. Such goals have led to this current investigation of how a warming winter climate is impacting the flowering and bud development of Tokyo cherry at its southern limit in Japan.

Materials and methods

Study sites

We used records of Tokyo cherry flowering collected during the period 1965–2024 by the Japan Meteorological Agency (JMA) at two sites: the Kagoshima Meteorological Office (M_KG) in Kagoshima City near the southern limit of Tokyo cherry, and the Kumamoto Meteorological Office (M_KM) in Kumamoto City, located 140 km north of M_KG (https://www.data.jma.go.jp/sakura/data/index.html). Throughout this paper, an M before a site acronym indicates a JMA meteorological office. Hourly temperatures were not recorded at M_KG before 1960, so it is difficult to calculate winter chilling index prior to that date. Therefore, we used data from 1965 to 2024, a 60-year period with hourly temperature data. In 2021, we established nine additional study sites in Kagoshima Prefecture at the southern limits of Tokyo cherry: Isa City (ISA), Aira City (AIR), Soo City (SOO), Kagoshima City (KGS1, 2 in the same city as M_KG), Ibusuki City (IBS1, 2), and Yakushima Town (YKS1, 2) (Table 1; Fig. 1). Two study sites were set up in each of three sites: Kagoshima, Ibusuki, and Yakushima. The average temperatures in winter (2023 Dec.–2024 Feb.) and spring (2024 Mar.–May) of the 12 sites where winter buds were observed were calculated using mesh data (Table 1).

At each study site, we selected 10 Tokyo cherry trees as observation trees that appeared healthy, and were as similar as possible in age and size within and among sites. The selected Tokyo cherry trees had been planted more than 20 years ago and had diameters at breast height ranging from 20 to 50 cm. The trees are believed to have come from the same grafted clone. In 2023, we also set up one cooler site at Kumamoto City (KMT; in the same city as M_KM) and four cooler sites in Okayama City (OKY1–4) for comparison as control flowering sites where winter chilling is sufficient (Fig. 1).

Flowering period

We estimated the flowering period at the nine study sites in 2024 according to the following procedure, utilizing

Table 1 Flower and leaf development in 2024 growing season, weather environment index, and the Pearson product-moment correlation coefficient (r) of each measure with cumulative chill units (cCU) at 12 sites. Sites arranged in descending order of cCU, that is, from coldest to warmest winter

Buds formed in 2023 (*N*)	OKY1	OKY2	OKY3	OKY4	KMT	AIR	SOO	KGS1	KGS2	IBS1	YKS1	YKS2	*r*
	148	197	213	157	195	87	219	127	229	111	147	136	
Flower buds/all buds (%)	72	64	42	66	50	82	59	72	59	68	31	27	0.498
Flower buds opened (%)	90	84	89	98	98	68	86	43	53	51	0	22	0.916*
Terminal leaf buds opened (%)	100	83	97	95	96	77	97	61	60	68	0	33	0.885*
Lateral leaf buds opened (%)	87	85	95	74	53	50	67	38	22	33	03	04	0.967*
Shoots from adventitious buds (%)	0	0	0	0	0	0	0	0	0	0	82	59	−0.745
North latitude	34°42’	34°42’	34°42’	34°42’	32°49’	31°45’	31°35’	31°35’	31°35’	31°15’	30°19’	30°19’	
Winter (Dec.–Feb.) temperature (°C)	6.5	6.5	6.5	6.5	8.6	9.7	9.6	11.1	11.3	10.8	14.1	14.1	−0.998*
Spring (Mar.–May.) temperature (°C)	14.6	14.6	14.6	14.6	16.6	16.7	16.5	17.7	17.8	16.9	19.0	19.1	−0.975*
cCU	2,394	2,394	2,394	2,394	1,787	1,568	1,576	1,190	1,151	1,340	393	393	

OKY Okayama City and *KMT* Kumamoto City are cooler, higher latitude sites. *AIR* Aira City, *SOO* Soo City, *KGS* Kagoshima City, *IBS* Ibusuki City, and *YKS* Yakushima Town are warmer sites at the southern edge of the range of Tokyo cherry. * indicates $P < 0.001$

methods described by Katsuki et al. (2024). We visited each study site once a week during the flowering period (from March 7 to June 2) and visually recorded the flowering degree (the proportion of buds that had reached anthesis) and the abscission degree (the proportion of buds that had reached petal abscission) in 10% increments. To supplement the visual measurements, we set up an automatic camera (SCURA DVR-Z4, Hanwha Q CELLS Japan) for one main observation tree suitable for photography at each study site from March to May. The camera took pictures of whole trees every two hours. From the photos, we assessed flowering degree and abscission degree. Such images taken by digital camera are useful for the observation of blooming phenology at multiple points (Nagai et al. 2018).

