植物生态学报 2022, **46** (12): 1573-1584
*Chinese Journal of Plant Ecology*
DOI: 10.17521/cjpe.2022.0036
http://www.plant-ecology.com

# 暖温带森林木本植物展叶始期对低温和热量累积变化的响应

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**摘 要** 为了解气候急剧变暖造成的冬春季节的低温和热量积累变化对自然环境中植物春季物候产生的影响，利用北京东灵山暖温带森林25种木本植物2003–2019年的展叶始期数据，采用偏最小二乘回归、动力学模型和生长度小时模型等方法模拟了各物种展叶始期所需的低温和热量累积量，并应用线性回归分析了展叶始期对低温和热量累积变化的响应，利用单因素方差分析对比了灌木和乔木展叶始期及其对低温和热量累积变化响应的差异。结果显示: (1) 25种木本植物展叶始期的平均低温和热量累积期分别在10月6日至次年3月17日和1月21日至4月26日之间，平均低温和热量累积量分别为66.16冷激份额(CP)和2 933.12生长度小时(GDH)。(2)展叶始期对低温和热量累积变化的响应敏感度均值分别为每10 CP延迟3.54 d和每1 000 GDH延迟7.09 d，各有2个和23个物种显著，说明暖温带木本植物展叶始期主要受热量累积的影响。(3)灌木的展叶始期比乔木早3.87 d，热量累积比乔木少543.56 GDH，且展叶始期越早的植物，所需热量累积也越少，可能与其采取机会主义生存策略有关。(4)灌木和乔木展叶始期对热量累积的响应敏感度分别为每1 000 GDH延迟8.10和延迟6.13 d，两者的差异呈边缘显著。这意味着随着气候变暖，灌木展叶始期提前的速度可能比乔木更快。

**关键词** 植物物候；展叶始期；气候变暖；低温累积；热量累积；暖温带森林；木本植物

于海英，杨莉琳，付素静，张志敏，姚琦馥 (2022). 暖温带森林木本植物展叶始期对低温和热量累积变化的响应. 植物生态学报，46，1573-1584. DOI: 10.17521/cjpe.2022.0036

## Response of leaf-unfolding dates of woody species to variation of chilling and heat accumulation in warm temperate forests

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**Abstract**

***Aims*** In recent decades, the rapid climate warming had affected chilling and heat accumulation during winter and spring and made profound changes in plant spring phenology. To date, most related studies focused on either a range of species grown in various gardens or on experimental research, which may be not necessarily applicable to real-world conditions.

***Methods*** By using leaf-unfolding data of 25 woody species during 2003–2019 in warm temperate forests of the Dongling Mountain, Beijing, we simulated the daily chilling and heat accumulation by applying partial least square regression, dynamic model and growing degree hour model. We then analyzed the response of leaf-unfolding dates to the variation of chilling and heat accumulation by linear regressions. Finally, the differences of leaf-unfolding dates and their responses to the variation of chilling and heat accumulation between shrubs and trees were compared by ANOVA.

***Important findings*** The chilling periods of 25 woody species were from October 6 to March 17 of next year, with the forcing periods from January 21 to April 26. The corresponding chilling and heat accumulation were 66.16 chill portion (CP) and 2 933.12 growing degree hour (GDH) on average. The leaf-unfolding dates were delayed 3.54 d per 10 CP and 7.09 d per 1 000 GDH as the chilling and heat accumulation changed, with 2 and

收稿日期Received: 2022-01-21 接受日期Accepted: 2022-02-23

基金项目：国家自然科学基金(32160287)、贵州省普通高等学校科技拔尖人才支持计划项目(黔教合KY字[2017]088)和贵州省科技计划项目(黔科合基础-ZK[2022]一般560)。Supported by the National Natural Science Foundation of China (32160287), the Talent Support Program for Common Colleges and Universities in Guizhou Province (Qian Education NO. [2017]088), and the Science and Technology Plan Project of Guizhou Province (Qian Science Basic-ZK[2022] General 560).

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23 species significant, respectively. This indicated that leaf-unfolding dates of woody species in warm temperate zone were mainly affected by heat accumulation. Moreover, the leaf-unfolding dates of shrubs were 3.87 d earlier and required 543.56 GDH less heat than trees. Species leafed earlier required less heat accumulation than those leafed out later, presumably due to the opportunistic strategy adopted by shrubs and early-leafing species. Sensitivity of leaf-unfolding dates of shrubs to heat accumulation (delayed 8.10 d per 1 000 GDH) existed marginally significant difference with trees (delayed 6.13 d per 1 000 GDH), which implied that leaf-unfolding dates of shrubs might advance faster than trees as global warming progresses.

**Key words** plant phenology; leaf-unfolding date; climate warming; chilling accumulation; heat accumulation; warm temperate forests; woody species

Yu HY, Yang LL, Fu SJ, Zhang ZM, Yao QF (2022). Response of leaf-unfolding dates of woody species to variation of chilling and heat accumulation in warm temperate forests. *Chinese Journal of Plant Ecology*, 46, 1573-1584. DOI: 10.17521/cjpe.2022.0036

近百年来, 全球平均气温升高了0.85 ℃ (IPCC, 2013), 而我国陆地的增温速率则高于全球平均值(《第三次气候变化国家评估报告》编写委员会, 2015)。植物物候在气候变暖的影响下发生了显著的变化(Keeling *et al*., 1996)。而物候变化会进一步改变物种间的相互作用和生态系统功能(Tylianakis *et al*., 2008), 引起生物圈与大气圈碳、水循环及能量平衡的改变, 甚至影响全球气候系统(Richardson *et al*., 2013)。因此, 准确理解植物物候对气候变化的响应对应对气候变化和预测未来物种及生态系统的改变具有重要意义。

温度被广泛认为是影响植物春季物候的主要因素(Chuine & Cour, 1999; Menzel & Fabian, 1999; Piao *et al*., 2019), 尤其是在北半球中高纬度地区(Hänninen, 2016)。在温带, 秋季低温会引起植物的应激反应使之进入休眠状态(Delpierre *et al*., 2016), 这是植物在不利环境下的自我保护策略(Jones *et al*., 2013)。此时植物会先后经历生理和生态两个休眠阶段(Lang, 1987)。在生理休眠阶段, 植物需要积累一定的低温才能解除休眠, 以防止早熟芽在秋冬季节的温暖期内因提前生长而在气温降低时遭受损害(Hänninen, 2016)。在生态休眠阶段, 植物则需满足一定的热量需求来促进分生组织的发育(Hänninen, 2016), 从而促使春季物候发生。这意味着冬春季节气温的上升可能会导致低温累积不足, 从而使芽的生长减缓甚至导致萌芽期延迟, 但同时也会促进热量的累积从而加速芽的生长并使植物提前发芽, 因此, 植物春季物候可能受低温和热量累积期温度变化的共同影响(Chen *et al*., 2017)。

