# RESPONSES OF FLORAL TRAITS OF HYSTERANTHOUS TREES TO TEMPERATURE IN SHANGHAI

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**Abstract.** The flower is the most sensitive organ of a plant and responds directly and rapidly to climate warming. Temperature influences floral traits, such as floral size, floral longevity, floral water content, and floral density. There are many hysteranthous tree species in urban forests, and these trees play a key role in landscape beautification and early spring greening. This study aimed to investigate the effects of temperature change on floral characteristics of eight hysteranthous tree species, with a particular focus on the regulatory effects of artificial emasculation and estrogen treatment on flower longevity, including *Prunus serrulata*, *Magnolia denudata*, *Magnolia liliiflora*, *Chaenomeles speciosa*, *Malus halliana*, *Cercis chinensis*, *Syringa oblata var. alba*, and *Syringa oblata*. It was hypothesized that experiments conducted at both elevated and reduced temperatures would demonstrate a substantial impact of temperature on floral characteristics, water content, and longevity. The artificial emasculation treatment was predicted to curtail floral longevity under elevated temperatures, while the estrogen treatment was anticipated to prolong it, particularly under such conditions. The outcomes of this study will contribute to the comprehension of the potential ramifications of climate change on the reproductive ecology of urban greening plants, thereby providing a scientific foundation for urban greening and plant protection initiatives.
**Keywords:** *artificial emasculation, artificial estradiol, climate warming, floral longevity, floral size, urban greening*

**Abbreviations:** HT site, high-temperature site; LT site, low-temperature site

## Introduction

The first publication on flower ecology, authored by Pammel (2018), focused on the relationship between floral traits and environmental factors (Buchmann, 2015; Harder and Barrett, 2006). Subsequently, scientists began investigating the interrelationships between flower development and insect interactions (Fouks and Wagoner, 2019), the evolution of flower coloration (Kellenberger and Glover, 2023), and the reproductive ecology of flowers (Takahashi et al., 2022; Van Doorn and Vojinovic, 1996). These studies have contributed to the rapid advancement of flower ecology (Massetti et al., 2015). In the natural environment, most woody plants unfold their leaves before blooming. However, some trees exhibit hysteranthous behavior, flowering early in the spring before leaf development. The timing of flowering relative to leaf unfolding has important ecological implications for pollination. Abundant flowers that emerge simultaneously are more likely to attract insects, while a lack of leaf cover facilitates wind pollination (Liang et al., 2014).


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Most hysteranthous plants are classified within the Rosaceae, Calycanthaceae, Magnoliaceae, and Oleaceae families. Most woody plants native to temperate climates enter a state of dormancy during the winter months, a process that serves to protect them from unfavorable conditions and to safeguard the delicate leaf and flower buds from the damaging effects of frost (Kumar et al., 2024; Luedeling et al., 2013). It is commonly assumed that dormancy is composed of an endodormancy phase followed by an ecodormancy period. The fulfillment of the chilling and heat requirements of plant buds is instrumental in breaking endodormancy and ecodormancy (Campoy et al., 2011). Nevertheless, in the subtropical zone, an increasing number of hysteranthous trees are becoming dominant in urban forest communities.

Shanghai, a famous international metropolis, is located at the northern edge of the subtropical zone (Li et al., 2018). Its climate is warm and moist, and the zonal climax is subtropical evergreen and deciduous mixed forest. In urban forests in Shanghai, the tree species are mainly local species or their artificial cultivated varieties, and many hysteranthous trees are widely used as ornamentals (Zhang et al., 2016). The demand for landscape aesthetics requires many hysteranthous tree species (trees and shrubs) for their aesthetic value in parks, roadsides, public green spaces and campuses. *Chimonanthus praecox* blooms in early January each year, and then many trees, such as *Magnolia* spp. (including *Magnolia denudata*, city flower of Shanghai, and *Magnolia liliiflora*), *Paulownia tomentosa*, *Amygdalus persica* var. *persica* f. *duplex*, *Prunus cerasifera* f. *atropurpurea*, *Armeniaca mume* and *Prunus serrulata*, flower and fructify one after another from February to April. There are some shrubs or dungarungas, such as *Syringa* spp. (including *Syringa oblate* and its variety *Syringa oblata* var. *alba*), *Malus halliana*, *Cercis chinensis*, and *Litsea cubeba*. There are also some bushes, such as *Jasminum nudiflorum*, *Chaenomeles speciosa*, and *Edgeworthia chrysantha*. In the category of herbs, there are also many hysteranthous plants, such as *Lycoris radiata* var. *radiata* and *Hippeastrum rutilum*, which can be planted in parks and public spaces.

A multitude of biotic factors, including competition, parasitism, allelopathy, and arbuscular mycorrhizal fungi, and abiotic factors such as temperature, moisture, light, soil organic matter, soil moisture, wind speed, and elevations, exert a profound influence on the growth and development of plants and regulate their function (Hyjazie and Sargent, 2024; Ren et al., 2012; Silva et al., 2024; Suni et al., 2023). The direct and indirect effects of temperature on plant physiology and ecology have become a focus in the context of global warming (Zahra et al., 2023). Climate change exerts a profound influence on ecosystems and biodiversity. As a living entity, plants possess the capacity to adapt to temperature change through a suite of mechanisms, including the intuitive flowering response due to the sensitivity of flowers to temperature fluctuations (Hedhly, 2011). Hysteranthous trees, whose flowers are exposed to the environment without the protection of leaves, demonstrate their response to environmental change in an intuitive manner (Liang et al., 2014; Sparks and Carey, 1995).