From these results, we evaluated the differences among the observed 10 trees, the first day when flowering of a main observation tree was confirmed with several opened flowers, and the full bloom day when the flowering degree reached 80% of open flowers. In addition, from visual observations, we recorded abnormal symptoms of development, such as bud drop-off, poor flower formation, and inflorescence withering.

For many JMA observation sites, data are available for both first flowering and full bloom for each year. In this study, we used full bloom dates of each year, as it is less affected by sample size than the first flowering dates (Hsu et al. 2023) and corresponds to the time of the annual cherry blossom festival. The full bloom date is greatly affected by the spring temperature after endo-dormancy is broken (Maruoka and Itoh 2009; Asakura et al. 2010) and can change from one year to the next (Shin et al. 2025a). To evaluate the effect of mild winter temperatures on flowering times, we used the day difference in the full bloom date at a particular site compared to a reference site where the chilling effect was sufficient.

Although spring temperatures are an important driver of flowering, our focus is on the impact of insufficient winter chilling at the warm edge of the cultivar's range. By comparing full bloom dates to a cooler reference site in the same year that always receives sufficient chilling, we were able to create an index for flower delaying that is less affected by yearly fluctuations in temperature. This approach allowed us to isolate the effect of winter chilling and test the hypothesis that insufficient winter chilling exerts a stronger delaying effect on flowering than advancing effects of warm spring temperatures. We verified this by confirming that our southern sites consistently had warmer spring temperatures than the reference site. Thus, any observed delays occurred *in spite of* conditions that would otherwise promote earlier flowering, highlighting the overriding impact of insufficient chilling at these warmer locations.

Specifically, we compared full bloom dates of Tokyo cherry trees at each of the nine sites with full bloom dates of a comparable site with a cooler climate that always has sufficient winter chilling: Kumamoto Meteorological Office (M_KM), located 140 km north of Kagoshima Meteorological Office (M_KG) at the southern limit of Tokyo cherry in Japan (Fig. 1). The average annual temperature (1991–2020) at M_KG is 18.8 °C and at M_KM is 17.2 °C. The day difference of full bloom at each site compared to M_KM was used as an indicator of flowering delay. We examined these differences for the nine study sites. We also examined these differences for observations collected during the period 1965–2024 at M_KG and M_KM, using data of full bloom date obtained from JMA.

Development of flower and leaf buds

In the autumn of 2023, we selected several branches at seven of the nine sites in Kagoshima that were experiencing warm winters (AIR, SOO, KGS1, KGS2, IBS1, YKS1, YKS2). We observed the state of the flower buds, terminal leaf buds, and lateral leaf buds on the branches—a total of 87 to 229 buds on branches from each site during the flowering period in 2024. In addition to these study sites, we set up five normal sites (KMT, OKY1–4) in cooler conditions, which were sufficient to meet winter chilling requirements. We recorded flower buds and their developmental stages: (0) dormant buds, (1) swollen buds, (2) flowers before anthesis, (3) flowers at anthesis, (4) flowers after abscission of petals, (5) fruiting infructescence, and (6) flower scar after abscission of inflorescence (Fig. 2). We also recorded terminal leaf buds and lateral leaf buds and their developmental stages: (0) dormant buds, (1) swollen buds, (7) leaf spreading, and (8) scar after abscission (Fig. 2). We recorded any failures to develop through these stages, such as bud drop or flower disorder. From these records for each site, we calculated the number of observed buds formed in 2023, and the following at the end of the flowering period in 2024: the ratio of flower buds to observed buds; the percentage of flower buds, terminal leaf buds, and lateral leaf buds that opened; and the ratio of leafy shoots from adventitious buds to total buds (meaning the number of leafy shoots developing from adventitious buds/number of leafy shoots developing from winter buds and adventitious buds; a greater value of leafy shoots developing from adventitious buds indicates a developmental disorder). Using data on the percentage of flowers open on each observation day, we estimated a logistic curve of flower opening in R using the glm() function (R Core Team 2024). This curve provides a measure of the intensity of the flower display—i.e., whether the flowers tend to open all at once or are spread out over a longer period.