在温带, 许多基于物候模型的研究显示不包含低温需求的模型比同时包含低温和热量需求的模型效果更好(Chuine, 2000; Morin *et al*., 2009; Vitasse *et al*., 2011; Xu & Chen, 2013; Martinez-Lüscher *et al*., 2017)。大部分温带地区低温累积量可能仍能满足植物解除休眠的需要(Chen *et al*., 2017), 暂时不会成为影响春季物候的限制因子。但也有研究发现秋冬季节温度上升使低温累积减少, 从而使一些物种的春季物候推迟, 如法国阿尔卑斯山的几种乔木(Asse *et al*., 2018)和喜马拉雅山区的部分杜鹃(*Rhododendron*)(Hart *et al*., 2014)等。尤其是具有高需冷量的物种, 可能会在较温暖的冬季积累不到足够的低温(Cannell & Smith, 1986; Roberts *et al*., 2015), 低温累积量的减少可能会进一步减缓甚至逆转热量累积带来的春季物候提前(Ford *et al*., 2016), 从而推迟春季物候。目前相关研究虽然较多, 但多利用园中植物或实验方法进行分析(Donnelly & Yu, 2021), 且一般针对的物种较少(Rollinson & Kaye, 2012), 不能完全代表真实的自然环境。因此, 探讨自然生境下植物的春季物候对气候变暖的响应具有非常重要的意义。

不同生活型植物(如灌木和乔木)的物候对气候变暖的响应具有差异性。研究发现灌木比优势乔木展叶早(Panchen, 2014; Donnelly & Yu, 2021)。这种差异可能与植物的演替过程(Lechowicz, 1984)和生存策略(Chuine & Cour, 1999)有关。通常来说, 灌木属于先锋种, 乔木属于顶极种(Chuine & Cour, 1999)。对德国36种木本植物的实验研究表明, 先锋种比顶极种具有更低的低温和热量需求(Laube *et al*., 2014)。而对中国东部白栎(*Quercus fabri*)林48种木本植物的野外调查则显示本地灌木和优势乔木的展叶时间没有显著差异(Sun *et al*., 2006)。此外, 在欧洲的实验研究还发现先锋种对气温上升的响应可能比顶极种更强烈(Caffarra & Donnelly, 2011)。但对美国宾夕法尼亚州130种植物的研究显示大乔木对

气温升高比较敏感, 而灌木则不受影响, 灌木受光周期的影响更多(Rollinson & Kaye, 2012)。可见, 由于物种类别、所处环境和研究手段等的不同, 对灌木和乔木春季物候对气候变暖响应方式的差异还存在一定争议。

据此, 本研究利用北京东灵山暖温带森林中25种木本植物2003–2019年的展叶始期数据, 采用最小二乘(PLS)回归、动力学模型和生长度小时模型模拟各物种展叶始期的低温和热量累积量, 分析展叶始期对气温及低温和热量累积变化的响应, 并对比不同生活型木本植物(乔木和灌木)之间的差异, 以增进对自然条件下暖温带植物春季物候对气候变暖响应机制的理解, 为应对气候变化对该区域生态系统的影响提供理论依据。

## 1 材料和方法

### 1.1 研究点概况

中国科学院北京森林生态系统定位研究站(简称北京森林站)位于北京市门头沟区东灵山, 115.43° E, 39.97° N, 海拔1 263 m。研究点属于暖温带半湿润大陆性季风气候, 冬季寒冷干燥, 夏季温暖湿润。年平均气温、最高和最低气温平均值分别为5.37、12.14和0.61 ℃, 最热月为7月, 最冷月为1月; 年降水量490.63 mm, 主要集中在6–8月。因时间跨度较短, 2002–2019年北京森林站的年平均气温并未表现出显著的增温趋势($p$ = 0.08), 但离研究点最近的怀来气象站年平均气温在过去的65年里以0.03 ℃·$a^{-1}$的速度上升(图1)。说明研究点气候总体呈变暖趋势。调查样地的植被为暖温带落叶阔叶林和人工常绿针叶林。落叶阔叶林以辽东栎(*Quercus wutaishensea*)为主, 在山沟等比较湿润的地区有椴(*Tilia* spp.)、胡桃楸(*Juglans mandshurica*)和黑桦(*Betula dahurica*)等其他树种。在人工常绿针叶林中, 乔木层的优势种为油松(*Pinus tabuliformis*), 灌木层主要为土庄绣线菊(*Spiraea pubescens*)。

### 1.2 物候和气象数据

物候资料为2003–2019年的展叶始期数据, 来源于国家生态科学数据中心(http://www.cnern.org.cn)。为保证有足够的样本量, 选择具有10年以上观测记录的植物作为研究对象, 共包括25种木本植物, 其中乔木13种, 灌木12种(表1)。展叶最早的是巧玲花(*Syringa pubescens*)(4月19日), 最晚的是油松(5月9日), 所有物种的平均展叶始期为4月27日, 平均观测年数为14年。

气象数据为北京森林站和河北省怀来县气象站2002–2019年的日平均、最高和最低气温(℃)数据。北京森林站气象数据来自国家生态科学数据中心, 为北京森林站在东灵山样地设置的气象站所收集。怀来县气象站位于东灵山以北54.6 km处, 是离东灵山最近的国家级气象站, 其数据可从国家气象科学数据中心(http://data.cma.cn/)获取。北京森林站气温数据有部分缺失, 缺失比例为6.88%–8.00%, 而该站数据与怀来县相应数据的线性回归拟合度很高(决定系数($R^2$)为0.96–0.98), 因此采用怀来县的气温数据对缺失数据进行插补。为了获取物候模型所需的逐时数据, 我们根据前人的方法采用日最低和最高气温值建立了日气温曲线, 该方法假设从日出至日落的气温遵循正弦曲线的变化规律, 而夜晚气温遵循对数曲线变化的规律, 计算公式见参考文献(Linvill, 1989, 1990)。