The development of urban areas and the worsening of air pollution have led to a diversification of ecological factors, which has also altered the timing of biological processes in some organisms (Oksanen and Kontunen-Soppela, 2021; Schoen and Ashman, 1995). The interaction between temperature and precipitation exerts a certain influence on the growth, development, and ecological characteristics of plants (Cong et al., 2024). Furthermore, the abnormal climate exerts a certain influence on the production of flowers (Tun et al., 2021). Low temperatures will result in delayed flowering, while excessive precipitation will impact the flowering and pollination of


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plants (Prevéy, 2020). Floral traits are a direct indicator of the impact of temperature on plants (Sparks et al., 1997; Weigel and Nilsson, 1995). There are notable contrasts between the temperature of the northern and southern sides of high-rise buildings in urban areas (Dimoudi and Nikolopoulou, 2003).

The primary objective of this study is to explore the effects of temperature on floral characteristics, particularly changes in flower lifespan. To this end, eight hysteranthous tree species were selected as research objects, and the effects of temperature changes on the water content, size, and lifespan of flowers were investigated by simulating high and low temperature conditions. A central objective of this study is to examine the impact of artificial emasculation and estrogen treatment on flower lifespan. This investigation aims to elucidate the regulatory mechanisms by which these treatments influence flower lifespan under diverse temperature conditions. The findings of this study will provide a scientific foundation for the implementation of urban greening and plant protection strategies in the face of future climate change. An experiment was conducted to assess the responses of floral traits (e.g., floral size, floral longevity, floral water content, etc.) to varying temperatures. The experiment was conducted on the sunny side and in the shade of the tall buildings on the campus of East China Normal University. The following hypothesis was tested: (1) In the context of HT site, artificial emasculation will result in a substantial reduction in the longevity of flowers. Conversely, under LT site, the longevity of flowers is found to be comparatively enhanced. (2) Estrogen treatment will extend the life of flowers, and this effect will vary at different temperatures, especially under high temperature conditions, the extension effect will be more obvious.

## Materials and methods

### *Target species*

In this study, eight hysteranthous tree species were selected for analysis: *P. serrulata, M. denudata, M. liliiflora, C. speciosa, M. halliana, C. chinensis, S. oblata var. alba, and S. oblata.* The selection of these tree species was primarily based on their representation of Shanghai's urban greening initiatives and their shared growth habits and flowering times. *M. denudata* and *M. liliiflora* and *S. oblata var. alba* and *S. oblata* belong to the same family and genus. In order to ensure the reliability of the study and the consistency of the results, the following criteria were used to select sample trees: (1) Age of the sample: trees ranged from five to 10 years, ensuring that they were in a relatively consistent growth stage. The age selection criteria were based on the premise that these trees exhibited stability in their growth performance at that stage and possessed the capacity to reflect the effects of temperature changes on floral characteristics. (2) Health of samples: The trees selected have been found to be free of any overt signs of pests or growth abnormalities. Furthermore, a thorough examination of the leaves and flowers reveals that they are exhibiting healthy growth characteristics. During the selection process, meticulous attention is paid to the health of the trees, ensuring that they are not affected by pollution or environmental stress. Distribution of sample: The sample trees were distributed uniformly within the designated study area, with both high temperature (HT) and low temperature (LT) sites being selected to ensure sufficient numbers of trees for comparative analysis. The number of sample trees in each site was set at three to ensure valid comparisons in both high and low temperature environments. The spatial distance between trees was sufficiently


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maintained to prevent interference from the growth of adjacent trees. The first flowering time (time of opening of the first flower of a plant), full flowering time (duration of flowering from 20% to 80% for a plant) and out of flowering time (time of withering of all flowers of a plant)) of 8 hysteranthous tree species were recorded by our daily observation, as well as the colors of flowers (*Table 1*).

***Table 1.*** *Flowering phenology of 8 hysteranthous tree species in 2018*

| Tree species | First flowering time | Full blooming period | Out of blooming time | Color of flower |
|---|---|---|---|---|
| *Prunus serrulata* | Feb 27 | Mar 5 – Mar 20 | Mar 28 | Pink |
| *Magnolia denudata* | Feb 26 | Mar 6 – Mar 17 | Mar 30 | White |
| *Magnolia liliiflora* | Mar 13 | Mar 20 – Mar 29 | Apr 11 | Purple |
| *Chaenomeles speciosa* | Mar 11 | Mar 20 – Apr 6 | Apr 18 | Red |
| *Malus halliana* | Mar 18 | Mar 25 – Apr 6 | Apr 13 | Pink |
| *Cercis chinensis* | Mar 19 | Mar 27 – Apr 14 | Apr 26 | Purple |
| *Syringa oblata* var. *alba* | Mar 19 | Mar 30 – Apr 10 | Apr 16 | White |
| *Syringa oblata* | Mar 21 | Apr 3 – Apr 14 | Apr 24 | Purple |

### *Selection of sample plots*

The city of Shanghai (31°14'N, 121°29'E) is situated at the northern edge of the subtropical zone, on the western coast of the Pacific Ocean, at the eastern edge of the Asian continent, and in the vicinity of the Yangtze River estuary. The climate is classified as monsoonal, with four distinct seasons, abundant light (1699.8 h per year), and significant rainfall (931.2 mm per year). The mean annual temperature is 17.4°C (Li et al., 2018; Zhang et al., 2016).