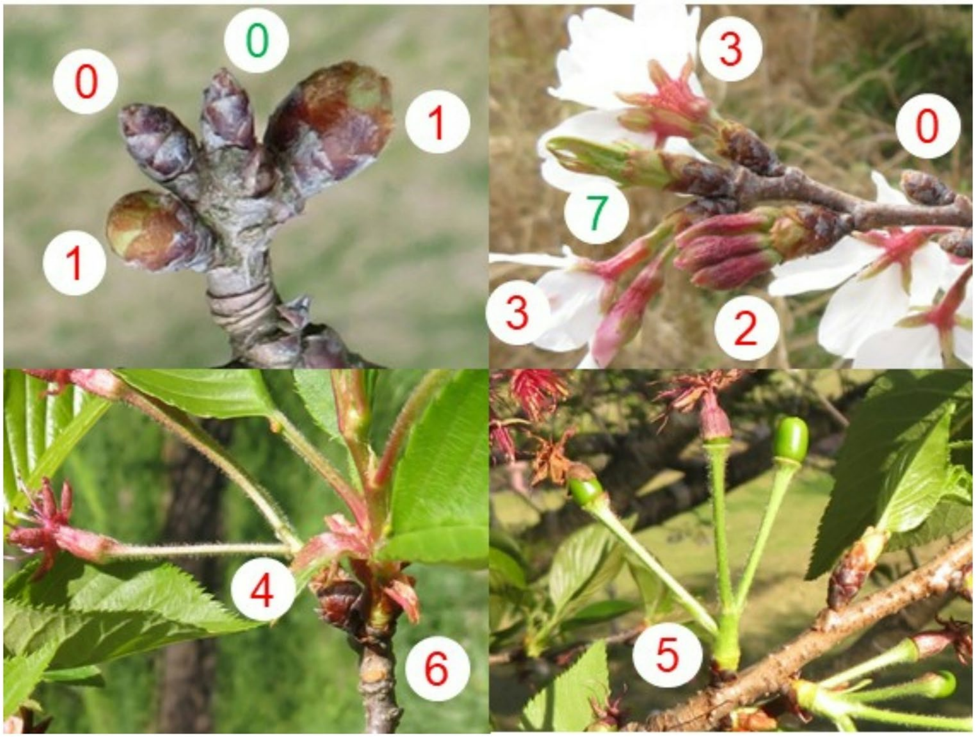

Fig. 2 The developmental stages of cherries from flower buds (red number) to fruiting and leaf buds (green number) to leafing out: (0) dormant buds, (1) swollen bud, (2) flowers before anthesis, (3) flowers at anthesis, (4) flowers after abscission of petals, (5) fruiting infructescence, (6) flower scar after abscission of inflorescence, and (7) leaf spreading. © 2025 T. Katsuki

Calculation of cumulative chilling units

Researchers have developed various methods to determine the amount of chilling plants experience over the winter season (Basler 2016; Luedeling 2012; Luedeling et al. 2021). For this project, we calculated the cumulative chill units (cCU) at K_KG and K_KM during the winter months as an index of winter chilling using methods developed by Asakura et al. (2010), based on earlier work (Aono and Omoto 1990; Aono and Moriya 2003; Maruoka and Itoh 2009). This index is based on the quantification of chilling units (CU), a limited variation of the Utah model, and establishes different ranges of temperatures with different contributions to dormancy completion (Richardson et al. 1974; Asakura et al. 2010; Luedeling and Brown 2011; Fadón et al. 2020). We did not use the full model developed by Asakura et al. (2010), but rather used just the cCU portion because it represents the best available chilling model developed specifically for Tokyo cherry. We did not use the model as a precise measure of chill required for breaking endo-dormancy, but as a comparative index for the approximate chilling experienced by Tokyo cherry trees to help us assess the effects of warm winters (low chilling) on trees at the margin of their range. In this model, the chilling unit accumulation during the endodormancy stage was expressed as a concave-down parabolic function, peaking at a maximum chill unit value of 1.0 at 4 °C, equal to 0 at −6 °C and 14 °C. On the high-temperature side, the function continues to decrease beyond 14 °C according to the same quadratic form until the chill unit value reaches −0.2, above which it remains fixed at −0.2. For temperatures below −6 °C, the chill unit value is set to 0 (Asakura et al. 2010). Since the hourly temperature at each study site was not observed, we calculated cCU using daily mean temperatures (T_{ave}), daily maximum temperatures (T_{max}), and daily minimum temperatures (T_{min}) at each of the study sites for each winter season using mesh data (latitude length is 30 s, longitude length is 45 s) supplied by the Agro-Meteorological Grid Square Data (https://amu.rd.naro.go.jp/wiki_open/) (Supplemental Table 1). The formula for estimating cCU from daily temperature was calculated using 3,939 sets of data from hourly temperatures at six meteorological stations in Kagoshima Prefecture in 2021–2024 (correlation coefficient is 0.992; Supplemental Fig. 1). cCU is calculated between September in the previous year to April in the current year as the sum of these daily chilling values from when they begin to increase in the autumn through the winter and when they cease accumulating at the first flowering date. Because plants respond to chilling experience only during the endo-dormancy period, the cCU, which includes the late winter period up to spring during eco-dormancy period, may be higher than the actual amount of chilling experienced by the plants during endo-dormancy period, particularly during long and cold winters. Prior research has shown that the minimum chilling requirement for Tokyo cherry in cool climates is around 1,450 cCU (Asakura et al. 2010). Therefore, once cCU values exceed 1,450, cherry trees transition from endo-dormancy to eco-dormancy. However, it has been suggested that in warm climates, Tokyo cherry trees can transition to eco-dormancy at lower chilling values (Aono and Moriya 2003; Maruoka & Itoh 2009; Asakura et al. 2010). Since it is difficult in practice to determine the exact endo-dormancy period, the cCU is considered a simple indicator or approximate threshold of chilling experience, rather than a rigid requirement, particularly in warm regions and years with mild winters less than 1,450 cCU. Even in a constant temperature environment of 4 °C, at least 62.5 days of exposure is required to meet its required winter chilling requirement, and these conditions may not be met in milder winters. cCU values are strongly negatively correlated with mean winter temperatures (Table 1; Supplemental Fig. 2), meaning that lower cCU values tend to be found in locations with milder (warmer) winters or growing in years with milder winters.