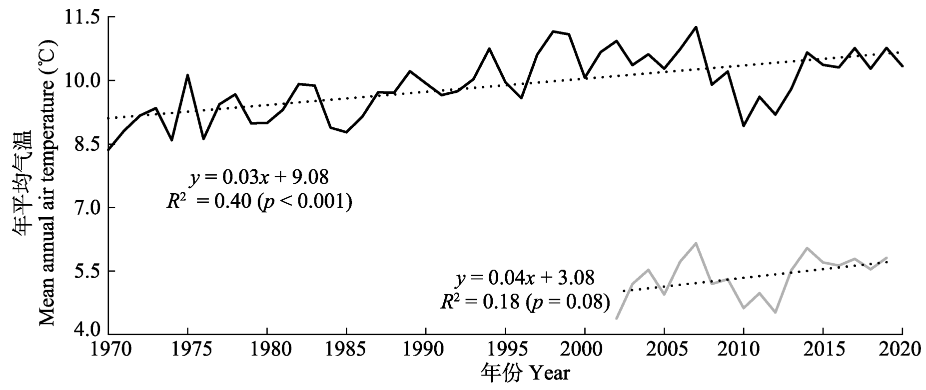


**图1** 1955–2020年怀来气象站(黑色曲线)和2002–2019年北京森林站(灰色曲线)年平均气温年际变化趋势。
**Fig. 1** Interannual change trend of mean annual temperature of the Huailai Meteorological Station during 1955–2020 (black curve) and Beijing Forestry Ecosystem Research Station during 2002–2019 (grey curve).

DOI: 10.17521/cjpe.2022.0036

**表1** 研究所选物种及相关信息
**Table 1** List of the species used in the study and related information

| 物种 Species | 生活型 Life form | 平均展叶始期 Mean leaf-unfolding date (month-day) | 最早展叶始期 The earliest leaf-unfolding date (month-day) | 最晚展叶始期 The latest leaf-unfolding date (month-day) | 观测年数 Number of observed years |
|---|---|---|---|---|---|
| 白桦 *Betula platyphylla* | 乔木 Tree | 05-04 | 04-27 | 05-17 | 15 |
| 大花溲疏 *Deutzia grandiflora* | 灌木 Shrub | 04-28 | 04-11 | 05-17 | 15 |
| 蒿柳 *Salix schwerinii* | 灌木 Shrub | 04-23 | 04-10 | 05-10 | 15 |
| 黑桦 *Betula dahurica* | 乔木 Tree | 05-04 | 04-25 | 05-13 | 11 |
| 胡桃楸 *Juglans mandshurica* | 乔木 Tree | 05-02 | 04-20 | 05-15 | 11 |
| 花曲柳 *Fraxinus chinensis* subsp. *rhynchophylla* | 乔木 Tree | 05-02 | 04-21 | 05-18 | 11 |
| 华北落叶松 *Larix gmelinii* var. *principis-rupprechtii* | 乔木 Tree | 04-22 | 04-09 | 05-08 | 11 |
| 金花忍冬 *Lonicera chrysantha* | 灌木 Shrub | 04-25 | 04-10 | 05-11 | 14 |
| 辽东栎 *Quercus wutaishansea* | 乔木 Tree | 05-03 | 04-20 | 05-15 | 16 |
| 裂叶榆 *Ulmus laciniata* | 乔木 Tree | 04-27 | 04-15 | 05-09 | 15 |
| 六道木 *Zabelia biflora* | 灌木 Shrub | 04-27 | 04-13 | 05-09 | 16 |
| 毛榛 *Corylus mandshurica* | 灌木 Shrub | 04-27 | 04-20 | 05-05 | 14 |
| 蒙椴 *Tilia mongolica* | 乔木 Tree | 04-30 | 04-17 | 05-08 | 15 |
| 巧玲花 *Syringa pubescens* | 灌木 Shrub | 04-19 | 04-03 | 05-06 | 11 |
| 青杨 *Populus cathayana* | 乔木 Tree | 04-27 | 04-12 | 05-07 | 15 |
| 山桃 *Prunus davidiana* | 乔木 Tree | 04-21 | 04-06 | 05-14 | 16 |
| 山杏 *Prunus sibirica* | 乔木 Tree | 04-26 | 04-10 | 05-10 | 16 |
| 土庄绣线菊 *Spiraea pubescens* | 灌木 Shrub | 04-28 | 04-18 | 05-14 | 11 |
| 卫矛 *Euonymus alatus* | 灌木 Shrub | 04-22 | 04-04 | 05-11 | 14 |
| 五角枫 *Acer pictum* subsp. *mono* | 乔木 Tree | 04-27 | 04-16 | 05-08 | 14 |
| 小花溲疏 *Deutzia parviflora* | 灌木 Shrub | 04-29 | 04-11 | 05-17 | 16 |
| 小叶鼠李 *Rhamnus parvifolia* | 灌木 Shrub | 04-21 | 04-09 | 05-15 | 15 |
| 迎红杜鹃 *Rhododendron mucronulatum* | 灌木 Shrub | 04-27 | 04-15 | 05-11 | 15 |
| 油松 *Pinus tabuliformis* | 乔木 Tree | 05-09 | 04-22 | 05-30 | 15 |
| 照山白 *Rhododendron micranthum* | 灌木 Shrub | 05-02 | 04-15 | 05-22 | 15 |

### 1.3 研究方法

动力学模型因具有严格的理论架构和强大的解释物候观测值的能力，在不同环境下的表现均优于其他模型(Campoy *et al*., 2011b; Luedeling & Gassner, 2012; Guo *et al*., 2015)。因此，本研究运用动力学模型，采用逐时气温数据估算了北京森林站2002–2019年的日低温和热量累积量。动力学模型假设低温的累积包括两步：首先低温会促进一种冷激相关的中介物质的形成，其次中等温度将此中介物质转化为永久的冷激份额(CP)，然后不断累积冷激份额一直到休眠期结束(Guo *et al*., 2019)。动力学模型的具体计算公式可见参考文献(Luedeling & Brown, 2011)。热量累积采用应用广泛的生长度小时(GDH)模型估算，计算公式见参考文献(Anderson *et al*., 1986; Guo *et al*., 2019)。动力学模型和生长度小时模型的模拟均应用R软件中的“chillR”程序包完成。

在应用物候模型时，一般是根据经验来设置低温或热量累积的起止日期或是从低温积累的第一天开始计算(Harrington *et al*., 2010; Luedeling & Brown, 2011; Harrington & Gould, 2015)。而PLS回归可以较清晰地识别出低温和热量的累积期，并已成功应用在前人的研究中(Luedeling & Gassner, 2012; Guo *et al*., 2015, 2019; Benmoussa *et al*., 2017; Martínez-Lüscher *et al*., 2017; 刘璐等, 2020)。此外，PLS回归也适用在自变量超出样本量的情况，并可通过建立潜在因子(类似主成分)解决自变量高度相