The experiment was conducted on the Minhang campus of East China Normal University. Three HT sites were selected for the experiment on flat ground devoid of surrounding buildings. Three LT sites were selected on the north side of the tall buildings. The heterogeneous environment created by the high buildings on the campus results in significant differences in temperature during the daytime (*Fig. 1*). In each of the HT site and LT site, all eight species of Hysteranthus trees were observed. From February 25 to April 25, the temperatures of the HT and LT sites were recorded with T110 digital probe thermometers (NTC 10k/3435 sensor) at 9:00, 12:00, and 15:00 each day. The average value of the three data points was considered to be the mean temperature of the day (*Fig. 1*). In Shanghai, the temperature continued to rise from February 25, but it was not stable. On rainy days, the temperature decreased. In both HT and LT sites, the temperature differences varied between 2°C and 4°C. On rainy days, there was a slight reduction in temperature, with a minimum difference of 0.3°C observed on March 18. Conversely, on sunny days, there was a larger increase in temperature, with a maximum difference of 16.5°C observed on March 28.

### *Measurement of floral size*

To ensure the accuracy and consistency of the flower size data, a vernier caliper was employed to meticulously measure the petal length and width of each flower. All measurements were conducted by a single observer to circumvent measurement bias arising from operational differences between observers. Prior to the experiment, the


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observer underwent standardized training to ensure that all measurements were performed in accordance with the same standard. Twenty flowers from each sample tree were randomly selected for measurement, and the maximum length and width of the petals were measured and the corresponding values were recorded. To enhance the reliability of the data, the two main dimensions of each flower were measured three times independently, and the average was taken as the final data.

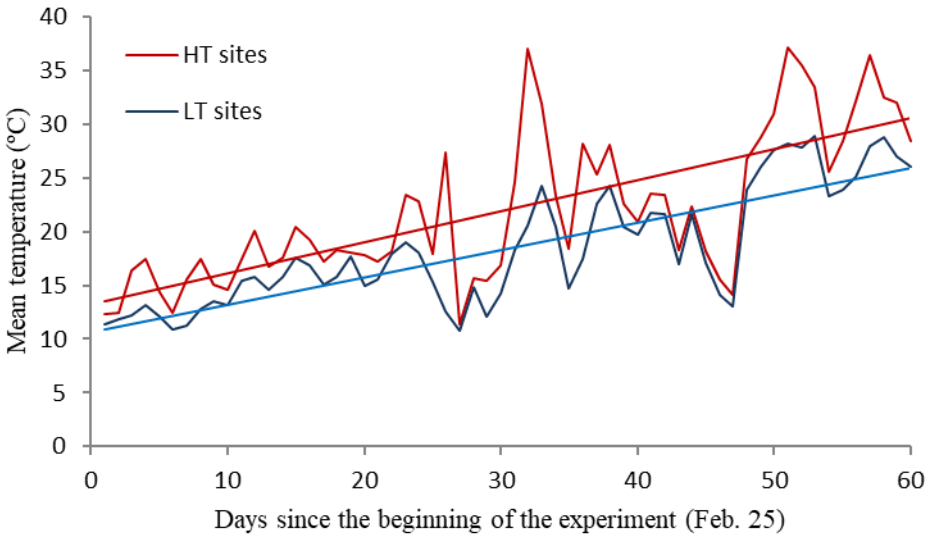


***Figure 1.*** *Variation of the mean temperature in high-temperature (HT) and low-temperature (LT) sites*

A total of 24 trees were randomly selected from the eight species of trees that flower first and leaf-follow. These trees were selected at two different sites, one at HT and the other at a LT sites. Twenty flowers were randomly selected from each sample tree and the maximum length and width of the petals were measured with a vernier caliper to the nearest 0.01 mm at 9 a.m. on each day of the flowering period. The mean and standard error were calculated.

According to length (L) and width (W) of the petal, the petal size (Area, A) could be calculated by the following formula according to area algorithm - parabola method (Feng and Shi, 2005).

$$A = L*W*2/3 \quad \text{(Eq.1)}$$

### *Measurement of floral longevity*

In the artificial de-stigmatization and estrogen treatment experiments of this study, an untreated flowers group was established as a control group to ensure the reliability and interpretability of the experimental results. The experiments consisted of three groups: an artificially demasculinized group (removal of stamens to prevent pollen production), an estrogen-treated group (application of an estrogen solution to the stigma to mimic hormone-regulating effects), and an untreated control group (flowers opened naturally without any intervention). All experiments were conducted under identical environmental conditions, and 20 flowers were randomly selected from each tree species and marked using different colored lines. The longevity of each flower was


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observed and recorded daily. The control group was established to verify the actual effects of desexing and estrogenic treatments on flower longevity, thereby enhancing the transparency of the research methodology and the scientific validity of the results.

Many scholars (Harder and Barrett, 2006; Ren et al., 2012; Zhang and Li, 2009) have different interpretations of the floral longevity. In this study, the floral longevity was defined as the duration (days) from petal opening to petal wilting without consideration for molecular biological factors, such as pollen activity. A random selection of 20 flowers (marked by different colors of threads) of sample trees from the two sites was observed every day to record the floral longevity.