Assessment of chilling effect

To examine the relationship between the chilling effect and flowering period, we assessed the relationship between cCU and the day difference in full bloom dates of M_KG and M_KM in 1965–2024, the assumption being that trees at southern sites often did not meet their winter chilling requirements in certain warm years, whereas trees at the cooler M_KM site always met their winter chilling requirements. We calculated the Pearson product-moment correlation coefficient for these values. All calculations in this section were done using R using the cor() function (R Core Team 2024).

We also examined if the nine southern study sites exhibited delayed flowering by comparing their full bloom dates to M_KM, and then comparing these flowering dates to the cCU of each study site. In addition to the data for 2024 studied in this article, we also added data for 2022 (ISA, AIR, SOO, KGS1, IBS1) and 2023 (ISA, AIR, SOO, KGS1, IBS1, 2, YKS1, 2) published in Katsuki et al. (2024).

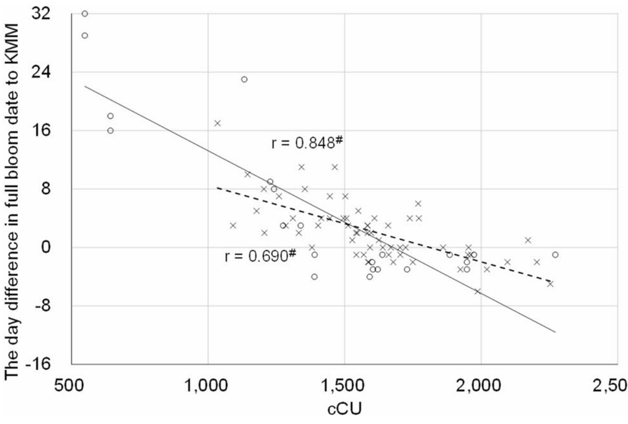

Fig. 3 The relationship between cumulative chill units (cCU) and the difference in full bloom dates between the warmer Kagoshima Meteorological Office (M_KG) site during the period 1965–2024 (cross) and nine study sites in 2022–2024 (circle), and the cooler Kumamoto Meteorological Office (M_KM) site. cCU measurements presented are from the warmer M_KG site and nine study sites. Dotted line is the regression line made from the data of M_KG; solid linear is the regression line of (M_KM); r shows the Pearson correlation coefficient; and # indicates $P<0.001$

To determine if the flowering period was highly concentrated or uneven and dispersed, we calculated the day difference between the first flowering date and the full bloom date for each main observation tree. We calculated the Pearson product-moment correlation coefficient for the relationship between cCU and the day difference using R.

Another way to determine flowering concentration is to look at the ratio of open flowers at peak flowering to the total number of flower buds. At the 12 sites, we examined the relationship between cCU and the percentage of flower buds that were open by calculating the Pearson product-moment correlation coefficient in R.

In Tokyo cherry, almost all buds on short shoots become flower buds, except for the end bud which forms a lateral leaf shoot (Ohba 2001). The terminal bud at the end of long shoots develops as a terminal leafy shoot (Katsuki et al. 2024). We examined the relationship between cCU and the opening of leaf buds by calculating the Pearson product-moment correlation coefficient in R. We also examined the relationship between cCU and average temperatures in winter and spring by calculating the Pearson product-moment correlation coefficient in R.

Results

Delays in flowering period

Records from the past 60 years (1965–2024) have shown that the full bloom date at M_KG, which has a warmer climate, occurs between 6 days earlier and 17 days later than at M_KM, which has a cooler climate, with an average of 2.3 days delay. As a result, cCU were accumulated from September 29–November 17 to March 17–April 5 in Kagoshima and from September 26–November 10 to March 15–April 1 in Kumamoto. The maximum delay in flowering occurred in 2020 when cCU at M_KG was about1,000 cCU (Fig. 3). In the period 1965–2024, the values of cCU at M_KG ranged from 1,034 to 2,253 (average: 1,596)—a range of mild to cold winters—and those at the cooler M_KM site ranged from 1,662 to 2,636 (average: 2,120). All of the cCU values in M_KM were above the winter chilling requirement of the Tokyo cherry. During this period, spring temperatures at M_KG were consistently 0.7 to 1.7 °C higher than at M_KM. The relationship between cCU and delayed days of the full bloom date was negative at M_KG: lower cCUs at M_KG were associated with greater delays in flowering ($P<0.001$).