关和模型过度拟合问题(Guo *et al*., 2015), 在自变量较多、相关度较高的情况下具有较强的优势。因此, 本研究采用PLS回归识别展叶始期的低温和热量累积期。

为了增强识别效果, 采用日低温和热量累积量的11天(即该日的前5天及后5天)滑动平均值来代替日值(Luedeling & Gassner, 2012)。将25种木本植物的展叶始期分别与其前一年的日低温和热量累积量的滑动平均值建立PLS回归, 可得到变量投影重要性(VIP)和标准化模型系数2个主要结果。VIP值反映低温和热量累积变化对展叶始期影响的显著性, 一般以0.8作为判定标准(Wold *et al*., 2001), 即VIP ≥ 0.8时, 模型系数显著, 反之则不显著。标准化模型系数表示影响的方向及强度, 系数为负表明低温或热量累积量增加会使展叶始期提前, 系数为正则表明会使展叶始期推迟。理论上讲, 在低温和热量累积期内, 较高的低温和热量累积会使树木展叶始期提前, 这些负相关关系可以被PLS识别出来。因此, 把PLS的回归结果中具有高VIP值(≥0.8)和负模型系数的连续时段认为是低温或热量的累积期(Luedeling *et al*., 2013; Martinez-Lüscher *et al*., 2017)。累积期内所积累的低温和热量则称为低温和热量累积量, 即植物的低温和积温需求。

为了解气候变暖对展叶始期的影响, 本研究利用线性回归分析了展叶始期与低温和热量累积期内平均气温及低温和热量累积量的关系。此外, 还利用单因素方差分析对比了灌木和乔木展叶始期、低温和热量累积及展叶始期对热量累积变化响应敏感度等的差异。

## 2 结果和分析

### 2.1 25种木本植物展叶始期的低温和热量累积时段及总量

基于PLS回归的VIP值和标准化系数, 可以较清晰地识别出暖温带森林木本植物展叶始期的低温和热量累积期(图2)。蒙椴(*Tilia mongolica*)和大花溲疏(*Deutzia grandiflora*)的低温累积期分别在10月26日至次年3月23日和9月30日至次年3月23日之间, 热量累积期分别在1月23日至4月29日和1月4日至4月27日之间。这些时段内大部分模型系数为负且

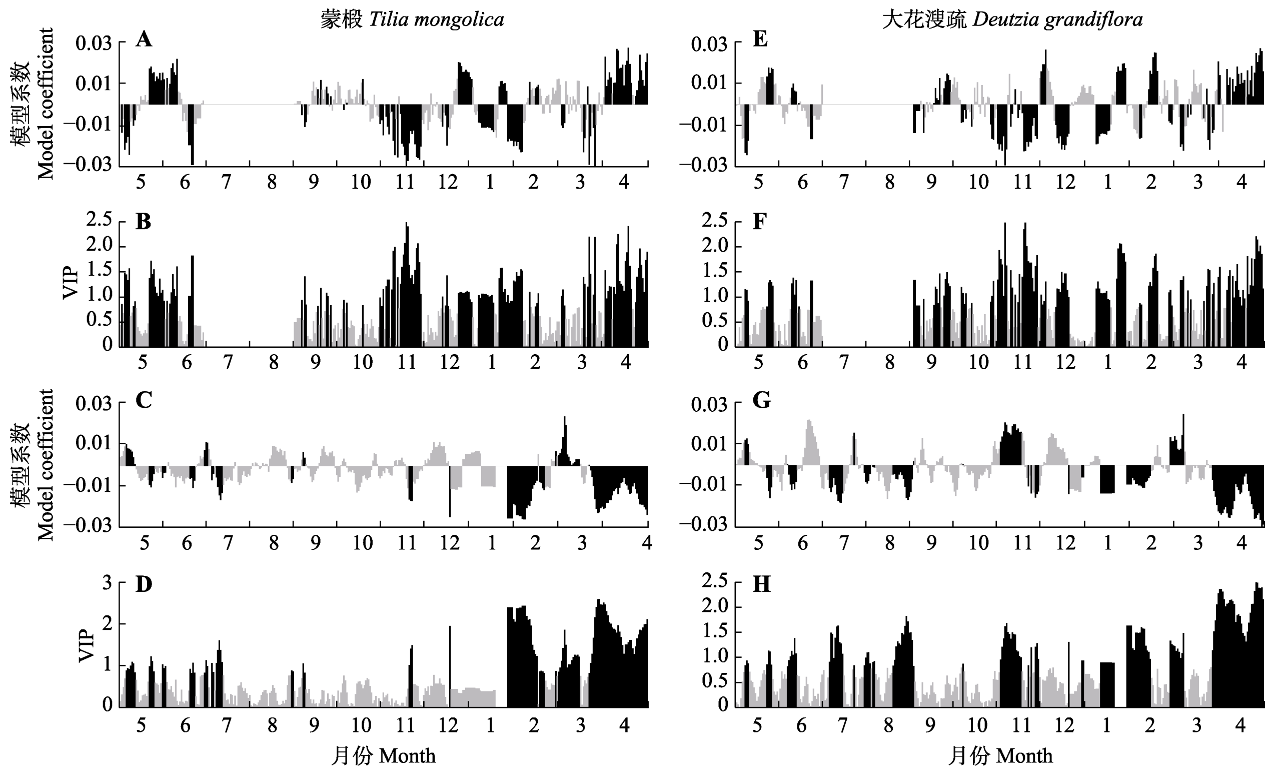


**图2** 东灵山蒙椴和大花溲疏展叶始期与日低温(**A, B, E, F**)和热量累积量(**C, D, G, H**)的偏最小二乘回归分析。图中黑色代表系数显著(变量投影重要性(VIP) ≥0.8)。

**Fig. 2** Results of Partial Least Squares regression between daily chilling (**A, B, E, F**) and heat accumulation (**C, D, G, H**) and leaf-unfolding dates of *Tilia mongolica* and *Deutzia grandiflora* in Dongling Mountain. Black bars indicate the coefficients are significant (variable importance in the projection (VIP) ≥0.8).