### *Measurement of the water content of flower*

In HT and LT sites, 3 sample trees of each 8 hysteranthous tree species were randomly selected. Twenty flowers as a group (a total of 3 groups for each tree species) were randomly picked from each sample tree, and the fresh weight was recorded ($W_F$). Then, the flowers were oven dried under 80°C for 48 h, and the dry weights were recorded ($W_D$). The flower water content ($C_W$) was calculated by *Equation 2*.

$$C_W = (W_F - W_D)/W_F * 100\% \quad \text{(Eq.2)}$$

### *Treatments of artificial emasculation and artificial estradiol administration*

Many studies have shown that the floral longevity of certain plants is significantly shortened after they have achieved the reproductive function of their males and females. After the pistil is pollinated, the whole flower will soon die. Therefore, the artificial emasculation and artificial estradiol treatment were conducted when flowers was formed, but the flower bud was not fully opened. In HT sites, 3 sample trees of each 8 hysteranthous tree species were randomly selected. Twenty flowers were randomly selected from each sample tree, and the stamens were carefully cut with medical scissors; 20 other flowers were randomly selected from each sample tree, and the stigma from the base were carefully cut with medical scissors; and another 20 flowers were randomly selected from each sample tree for controlled observation treatment. The flowers were marked by different color threads tied close to the branch. All of these flowers were observed daily, and the floral longevity after artificial emasculation and artificial estradiol and control treatments were recorded. Because the stamens of *C. speciosa* are too dense to cut off while leaving other parts of the flower intact, emasculation treatment was not performed for *C. speciosa*. Similarly, because the stigmas of *Syringa* spp. (*S. oblata* var. *alba* and *S. oblata*) are too deep to cut off, artificial estradiol treatment was not performed for *Syringa* spp.

### *Measurement of floral density*

The floral density of this study refers to the number of flowers on the unit length branches. Because *Syringa* spp. (*S. oblata* var. *alba* and *S. oblata*), *Magnolia* spp. (*M. denudata* and *M. liliiflora*), and *P. serrulata* have inflorescences of panicles or umbels, their floral density was not able to be determined by this method. Therefore, only *C. speciosa*, *M. halliana* and *C. chinensis* were selected for determining the response of floral density to temperature. The branch length (L) was measured with a ruler from the last bifurcation point of the branch to the end of the branch; 5 branches were selected in each sample tree; and the number of flowers on the branches were counted (N) during


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the blooming period of the HT and LT sites. The floral density ($D_F$) (individuals per meter) was calculated by using *Equation 3*.

$$D_F = N/L \quad \text{(Eq.3)}$$

### *Statistical analysis*

The differences between the floral traits of HT and LT sites were examined by a t-test ($\alpha = 0.05$). All of the statistical analyses were performed by Microsoft Excel 2010 and SPSS 18.0.

## Results

### *Response of floral size to temperature*

The petal lengths (*Table 2*) were significantly longer for *P. serrulata*, *M. denudata*, *M. liliiflora* and *S. oblata* var. *alba* in HT sites than in LT sites. The petal width (*Table 2*) was significantly longer for *P. serrulata*, *M. liliiflora*, *S. oblata* var. *alba* and *S. oblata* in HT sites than in LT sites. The petal size (*Table 2*) was significantly larger for *P. serrulata*, *M. denudata*, *M. liliiflora*, *S. oblata* var. *alba*, and *S. oblata* in HT sites than in LT sites.

***Table 2.*** *Length (cm), width (cm) and size ($cm^2$) of the petal in two sites*

| Species | Petal length | | Petal width | | Petal size | | Cohen's d |
|---|---|---|---|---|---|---|---|
| | HT sites | LT sites | HT sites | LT sites | HT sites | LT sites | |
| *Prunus serrulata* | 1.43±0.17** | 1.27±0.08 | 1.27±0.11** | 1.14±0.05 | 1.22±0.11** | 0.97±0.22 | 1.20 |
| *Magnolia denudata* | 9.15±2.02** | 6.79±2.61 | 4.86±0.62ns | 4.97±0.74 | 30.13±3.88** | 22.28±4.13 | 1.01 |
| *Magnolia liliiflora* | 11.7±1.76* | 9.98±0.81 | 5.23±1.11* | 4.12±0.95 | 41.18±4.15** | 28.15±5.09 | 1.26 |
| *Chaenomeles speciosa* | 1.76±0.56ns | 1.67±0.39 | 1.64±0.54ns | 1.68±0.53 | 1.89±0.43ns | 1.83±0.53 | 1.09 |
| *Malus halliana* | 1.83±0.07ns | 1.90±0.02 | 1.35±0.05ns | 1.33±0.11 | 1.62±0.06ns | 1.66±0.12 | -1.36 |
| *Cercis chinensis* | 0.90±0.05ns | 0.91±0.06 | 0.60±0.03ns | 0.61±0.03 | 0.37±0.12ns | 0.36±0.08 | -0.18 |
| *Syringa oblata* var. *alba* | 0.66±0.04* | 0.60±0.04 | 0.48±0.04* | 0.43±0.04 | 0.21±0.07* | 0.16±0.09 | 1.50 |
| *Syringa oblata* | 0.67±0.04ns | 0.65±0.05 | 0.53±0.05* | 0.47±0.05 | 0.25±0.08* | 0.20±0.06 | 0.44 |

* Represents significant differences ($P < 0.05$); ** represents extremely significant differences ($P < 0.01$); ns represents no significant differences. Cohen's d values represent the effect size of the difference in petal size between the high temperature (HT) and low temperature (LT) groups. The calculation method uses the ratio of the difference in means between the HT and LT groups to the pooled standard deviation. The Cohen's d values in the table are the effect sizes for petal length, petal width, and petal size for each tree species

### *Response of floral longevity to temperature*

Except for *S. oblata* var. *alba*, all floral longevity in LT sites is significantly higher than that in HT sites (*Fig. 2*).

### *Response of water content of flower to temperature*

The flower is the most tender organ, and the water content of flowers is higher than that of other organs. Except for *M. denudata* and *S. oblata* var. *alba* (white flower), the water content of all flowers in HT sites is significantly lower than that in LT sites (*Fig. 3*).