Based on a visual examination of the data, it appears that a cCU of 1,500 is approximately where the winter chilling requirement of the Tokyo cherry is met, though this is not a rigid requirement. In 36 years where cCU at M_KG was above 1,500, the difference in flowering from M_KM ranged from −6 to 6 days, that is little overall difference; whereas in 19 years where cCU at M_KG was less than 1,500, the difference in flowering from M_KM ranged from 0 to 17 days, that is, often considerably delayed.

The relationship between cCU and flowering time was also negative at the nine study sites at Kagoshima Prefecture in 2022–2024 ($P<0.001$). In the 22 cases where there was complete information, cCU were accumulated from October 2–November 30 to March 18–April 18. Values of cCU at these nine sites ranged from 548 to 2,271 (average:1,417). In 11 cases where cCU was above 1,500, the delay in flowering in relation to M_KM ranged from −4 to −1 days, whereas in 11 cases where cCU was less than 1,500, the differences were stronger, ranging from −4 to 32 days, that is often delays of several weeks (Fig. 3). In the cases where cCU was less than 1,000 cCU, flowering was delayed even more strongly, consistently by 16 days or more.

At the nine southern study sites, there was also a significant negative correlation between cCU and the day difference between first flowering and full bloom ($P<0.001$), an index of flowering duration (Fig. 4). Lower cCU values were associated with longer flowering durations. Stating this in a different way, higher cCU values tended to create shorter, more concentrated flowering periods whereas lower cCU values tended to create spread out flowering periods. In 11 cases where cCU was above 1,500, the time between first and full bloom ranged from 5 to 9 days, whereas in 11 cases where cCU was less than 1,500, it ranged from 6 to 19 days.

Development of dormant buds

Years and sites with low cCU can strongly affect the development and opening of flower buds (Fig. 5). In 2024, KMT met the chilling requirements (1,500 cCU) on February 24 and experienced a relatively high cCU value of 1,804: 96 of 98 flower buds (98%) opened (Fig. 5; Table 1). In 2024, KGS2 did not meet the chilling requirements and experienced a relatively low cCU value of 1,241: only 69 of 129 flower buds (53%) opened (Fig. 5; Table 1). Of the flower buds that did not open at KGS2, two dormant buds remained closed, 51 buds dropped off, and seven buds were damaged by broken branches.

Using the data on developmental stages, we estimated logistic curves for the flower opening ratios and the flower abscission ratios, and calculated the visual flowering ratio from the difference between them. The maximum visual

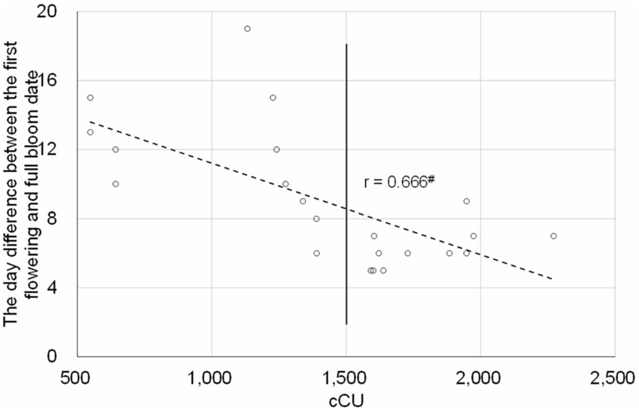

Fig. 4 The relationship between cumulative chill units (cCU) and the difference between first flowering and full bloom dates at nine study sites in 2022–2024. The difference between first flowering and full bloom (y-axis value) represents approximately half of the flowering duration. Dotted line is a regression line, with r showing the Pearson correlation coefficient, and # indicates $P<0.001$