DOI: 10.17521/cjpe.2022.0036

VIP值多大于等于0.8, 说明该时段内低温或热量累积增加会使展叶始期提前。虽然其中有的系数为正或者VIP值小于0.8, 但时间较为短暂, 因此仍把整个时期作为展叶始期对低温或热量累积的响应期。其他物种也以同样的方法来识别。

结果显示, 25种木本植物展叶始期的低温累积开始日期在9月2日至12月5日之间, 平均在10月6日, 结束日期多在3月份(除白桦(*Betula platyphylla*)外), 平均为3月17日(表2)。低温累积量为36.79–79.72 CP, 均值为66.16 CP。热量累积开始日期在12月13日至次年3月22日之间, 平均在1月21日; 结束日期则集中在4月17日至5月8日之间, 平均在4月26日。热量累积量在1 879.42–4 829.02 GDH之间, 均值为2 933.12 GDH。除白桦外, 其余24个物种的低温和热量累积期都有不同程度的重叠。

### 2.2 25种木本植物展叶始期对气温及低温和热量累积变化的响应

从图3来看, 25种木本植物展叶始期对低温和热量累积期内的平均气温响应的敏感度分别在–7.28–0.46 d·$℃^{-1}$ (均值–3.78 d·$℃^{-1}$)和–7.01– –2.36 d·$℃^{-1}$ (平均值–4.51 d·$℃^{-1}$)之间, 各有6个和20个物种显著。展叶始期对低温和热量累积量的敏感度分别为

**表2** 东灵山25种木本植物展叶始期的低温和热量累积期及累积量(平均值±标准差)
**Table 2** Chilling and heat accumulation (mean ± *SD*) during each chilling and forcing periods for 25 woody species in Dongling Mountain

| 物种 Species | 低温累积期 Chilling periods | | 低温累积量 Chilling accumulation (CP) | 热量累积期 Forcing periods | | 热量累积量 Heat accumulation (GDH) |
|---|---|---|---|---|---|---|
| | 开始日期 Start date (month-day) | 结束日期 End date (month-day) | | 开始日期 Start date (month-day) | 结束日期 End date (month-day) | |
| 白桦 *Betula platyphylla* | 09-30 | 01-11 | 43.37 ± 5.79 | 03-22 | 05-03 | 3 640.58 ± 963.76 |
| 大花溲疏 *Deutzia grandiflora* | 09-30 | 03-23 | 73.26 ± 6.64 | 01-04 | 04-27 | 2 924.49 ± 824.72 |
| 蒿柳 *Salix schwerinii* | 10-06 | 03-07 | 60.57 ± 6.14 | 03-03 | 04-22 | 2 304.28 ± 699.59 |
| 黑桦 *Betula dahurica* | 10-31 | 03-23 | 55.55 ± 7.03 | 01-26 | 05-03 | 3 887.06 ± 1 105.56 |
| 胡桃楸 *Juglans mandshurica* | 09-29 | 03-23 | 74.46 ± 7.52 | 12-19 | 05-01 | 3 562.93 ± 1 066.70 |
| 花曲柳 *Fraxinus chinensis* subsp. *rhynchophylla* | 10-04 | 03-20 | 70.33 ± 6.99 | 01-04 | 05-01 | 3 562.62 ± 1 066.71 |
| 华北落叶松 *Larix gmelinii* var. *principis-rupprechtii* | 10-26 | 03-07 | 48.92 ± 6.77 | 01-26 | 04-21 | 2 279.80 ± 775.96 |
| 金花忍冬 *Lonicera chrysantha* | 09-30 | 03-23 | 73.28 ± 6.84 | 12-22 | 04-24 | 2 566.87 ± 783.05 |
| 辽东栎 *Quercus wutaishansea* | 10-26 | 03-23 | 58.23 ± 6.29 | 01-26 | 05-02 | 3 669.40 ± 928.35 |
| 裂叶榆 *Ulmus laciniata* | 09-29 | 03-23 | 73.62 ± 6.74 | 01-26 | 04-26 | 2 799.27 ± 797.50 |
| 六道木 *Zabelia biflora* | 09-30 | 03-23 | 73.07 ± 6.47 | 12-13 | 04-26 | 2 750.16 ± 796.11 |
| 毛榛 *Corylus mandshurica* | 09-28 | 03-02 | 61.20 ± 6.76 | 12-22 | 04-26 | 2 808.29 ± 931.77 |
| 蒙椴 *Tilia mongolica* | 10-26 | 03-23 | 58.52 ± 5.89 | 01-23 | 04-29 | 3 200.84 ± 884.28 |
| 巧玲花 *Syringa pubescens* | 09-02 | 03-24 | 79.72 ± 7.54 | 01-26 | 04-17 | 1 949.79 ± 711.70 |
| 青杨 *Populus cathayana* | 12-05 | 03-24 | 36.79 ± 5.91 | 03-02 | 04-26 | 2 777.00 ± 512.17 |
| 山桃 *Prunus davidiana* | 09-02 | 03-23 | 78.39 ± 6.43 | 03-20 | 04-20 | 1 879.42 ± 652.17 |
| 山杏 *Prunus sibirica* | 09-30 | 03-22 | 72.40 ± 6.47 | 12-22 | 04-25 | 2 626.39 ± 773.89 |
| 土庄绣线菊 *Spiraea pubescens* | 10-05 | 03-23 | 71.86 ± 6.97 | 12-17 | 04-27 | 2 995.08 ± 936.94 |
| 卫矛 *Euonymus alatus* | 09-30 | 03-23 | 73.28 ± 6.84 | 03-19 | 04-21 | 2 059.65 ± 709.69 |
| 五角枫 *Acer pictum* subsp. *mono* | 09-30 | 03-22 | 72.60 ± 6.84 | 01-22 | 04-26 | 2 808.06 ± 831.75 |
| 小花溲疏 *Deutzia parviflora* | 09-29 | 03-23 | 73.44 ± 6.56 | 12-22 | 04-28 | 3 012.81 ± 844.57 |
| 小叶鼠李 *Rhamnus parvifolia* | 09-30 | 03-23 | 73.26 ± 6.64 | 01-22 | 04-20 | 2 106.40 ± 666.57 |
| 迎红杜鹃 *Rhododendron mucronulatum* | 09-29 | 03-23 | 73.62 ± 6.74 | 12-22 | 04-26 | 2 799.54 ± 797.67 |
| 油松 *Pinus tabuliformis* | 10-22 | 03-08 | 51.62 ± 6.26 | 03-03 | 05-08 | 4 829.02 ± 1 002.10 |
| 照山白 *Rhododendron micranthum* | 09-30 | 03-22 | 72.60 ± 6.63 | 12-22 | 05-01 | 3 528.25 ± 932.79 |
| 均值 Average | 10-06 | 03-17 | 66.16 ± 11.26 | 01-21 | 04-26 | 2 933.12 ± 677.50 |

CP, 冷激份额; GDH, 生长度小时。
CP, chill portion; GDH, growing degree hour.