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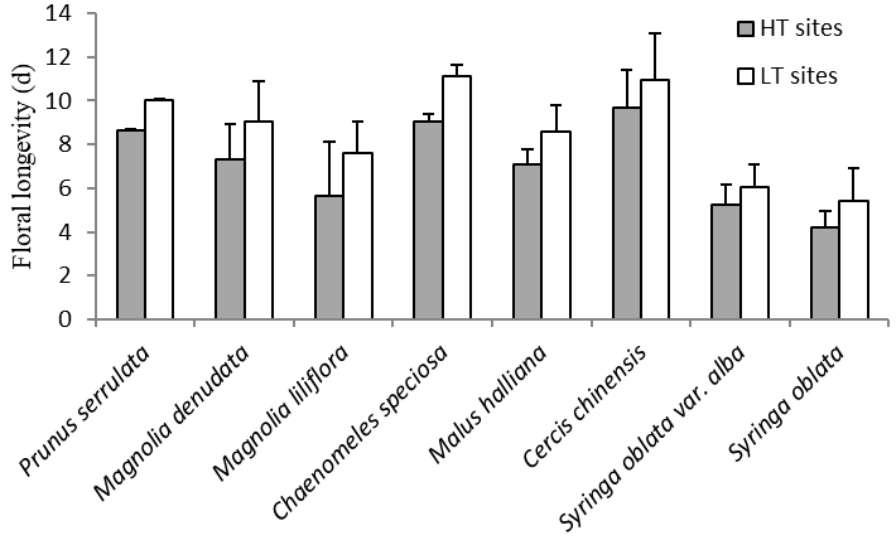


***Figure 2.*** *Floral longevity in two sites (d). * Represents significant differences (P < 0.05); ** represents extremely significant differences (P < 0.01); ns represents no significant differences)*

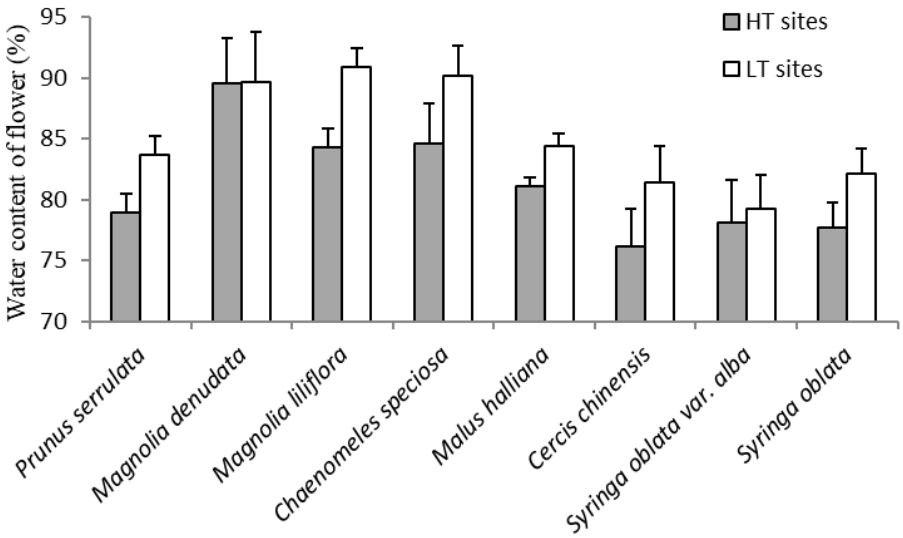


***Figure 3.*** *Water content of flower in two sites (%) (Note: * represents significant differences (P < 0.05); ** represents extremely significant differences (P < 0.01); ns represents no significant differences)*

## Discussion

### *Climate warming and biological reaction*

Climate warming represents a global environmental trend that has resulted in a significant impact on biodiversity. All organisms must adapt to this change (Jakobsen and Olsen, 1994; Wilde and Maxwell, 2018). To ascertain the biological response in the context of climate change, it is possible to artificially simulate the temperature increase or to seek out the heterogeneity caused by the microclimate in urban areas. In our study, the shadow cast by tall buildings results in temperature differences between HT and LT sites, which facilitates our investigation into the effects of climate warming.


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As flower growth and development are closely related to temperature, it can be expected that if different individuals of a plant species grow in habitats with different temperatures for a long period, the size of flowers will differ. This is supported by the findings of Vesprini and Pacini (2005) and Wang et al. (2021). The daytime temperature differences between the two sites in this study were maintained above 2°C, which resulted in significant differences in floral size between the two sites for most plant species examined. A number of studies have indicated that elevated temperatures can stimulate larger sizes and higher flower densities in flowers. This phenomenon may be attributed to the attraction of pollinators, such as insects and birds, to the increased floral abundance. However, this accelerated growth and flowering process may come at the cost of a reduction in flower longevity. For instance, observations in hot environments have revealed that flowers tend to have shorter lifespans, resulting in diminished time available to pollinators, which can potentially compromise pollination success. In certain species, such as *P. serrulata*, the reduction in floral longevity due to elevated temperatures may diminish the opportunity for pollination, consequently affecting the plant's reproductive success.

The environmental factors required by different types of flowers vary considerably. For instance, long-day plants require long-term light. Consequently, in order to investigate the influence of other environmental factors on flowers, it is essential to gain a deeper insight into the molecular mechanisms underlying the floral varieties (Endress, 2001) and the growth and reproduction stages of flowers. On the other hands, the acclimatization of plants is contingent upon the equilibrium of temperature and ancillary environmental factors. In HT site environments, certain species of plants have adapted to harsh conditions through the reduction of flowering cycles and the acceleration of growth and development. However, such adaptations may not be universally beneficial, particularly for species that depend on prolonged floral lifespans to enhance pollination prospects. For instance, *Magnolia denudata* exhibits a substantially extended floral longevity at lower temperatures, which could potentially amplify its pollination success at these lower temperatures. Conversely, elevated temperatures may impede the completion of reproductive cycles in certain species, thereby influencing plant acclimatization processes.