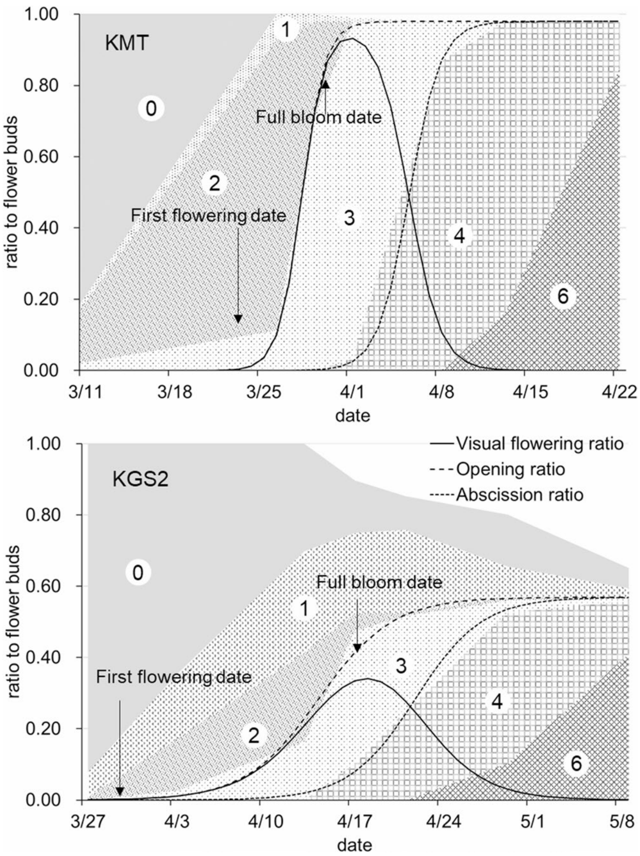

Fig. 5 The observed ratios between flower buds and each stage of development at two example sites of KMT and KGS2 in 2024: (0) dormant buds, (1) swollen bud, (2) flowers before anthesis, (3) flowers at anthesis, (4) flowers after abscission of petals, and (6) flower scar after abscission of inflorescence

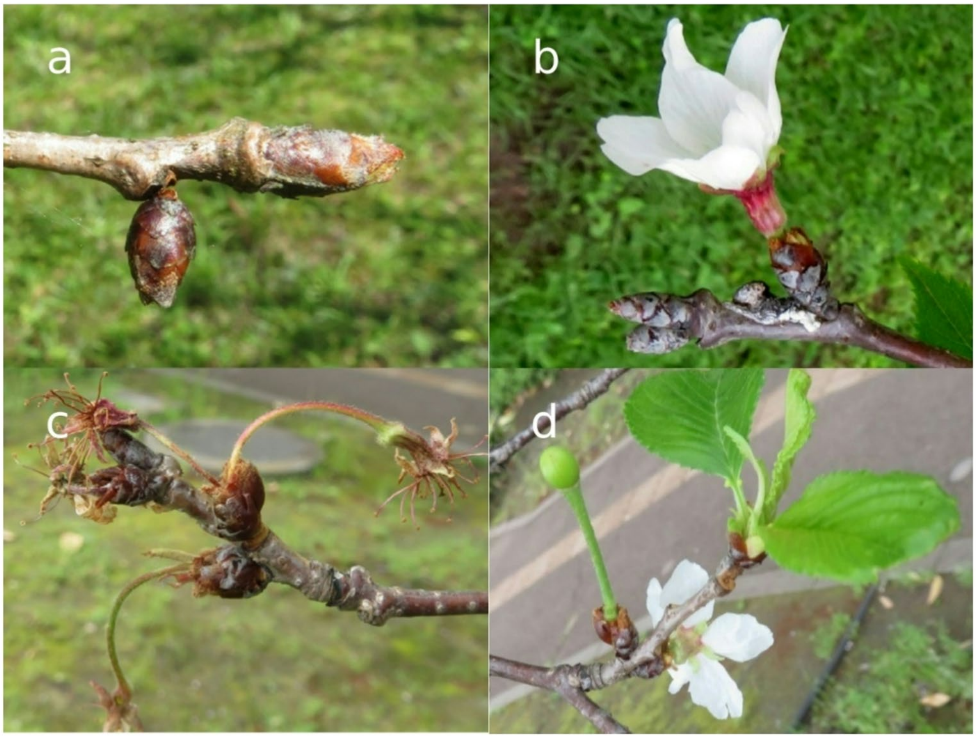

Fig. 6 Abnormalities of flowering observed at the study sites in Kagoshima Prefecture: **a** abscission of swollen bud, **b** immature inflorescence, **c** withered inflorescence during flowering, and **d** flower that opened after leafing or fruiting. © 2025 T. Katsuki

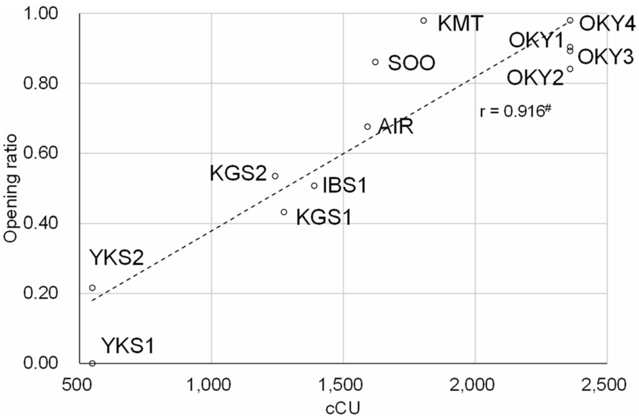

Fig. 7 The relationship between cumulative chill units (cCU) and percentage of flower buds that opened at 12 sites in 2024. Sites include: Aira City (AIR), Ibusuki City (IBS1), Kagoshima City (KGS1, 2), Kumamoto City (KMT), Okayama City (OKY1–4), Soo City (SOO), and Yakushima Town (YKS1, 2), Dotted line is regression line, r show the Pearson correlation coefficient, and # indicates $P < 0.001$

flowering ratio in KMT was 93%, while in KGS2 it was 34% (Fig. 5). That is, at peak flowering, 93% of the flowers were open at KMT where cCU values were relatively high, and only 34% of the flowers were open at KGS2 where cCU values were relatively low. A smaller portion of flower buds opened and the flowering period was more spread out at the warmer KGS2 site compared to the cooler KMT site.