每10 CP –6.63–1.71 d (平均值–3.54 d)和每1 000 GDH –12.37– –3.14 d (平均值–7.09 d), 各有2个和23个物种显著。这说明暖温带绝大多数木本植物的展叶始期主要受热量累积(或热量累积期内平均气温)的影响, 热量累积得越多, 展叶始期开始得就越早, 而低温累积(或低温累积期内平均气温)的影响则很小。展叶始期对低温累积期内的平均气温变化的响应敏感度只有一个正值(0.46)且不显著, 说明各物种均没有出现因气温升高使低温累积量不足从而推迟展叶始期的现象。

### 2.3　灌木和乔木的展叶始期及其对气候变暖响应的对比

灌木和乔木的展叶始期及其对气候变暖的响应存在一定差异(图4)。对于展叶始期, 灌木比乔木早

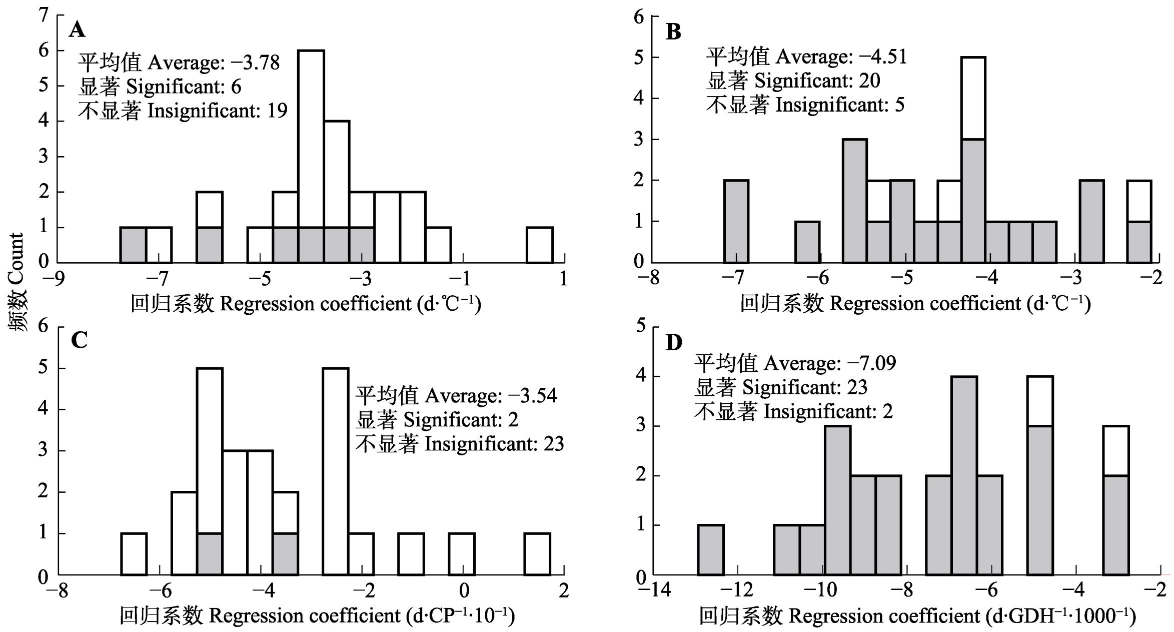


**图3**　东灵山25种木本植物展叶始期与低温和热量累积期内平均气温及低温和热量累积量的回归系数。**A,** 低温累积期平均气温。**B,** 热量累积期平均气温。**C,** 低温累积量。**D,** 热量累积量。图中灰色代表回归系数显著($p < 0.05$), 白色代表回归系数不显著。CP, 冷激份额; GDH, 生长度小时。

**Fig. 3**　Regression coefficients between mean temperature, chilling and heat accumulation and leaf-unfolding dates during chilling and forcing periods for 25 woody species in Dongling Mountain. **A,** Mean temperature during chilling period. **B,** Mean temperature during forcing period. **C,** Chilling accumulation. **D,** Heat accumulation. Grey bars indicate regression coefficients are significant ($p < 0.05$), and white bars indicate regression coefficients are insignificant.CP, chilling portion; GDH, growing degree hour.

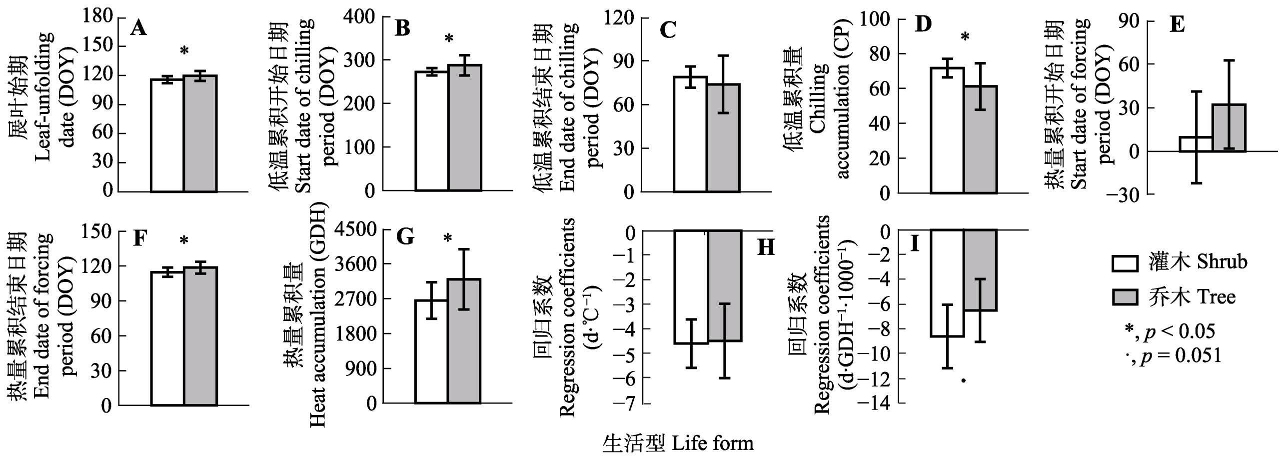


**图4**　东灵山灌木和乔木的展叶始期及其对气候变暖响应的差异比较(平均值±标准差)。**H,** 展叶始期与热量累积期平均气温的回归系数。**I,** 展叶始期与热量累积量的回归系数。DOY, 年序日。CP, 冷激份额; GDH, 生长度小时。

**Fig. 4**　Difference between leaf-unfolding dates of shrubs and trees and their responses to climate warming in Dongling Mountain (mean ± *SD*). **H,** Regression coefficients between leaf-unfolding dates and mean temperature during forcing period. **I,** Regression coefficients between leaf-unfolding dates and heat accumulation. DOY, day of the year. CP, chilling portion; GDH, growing degree hour.