The present study demonstrated that the flowering time of *C. speciosa* was advanced in HT sites. The sole distinction observed was between daytime temperatures. If the diurnal temperature differs, the flowering time is more pronounced (Zhang et al., 2014). The prolongation and advance of flowering time represent a physiological process adjustment that plants undergo in response to and as a means of adapting to environmental changes (Cho et al., 2017; Zhang et al., 2014). This phenomenon, which modifies the flowering time in response to ambient temperature fluctuations, is referred to as the heat-sensing pathway of flowers (Li et al., 2016). The results demonstrate that the longevity of flowers in HT sites is significantly reduced. One possible explanation for this phenomenon is that once the temperature exceeds a certain threshold, C. speciosa initiates the closure process due to excessive temperature stimulation (Vesprini and Pacini, 2005; Weigel and Nilsson, 1995). The mean temperature for flowering in *C. speciosa* was approximately 18°C. When the mean temperature exceeds 22°C, the floral longevity of *C. speciosa* is significantly shortened.

*Syringa spp.* is a species of tree that has been identified as having a number of beneficial characteristics in an urban forest setting (Kronenberg, 1994). These include the ease with which it can be reproduced, its high survival rate, and its value for


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afforestation purposes. *Syringa spp.* has been introduced into Shanghai as a tree species for the purpose of city greening, with certain ecological and economic benefits. In a special study on the phenological characteristics of *Syringa spp.* in the context of climate change, the variation in the leaf phenology of *Syringa spp.* with the increase of temperature was analyzed using space for time substitution. Recent studies (Xiao et al., 2015) have demonstrated that, as a consequence of global warming, the flowering and leaf phenology of *Syringa spp.* in spring has exhibited an advanced trend, while the defoliation in autumn has demonstrated a delayed trend (Marks and Simpson, 2000; Rose et al., 2000).

### *Floral longevity after artificial emasculation and artificial estradiol*

Floral longevity is the duration of a flower to remain open and functional (Ashman and Schoen, 1997; Primack et al., 2009). It can also be defined simply as the time from flowering to withering of a flower. Floral longevity encompasses the biological characteristics of species that are not only influenced by genetic factors but are also contingent upon environmental temperature (Tisserat et al., 1990; Vesprini and Pacini, 2005). Floral longevity may vary according to habitat, breeding system, pollinator class, and sexual expression (Ashman and Schoen, 1994; Endress, 2001; Primack et al., 2009). It is an important functional trait of flowering plants and has very important significance in plant reproductive ecology (Massetti et al., 2015; Primack et al., 2009). A flower's longevity allows for a certain degree of pollinator visitation, which in turn affects the quantity of pollen received on the stigma and the genetic diversity of the plant, as well as the production of flowers' own pollen. Floral longevity represents a crucial factor influencing the success of plant reproduction. Research has demonstrated that flowers of a specific plant will rapidly wither once their male and female reproductive functions have been fulfilled (Weigel and Nilsson, 1995). Following pollination of the pistil, floral longevity is significantly reduced. Artificial emasculation or the administration of artificial estradiol prevent flowers from completing their male or female reproductive function, which will undoubtedly affect floral longevity. The flowers that have been pollinated, regardless of whether or not their pollen has been removed, enter the closed-flower state at a faster rate than the control group. In contrast, the flowers that have had their pollen removed only experience a marginal reduction in longevity compared to the control group (Ai et al., 2007; Putterill et al., 2004). A study on the pollination of *Cymbidium hybridum* revealed that following pollination, all amplification sites exhibited a lower methylation rate and a total methylation level than before pollination (Chen et al., 2008).

The model proposed by Ashman and Schoen (1994) suggests that the realization of female function will result in a reduction in the longevity of floral organs. If artificial estradiol administration is carried out, flowers cannot be successfully pollinated, the female function cannot be achieved, and the floral longevity of a single flower is assumed to be prolonged (Zeng et al., 2004). These predictions were corroborated by the results of the study, which indicated that the floral longevity of the trees was significantly prolonged after the administration of artificial estradiol, with the exception of *P. serrulata* (*Table 3*).

The results of the emasculation treatment were not uniform. Following the application of the emasculation treatment, the floral longevity of *P. serrulata*, *S. oblata var. alba*, and *S. oblata* was found to be significantly reduced (*Table 3*). In contrast, the floral longevity of *M. denudata*, *M. liliiflora*, *M. halliana*, and *C. chinensis* was


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observed to be significantly extended. Putterill et al. (2004) proposed that floral longevity is contingent upon the regulation of biotic and abiotic factors and species properties within a given region. In addition to the influence of pollination, sudden alterations in temperature, illumination, precipitation, and wind may also impact floral longevity. Furthermore, in the process of artificial emasculation and artificial estradiol administration, we observed that the experimental equipment and techniques employed in the process of cutting the stigma were more or less likely to poke and injure the petals. This treatment was found to accelerate the decline of injured petals. All eight tree species included in the experiments were entomophilous, with *C. speciosa* exhibiting monoecious and self-incompatible characteristics (Harder and Barrett, 2006). According to the aforementioned characteristics, it is possible to enhance the experimental methods and impede the fertilization process through the gauze netting treatment, which isolates the pollinating insects, if one is only concerned with the functions of male or female.