We observed disorders of flower buds at all study sites, but at five study sites where cCU was less than 1,500, disorders were particularly common, including drops of swollen buds and flowers, and immature or withered inflorescences (Fig. 6). At all study sites, most of the defective flower buds dropped during growth.

The effect of cCU on flower opening was also demonstrated at our 12 study sites in 2024. At the seven sites where cCU was above 1,500, the opening ratio of flower buds ranged from 68% to 98%, whereas at the five sites where cCU was less than 1,500, the ratio ranged from 0% to 53% (Fig. 7; Table 1). There was a strikingly clear linear relationship ($r = 0.916$) between cCU and flowering opening ratio.

cCU values were also related to the opening of terminal and lateral leaf buds in 2024. At the seven sites where cCU was above 1,500, the opening ratio of terminal leaf buds ranged from 77% to 100%, whereas at the five sites where cCU was less than 1,500, the ratio ranged from 0% to 68%. At the seven sites where cCU was above 1,500, the opening ratio of lateral leaf buds ranged from 50% to 95%, whereas at the five sites where cCU was less than 1,500, the ratio ranged from 3% to 38% (Table 1). These results suggest that lack of winter chilling had a strong effect on leaf bud development and flower bud development.

Discussion

Our study shows that peak flowering of Tokyo cherry occurs later and is less spectacular following winters with little chilling. Specifically, flowering is delayed by up to 32 days at many sites in Kagoshima Prefecture when the approximate winter chilling requirement of 1,500 is not met. In addition, lack of adequate chilling results in extended flowering periods with lower proportions of flowers open at peak flowering, and numerous flower buds exhibiting poor development, with many never opening at all. In contrast, in years with cCU values above 1,500, plants do not show notable delay in flowering and almost all of their flowers open at one time. These phenomena are highly correlated with cCU and are likely caused by insufficient winter chilling effects in some winters, as has been reported elsewhere for Tokyo cherry (Hsu et al. 2023) and other fruit trees (Bartolini et al. 2019). It is important to note that this approximate value of 1500 cCU is not rigid and isolated requirement and flowering may be influenced by other factors such as spring warming and the physiological health of the tree.

Currently, JMA defines the full bloom date as when 80% of the flowers, including abscission, have opened. Consequently, in years when winter chilling requirements are not met, Tokyo cherry trees may simply not reach “full bloom” even at the date of peak flowering. This phenomenon is likely responsible for years of “flowering without full bloom” described by Maruoka and Itoh (2009) and Asakura et al. (2010) and observed at M_KG in 2024.

Other studies have reported similar chilling requirements for breaking dormancy in Tokyo cherry, specifically, such as the studies of Asakura et al. (2010) reporting CU values of 1,450. Our study shows additionally that the impact of warmer winters on flowering becomes more pronounced as chilling is further reduced. These effects are particularly striking at cCU values below approximately 1,000, with large delays in flowering, low proportions of flowers open at any one time, and many flowers failing to open or failing to develop normally. At cCU values close to 500, only 0–22% of the buds opened.

Similar problematic responses to low chilling have been reported for Japanese pear (*Pyrus pyrifolia*) and apricot (*Prunus domestica*), including flowering delays and development disorders of flower buds (Ito et al. 2018; Tominaga et al. 2022; Acarsoy and Misirli 2018). Warmer autumn–winter temperatures may result in poor flowering of Japanese pear because buds do not develop freezing tolerance, endo-dormancy progression is abnormal, and floral organ development is disrupted thereby causing developmental problems for flower buds (Ito et al. 2018; Tominaga et al. 2022). More detailed physiological and anatomical research is needed to clarify the relative importance of these factors in the Tokyo cherry and how they interact with late frost events.

Our study also demonstrated that the lower cCU values associated with milder winters decreased the probability of terminal and lateral leaf buds opening (Table 1). Over successive years, this phenomenon reduces the number of leaves on trees, limiting the production of flower buds in following years. In addition, in years with lower cCU values, we also observed lateral buds and shoots growing out of short shoots. Such conversions of short shoots to long shoots also reduce flower production.

Potential management responses and future research

As temperatures in temperate zones continue to rise in the future, the impacts of insufficient chilling are expected to become more severe and widespread (Maruoka and Itoh 2009; Guo et al. 2015; Fernandez et al. 2023; Hsu et al. 2023). People growing trees and shrubs for fruit production and ornamental purposes may need to shift to species or cultivars that have lower chilling requirements (Alburquerque et al. 2008; Fadón et al. 2023; Osorio-Marín et al. 2024). This has special significance for Japan, where Tokyo cherries are so widely cultivated. Cherry blossom festival culture, associated with the flowering of the Tokyo cherry, has spread from Tokyo and Kyoto throughout Japan, and is now practiced even in Okinawa, where cherries are not native. It is an important part of the lifestyle for Japanese people, involving city-wide celebrations and large-scale tourism with great economic and social significance. Landscape designers need to consider planting other cultivars of flowering cherry to replace Tokyo cherry as temperatures continue to warm in the future.