DOI: 10.17521/cjpe.2022.0036

3.87 d, 两者的平均值差异显著。灌木的低温累积开始日期也比乔木早14.90 d, 不过结束日期比乔木晚5.07 d (差异未达显著), 所需低温累积量比乔木多10.46 CP。此外, 灌木热量累积的开始日期也比乔木早22.57 d, 但因数据波动较大, 差异未达到显著, 结束日期则比乔木早3.96 d, 热量累积比乔木少543.56 GDH。由此可以推断热量累积的多少可能与累积期的结束日期(通常为展叶始期)关系密切。进一步分析则发现, 12种灌木和13种乔木的热量累积量和展叶始期均呈显著的正相关关系(图5)。这说明无论是灌木还是乔木, 展叶始期越晚的物种, 其所需累积的热量也越多。此外, 研究还发现灌木和乔木的展叶始期与热量累积期内平均气温的回归系数虽无显著差别, 但两者与热量累积量系数的差异呈边缘显著(灌木和乔木的平均值分别为每1 000 GDH –8.10和–6.13 d)(图4H–4I)。这说明灌木对热量累积量的响应敏感度比乔木高。

## 3 讨论

### 3.1 25种木本植物展叶始期的低温和热量累积期及累积量

PLS回归在暖温带25种木本植物展叶始期的低温和热量累积期的识别上体现了较好的应用。累积期内存在短暂的不连续性, 这在前人的研究中(Guo *et al*., 2015; Martinez-Lüscher *et al*., 2017; Guo *et al*., 2019)也出现过。可能是由休眠相关基因的表达差异引起生理过程的不同而造成(Leida *et al*., 2012; Benmoussa *et al*., 2017), 也可能是由芽的"基因闹钟" (Ríos *et al*., 2014)或其他未知因素引起的(Luedeling *et al*., 2013)。

25种木本植物展叶始期的平均低温及热量累积期的起止时间与北京市区4种树木(低温累积期10月2日至次年3月21日; 热量累积期1月17日至4月17日)较为相近, 除了低温累积结束日期早4天外, 其他日期晚4–9天(Xu *et al*., 2021)。因本研究地点位于北京市西郊东灵山, 海拔1 263 m, 年平均气温比市区低5 ℃左右, 存在这种差别是正常的。此外, 研究中多数木本植物的低温和热量累积期存在不同程度的重叠, 这在基于控制实验和实地观测的研究中(Murray *et al*., 1989; Luedeling *et al*., 2013; Guo *et al*., 2014, 2015)都有证明, 说明热量的累积在低温累积还未结束时就已经开始了(Campoy *et al*., 2011a), 展叶始期对温度的响应可能存在低温和热量累积同时有效的阶段(Luedeling *et al*., 2013; Guo *et al*., 2014, 2015; Martínez-Lüscher *et al*., 2017), 其深层机制有待进一步探讨。

本研究中25种木本植物展叶始期平均所需的低温累积量(66.16 CP)与北京市区4种树木(66.83 CP)非常接近; 热量累积量(2 933.12 GDH)则与该4种树木的平均值(6 170.55 GDH)相差较多, 不过与榆树(*Ulmus pumila*)(3 996.7 GDH)较为接近(Xu *et al*., 2021)。可能是研究地点和北京市区的气温差异所致。有研究证实来自寒冷地区的树木比生长在较温暖地区的树木所需的热量少(Sanz-Pérez *et al*., 2009; Olson *et al*., 2013; Zohner & Renner, 2014)。东灵山相较市区气温偏低, 物种可能更能适应寒冷的环境, 对极端低温也具有更强的适应性, 因此所需热量较少。而北京市区的4种树木所需热量则较多, 尤其是来自温暖地区的非本地物种, 如亚热带树木紫薇(*Lagerstroemia indica*)所需热量最多。此外, 前人研究发现板栗(*Castanea mollissima*)树在低温需求一致的情况下, 展叶晚的基因型比展叶早的所需热量

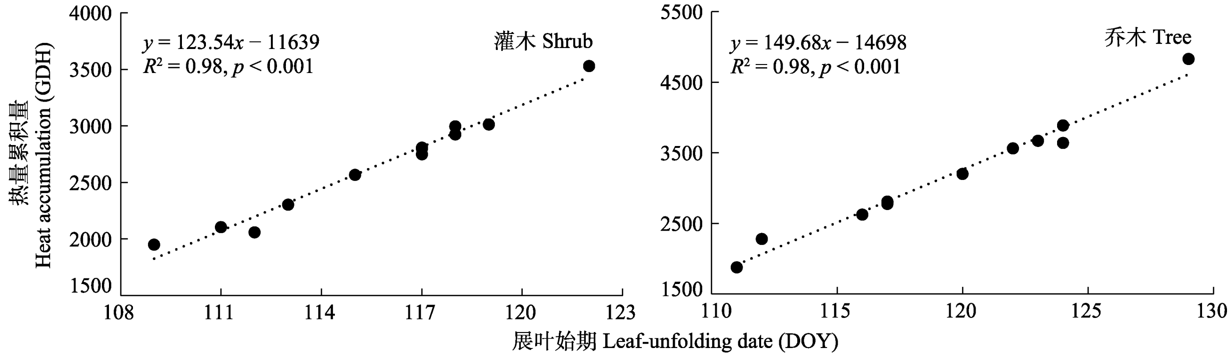


**图5** 东灵山12种灌木和13种乔木的热量累积量与展叶始期的关系。DOY, 年序日; GDH, 生长度小时。

**Fig. 5** Linear regression between heat accumulation and leaf-unfolding dates of 12 shrubs and 13 trees in Dongling Mountain. DOY, day of the year; GDH, growing degree hour.