***Table 3.*** *Floral longevity (d) after artificial emasculation and artificial estradiol administration in two sites*

| Tree species | Artificial emasculation | Artificial estradiol | Control |
|---|---|---|---|
| *Prunus serrulata* | $7.06 \pm 0.87^{**}$ | $6.97 \pm 0.61^{**}$ | $9.71 \pm 1.06$ |
| *Magnolia denudata* | $10.56 \pm 2.12^{*}$ | $11.42 \pm 2.45^{**}$ | $8.43 \pm 1.35$ |
| *Magnolia liliiflora* | $8.52 \pm 1.21^{**}$ | $9.22 \pm 1.46^{**}$ | $6.75 \pm 1.89$ |
| *Chaenomeles speciosa* | / | $9.62 \pm 0.34^{*}$ | $8.92 \pm 0.27$ |
| *Malus halliana* | $8.72 \pm 1.65^{**}$ | $8.17 \pm 1.32^{**}$ | $6.46 \pm 1.41$ |
| *Cercis chinensis* | $11.05 \pm 2.05^{*}$ | $11.74 \pm 2.31^{*}$ | $9.70 \pm 1.71$ |
| *Syringa oblata* var. *alba* | $4.10 \pm 0.97^{**}$ | / | $6.03 \pm 1.08$ |
| *Syringa oblata* | $3.95 \pm 1.10^{**}$ | / | $5.43 \pm 1.47$ |

* Represents significant differences ($P < 0.05$); ** represents extremely significant differences ($P < 0.01$)

### *Relationship between the floral density and temperature*

Floral density is one of the biological characteristics of plants and is closely related to environmental conditions (Zieslin and Khayat, 1990). The high floral density is beneficial for landscape aesthetics. However, the production of flowers requires a significant amount of energy, and thus temperature, light, and other environmental conditions will influence the plant's floral density (Zhang et al., 2016). There are numerous methods for measuring floral density, including the number of flowers per unit area and the number of flowers per unit volume (Zhang and Taylor, 2011). The floral density of this study is defined as the number of flowers on a branch of a given length. Consequently, trees may exhibit a greater propensity to develop flowers in HT sites, while the floral density is significantly diminished at LT sites (*Fig. 4*).

The number of flowers is influenced not only by environmental factors but also by traits of the tree itself. In the case of *C. chinensis*, which is cauliflorous, the thickness and age of the branch have been found to influence the number of flowers. Consequently, if the objective is to determine floral density with precision, it is necessary to select branches of the same age (in this study, two-year-old branches) for


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statistical analysis. Alternatively, it is advisable to establish a relationship between branch thickness and the number of flowers in advance.

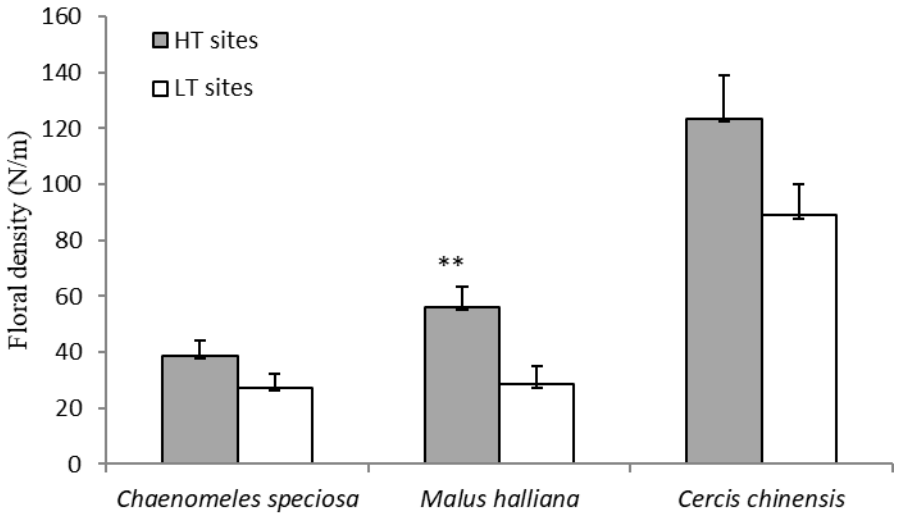


***Figure 4.*** *Floral density in two sites (N/m). * Represents significant differences (P < 0.05); ** represents extremely significant differences (P < 0.01))*

### *Management implications*

Color of flower is one of the important ecological characteristics, which is closely related to genetic factors (Narbona et al., 2021; Zhang and Li, 2009). In this study, flower water content is related with flower color, which might be caused by the effect of solar radiation on different color. In LT sites, the light intensity is relative weak, and the petal is not easy to lose water, so the water content is high. Interestingly, there is no significantly difference of the water content of white flowers (*M. denudata* and *S. oblata* var. *alba*) in the two sites while the water content of the dark (pink to purple) flower (other 6 tree species) is significantly lower in HT sites than in LT sites (*Fig. 3*). Whether flower color and longevity are related is not determined by our research, but the question will be for follow-up study in the future.

The temperature difference of HT sites and LT sites maintains a certain value during daytime in our research (*Fig. 1*), but at night there is only a minor difference in temperature between these two kinds of sites. Shanghai is a highly urbanized metropolis, and, considering the urbanization gradient (urban center-suburb-countryside), real-time monitoring to measure the night temperature may obtain further results (Sparks et al., 2000; Yin et al., 1996).