Over the past 150 years, people have learned by experience that the climate is too warm for the Tokyo cherry to grow on Okinawa Island, which is subtropical. Following efforts to introduce various flowering cherry species to Okinawa, only *Cerasus campanulata* has shown some success (Higa 1986). In addition, *C. jamasakura* and *C. kumanoensis* are native to the warm temperate zone of Japan (Ohba 2001; Katsuki 2018), and selection of these species and their hybrids may yield cultivars with reduced winter chilling requirements. One possible cherry already available with a low chilling requirement is *C. jamasakura* var. *chikusiensis*, a native to Yakushima Island off the southern coast of Kyushu in Kagoshima Prefecture (Ohba 2001). It is considered a promising alternative species for use in cherry blossom festivals in southwestern Japan.

Additional research can explore how cCU values will likely change at sites across Japan, particularly in key tourist locations and population centers in southern Japan. For example, Miyazaki on Kyushu Island has already shown cCU values below 1,500, and Shizuoka on the southern coast of Honshu Island and Kochi on Shikoku Island have shown values close to 1,500. It seems likely that the warming climate in coming years will cause delays in flowering and weaker flowering at these sites. With present trends towards warming, at some point Tokyo cherry trees growing in many other places will be affected, including major urban areas further north.

Plant phenology researchers should also consider the relative advantages of using cCU or mean winter temperatures in research projects. As we have observed in this study (Table 1), and others have noted (Basler 2016), CU values are highly correlated with mean winter temperatures. CU values have the advantage of corresponding to plant physiological processes, but they are complicated to calculate and are more challenging to explain to the public. At two sites in Kagoshima and Kumamoto, cCU values of 1,500 and 1,000 correspond to mean winter temperatures of 10 and 12 degrees Celsius, respectively (Supplemental Fig. 2). These mean temperature values are easier to understand intuitively and explain to the public, but they are merely indicators. In some research applications, such as some applications in horticulture or fine-scale forecasts of phenological change, physiological models are still necessary and preferable.

Much of the results of this study have been built on the phenological observations made by the staff of JMA. For over 70 years, the JMA has been recording the flowering period of Tokyo cherry and other species at various sites throughout the Japanese archipelago. These records are an outstanding example of how long-term high-quality phenology data can be useful in climate change research (Maruoka and Itoh 2009; Primack et al. 2009a; Ibáñez et al. 2010; Hsu et al. 2023; Miyawaki-Kuwakado et al. 2024), and such monitoring should be continued (Doi et al. 2021). However, we argue that the observations should be expanded to include developmental disorders associated with insufficient winter chilling, rather than just recording that species are "flowering without full bloom." One such change would be to label one or more branches on each plant in phenology gardens several weeks before a plant comes into flower, and count the number of flower buds on each branch. Then when the plant is in full bloom, observers could count the number of open flower buds in total and the number of flowers per flower bud. With this information, researchers would know the percent of flower buds that are open and the degree to which plants are displaying developmental disorders. Observers could also count the number of healthy and deformed flowers. This perhaps could be supplemented by taking photographs of each plant when it is in full flower, taken from a fixed position.

Conclusions

As the climate continues to warm in Japan and other countries, ornamental plants growing at the southern limits of their plantings are facing increasing difficulties due to inadequate winter chilling. This is a special problem in Japan where the Tokyo cherry is widely planted and crucial to cherry blossom festivals, events of enormous cultural and economic significance. In this study, we have shown that when cumulated chilling units fall below 1,500 there is a noticeable decrease in flower displays. Mild winters that can trigger such events are already occurring in Kagoshima Prefecture and will likely spread to other areas of Japan in coming years and decades. City managers, tourism officials, and parks departments should begin planning to deal with this impending problem. In some cases, this will involve interplanting Tokyo cherries with alternative cherry species, hybrids, and cultivars with lower winter chilling requirements, or in more extreme cases, this might involve completely replacing Tokyo cherry trees with alternative plants.

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Authors' contributions T.K. conceived of and designed the study, and analyzed data; S.K., Y.K., T.F., and H.I. collected data; A.J.M.-R., and R.B.P. contributed to the drafting and revision of the manuscript.

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Data availability The datasets generated during and/or analysed during the current study are available in Forest Research and Management Organization Repository (https://repository.ffpri.go.jp/).

Declarations

Ethics approval Not applicable.

Consent to participate Not applicable.

Consent for publication Not applicable.

Conflict of interest The authors declare that they have no conflicts of interest.

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