多(Charrier *et al*., 2011; Dantec *et al*., 2014)。相对低温需求，树木对热量的需求变化较大，其影响因素可能较多。

### 3.2 25种木本植物的展叶始期对低温和热量累积量变化的响应

暖温带25种木本植物展叶始期的变化主要受热量累积量(或热量累积期内平均气温)的影响，而受低温累积量(或低温累积期内平均气温)的影响较小，且未发现因气温升高而使春季物候推迟的现象。这与前人的研究结果(Fu *et al*., 2012; Guo *et al*., 2014; Chen *et al*., 2017; Yang *et al*., 2020)一致。如很多基于过程的物候模型研究发现，在温带地区，只考虑热量而不考虑低温需求的模型效果较好，而两者均考虑的效果则较差(Chuine, 2000; Morin *et al*., 2009; Vitasse *et al*., 2011; Fu *et al*., 2012; Xu & Chen, 2013)。其原因可能是，虽然冬季气温上升速度较快，但目前在自然环境下大部分温带及高寒地区的低温累积仍能满足春季植物解除休眠的需要，不会成为影响其春季物候的限制因子(Chen *et al*., 2015)。不过在冬季较温暖的地区，如热带及亚热带地区，随着气温的上升，低温累积的作用可能会变得越来越重要，使植物的春季物候受低温和热量累积的共同作用(Guo *et al*., 2014, 2019; Chen *et al*., 2017)。除了温度之外，有研究发现降水可能会通过改变积温和太阳辐射间接地影响温带树木春季物候(Fu *et al*., 2014, 2015)，在将来的研究中可加入降水和太阳辐射因子，以全面理解气候因子对暖温带树木春季物候的影响。

### 3.3 灌木和乔木的展叶始期及其对气候变暖的响应对比

本研究发现灌木的平均展叶始期比乔木早，且灌木热量累积的起止日期都比乔木早，与前人的研究结果(Rollinson & Kaye, 2012; Vitasse, 2013; Panchen *et al*., 2014; 陶泽兴等, 2020)一致。这可能是植物为了适应外界环境在物候上表现出来的差异。灌木属于演替早期出现的、生活史较短的机会种，这样的物种一般采取机会主义生存策略(Caffarra & Donnelly, 2011)，如倾向于较早地萌芽和展叶等，以便在林冠郁闭前争取光照资源(Panchen *et al*., 2014; 陶泽兴等, 2020; Donnelly & Yu, 2021)。其次，物候期早的物种可能对极端低温具有更强的适应性，而物候期晚的物种则适应性较差，提前展叶容易使它们遭受春季晚霜的损害(Scheifinger *et al*., 2003; Ge *et al*., 2013)。

本研究中灌木展叶始期所需的低温累积量高于乔木，与前人的研究结果(Polar *et al*., 2014; Wang *et al*., 2020a)不同。前人研究一般通过实验完成，与自然条件下植物的响应可能存在一定差异，这有待进一步探讨。本研究中灌木所需的热量低于乔木，这与前人的结果一致，如两种温带灌木的热量需求显著低于3个乔木树种(Wang *et al*., 2020a)。本研究也发现无论是灌木还是乔木，展叶始期较早的物种其热量需求也较低，这也与前人的研究一致。如北京展叶最早的榆树其所需热量最少，而展叶最晚的紫薇所需热量最多(Xu *et al*., 2021)。这可能也与植物采取机会主义生存策略有关(Chuine & Cour, 1999)，使其在春季升温时能够快速响应(Polgar等, 2013; 陶泽兴等, 2020)。此外，灌木和乔木对低温和热量需求的相反关系，与多数研究结果(Laube *et al*., 2014; Fu *et al*., 2015; Flynn & Wolkovich, 2018; Wang *et al*., 2020b)一致。很多研究表明如果植物所需低温量较多，则需要的热量就较少(Laube *et al*., 2014; Fu *et al*., 2015; Flynn & Wolkovich, 2018; Wang *et al*., 2020b)。低温和热量累积互相配合保证植物在较适宜的环境下萌芽和展叶，这在大量的研究中得到了证实(Wang *et al*., 2020b)。

本研究还发现灌木对热量累积变化的响应比乔木更高，这也与前人的研究相近。如灌木或其他机会种比演替后期物种(如乔木)对气温的上升响应更敏感(Caffarra & Donnelly, 2011)。这意味着在气候变暖的情况下，灌木展叶始期提前的速度比乔木更快，能够更加紧密地跟随气候的变化。不同生活型植物对气候适应的差异性，也可能会使一些适应性较差或不能与互作物种同步的物种面临减少的风险(Rosbakh *et al*., 2021)，从而对林下和林冠的物种组成及生态系统功能产生较大影响。此外，文中灌木和乔木的展叶始期与热量累积期内平均气温的回归系数无显著差别，可能是因为在一定范围内的气温才能进行有效的热量累积，使得平均气温对物候的影响与热量累积存在一定的差异。

## 4 结论

本研究模拟了2003–2019年暖温带25种木本植物展叶始期的低温和热量累积，分析了各物种展叶

DOI: 10.17521/cjpe.2022.0036

始期对气候变暖的响应及差异, 主要结论如下:

(1) 25种木本植物展叶始期的低温累积期为10月6日至次年3月17日, 平均低温累积量为66.16 CP; 热量累积期为1月21日–4月26日, 平均热量累积量为2 933.12 GDH。低温和热量累积期有不同程度的重叠。

(2)展叶始期对低温和热量累积量变化响应的敏感度均值分别为每10 CP –3.54 d和每1 000 GDH –7.09 d, 各有2个和23个物种显著。说明暖温带木本植物展叶始期主要受热量累积的影响, 而低温累积可能仍能满足植物打破休眠的需求, 暂时不成为春季物候的限制因子。

(3)灌木的展叶始期比乔木早3.87 d, 低温需求比乔木多10.46 CP, 热量需求比乔木少543.56 GDH。无论是灌木还是乔木, 展叶始期越早的植物, 其所需的热量累积也越少。灌木或展叶早的植物热量需求相对较低, 这可能与其采取机会主义生存策略有关。

(4)灌木展叶始期对热量累积的响应敏感度(边缘)显著高于乔木(分别为每1 000 GDH –8.10和–6.13 d, $p$ = 0.051)。这意味着灌木能够更加紧密跟随气候的变化, 在气候变暖的情况下, 其展叶时间提前的速度可能比乔木更快。

**致谢** 感谢国家生态科学数据中心, 特别感谢中国科学院北京森林生态系统定位研究站提供数据支撑。

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DOI: 10.17521/cjpe.2022.0036

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