The results demonstrate that the discrepancy in temperature between sampling sites within the same region can influence the floral dimensions, longevity, and water content of hysteranthous tree species. This finding can assist managers in adjusting the flowering time by modifying the planting position and planting temperature of the plants in order to enhance the aesthetic appeal of the city and promote its vitality. The study of floral traits has been shown to have positive effects on landscape construction and landscape reconstruction (Zhang et al., 2014). In the context of contemporary urban eco-economic construction, the development of gardens is progressing towards an open, integrated, and sustainable trajectory (Buccolieri et al., 2018; Schindler et al., 2018). Landscape construction must be continuously enhanced to accommodate climate change


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and the urban heat island effect. This necessitates a more profound comprehension of plant location, planting time, and environmental control (Bell et al., 2003; Feltynowski et al., 2018). The future green city will adjust its urban vegetation structure and location according to the ecological characteristics of plants (Arnberger and Eder, 2012; Zhang et al., 2014). Conversely, during the construction of urban areas, builders may also consider the sustainable development of urban landscapes. This may entail modifying the density of buildings and calculating the distribution and influence of heat release in order to reduce the discomfort caused by heat island effects and create healthy green spaces (Cui et al., 2009).

The value of many plants in the natural world lies in the ornamental value of their flowers (Altman et al., 2022). Consequently, pollination and fruit may not be necessary for the survival of these plants. The application of artificial emasculation and estradiol administration may result in an extension of floral longevity, thereby enhancing the ornamental value of flowers (Van Doorn and Vojinovic, 1996).

### *Management recommendations*

This study provides an exhaustive analysis of the disparities in floral characteristics exhibited by hysteranthous tree species under varying thermal conditions. Drawing upon the findings of this study, we are able to formulate the following recommendations for urban planners and landscape architects, with the objective of optimizing urban greenery and enhancing ecological resilience.

Firstly, it is evident that high and low temperatures significantly affect the floral characteristics of early-flowering tree species, especially in terms of flower longevity and petal size. In order to maximize pollination success and plant adaptation, urban greening planners should select appropriate tree species according to the microclimatic conditions of different regions. For instance, in hot areas, species that flower quickly and can complete the pollination process within a short flowering period, such as *P. serrulata* and *M. liliiflora*, are recommended, while in cooler environments, selecting species that have longer flower longevity and can provide a longer pollination period, such as *M. halliana* and *S. oblata*, will help improve pollination success and plant reproduction.

Secondly, the urban heat island effect leads to elevated temperatures in urban centers, which has a differential effect on plant growth, particularly in large cities. To address this challenge, landscape architects can optimize the planting locations of early flowering tree species according to the distribution of the heat island effect. Higher temperature areas can be planted with heat-tolerant and adaptable tree species, such as *Cercis chinensis*, which not only grow at higher temperatures but also help to mitigate the heat island effect. Concurrently, the strategic planting of long-flowering tree species in temperate regions is instrumental in preserving ecological equilibrium between high and low temperatures, thereby enhancing the diversity and ecological functionality of urban green spaces.

Finally, as climate change intensifies, enhancing the ecological resilience of urban green spaces becomes particularly important. By optimizing the selection and placement of tree species, urban greening can be better adapted to extreme climatic events (e.g., high temperatures, droughts and heavy rainfall). It is recommended to adopt the principle of diversity in greening design by planting a variety of hysteranthous tree species in one area to ensure that adaptable tree species are available under different climatic conditions. This will not only improve the stability of the ecosystem, but also provide richer resources for pollinators and contribute to the maintenance of biodiversity.


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## Conclusion

In this study, we conducted a systematic investigation of the effects of temperature on floral traits in eight tree species at the pre-flowering and post-foliar stages. Our findings indicate that petal length and width, as well as flower longevity, were significantly increased in HT site environments. Specifically, high temperatures promoted cell elongation and division of petals, resulting in larger petals. Additionally, the protective effect of high temperatures on floral tissues prolonged flower longevity. These results are consistent with existing studies and further confirm the important impact of climate change on plant flowering characteristics.

This study addresses a gap in the existing literature by examining the response of flowering traits of pre-flowering and post-foliar tree species under different temperature conditions. It also provides new perspectives for understanding plant adaptation to climate change during urbanization. However, the study is limited by a small sample size and a single study site. To enhance the generalizability of the findings, future studies should expand the sample size and study area.

In order to further advance this research area, future research could focus on the following directions: first, exploring more variations in floral characteristics, such as flower color, pollen quality and nectar content, in order to comprehensively understand the effects of temperature changes on plant reproduction. Secondly, the capacity of plants to adapt to diverse climate zones should be investigated, with a particular focus on the performance of hysteranthous species in different climates. Additionally, the impact of urbanization on plant diversity should be analyzed, with the optimization of urban green spaces to enhance ecological functions being a key objective. The interrelationship between plants and pollinators should be delved into, and the relationship between plants and pollinators should be examined. Finally, the impact of urbanization on plant diversity and the optimization of urban green spaces to improve ecological functions will be studied. Through these future research directions, we will not only be able to gain a deeper understanding of how plants adapt to different climatic conditions, but also provide a more comprehensive scientific basis for urban ecological restoration and climate change adaptation strategies. Ongoing research will help optimize the design of urban greening and enhance the ecological resilience and biodiversity of urban green spaces to meet the growing challenges of climate change.

In conclusion, this study provides valuable experimental evidence in the fields of botany, urban ecology, and climate change, revealing the important role of temperature as a key environmental factor in plant growth and reproduction. These findings serve as important guidelines for urban greening and plant conservation, helping to develop more effective urban ecological management strategies.

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