Journal of
Plant Ecology

Research Article

Flowering responses of the woodland strawberry to local climate and reduced precipitation along a European latitudinal gradient

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Handling Editor: Peter Alpert

Received: 14 November 2024, **First Decision:** 1 March 2025, **Accepted:** 9 June 2025, **Online Publication:** 19 July 2025

Citation: De-la-Cruz Ivan M., Batsleer Femke, Bonte Dries, Diller Carolina, Izquierdo José Luis, Still Sonja, Osorio Sonia, Posé David, de la Rosa Aurora, Vandegehuchte Martijn L., Muola Anne, Hytönen Timo, Stenberg Johan A. (2025) Flowering responses of the woodland strawberry to local climate and reduced precipitation along a European latitudinal gradient. *J Plant Ecol* **18**:rtaf105. https://doi.org/10.1093/jpe/rtaf105

Abstract

Climate change creates novel environmental conditions that plant species must adapt to. Since plants are finely tuned to the seasonality of their environments, shifts in their phenology serve as some of the most compelling evidence of climate change's impact. Understanding how key fitness-related phenological traits, such as flowering onset, respond to novel environments is crucial for assessing species' plasticity and/or adaptive potential under climate change. Here, we investigated the onset of flowering in *Fragaria vesca* (woodland strawberry; Rosaceae) by translocating genotypes between four sites along a south–north gradient in Europe, encompassing its entire latitudinal distribution range with varying temperatures, precipitation patterns, and photoperiods. At each site, we included a reduced precipitation treatment using rainout shelters to simulate drought conditions and assess their impact on flowering onset. Our findings revealed that southern and central European genotypes exhibited a delayed onset of flowering when translocated to the northernmost site. In contrast, no difference among genotypes was found in the onset of flowering when grown in more southerly sites. Reduced precipitation accelerated flowering across several sites and all genotypes, irrespective of their latitudinal origin. Overall, northern European genotypes showed a greater capacity to adjust their onset of flowering in response to the different photoperiods and temperatures across the latitudinal gradient compared to southern European genotypes, suggesting that they may be more resilient to shifting environmental conditions. Differences in phenotypic plasticity among genotypes translocated to higher versus lower latitudes highlight the role of photoperiod in evaluating a species' capacity to cope with climate change.

Keywords: drought, *Fragaria vesca*, growing degree days, onset of flowering, photoperiod, plant phenology

欧洲林地草莓开花物候沿纬度梯度的变化以及对降水减少的响应

摘要：气候变化背景下，植物需适应新的环境条件。由于植物对其生长环境的季节性变化高度敏感，物候期变化成为反映气候变化影响的最有力证据之一。研究关键适应性物候性状(如开花起始时间)如何响应新环境，对评估物种在气候变化下的表型可塑性和/或适应潜力至关重要。本研究通过不同基因型林地野草莓(*Fragaria vesca*, 蔷薇科)沿欧洲南北梯度的4个样点移植实验，探究其开花起始时间的变化。这些样点覆盖了其全纬度分布范围，包含不同气温和降雨格局及光周期。此外，各样点设置了减雨处理(利用遮雨棚模拟干旱条件)以评估干旱对开花起始时间的影响。结果表明，当南欧和中欧基因型被移植至最北端时，开花起始时间显著延迟；而在南部样点栽培时，不同基因型的开花起始时间无显著差异。在一些样点，减雨处理加速了所有基因型(无论其纬度来源)的开花进程。总体而言，在应对不同纬度的光周期和温度变化时，北欧基因型比南欧基因型表现出更强的开花起始时间调节能力，表明其对环境变化的适应韧性更强。基因型向高/低纬度移植时表现出的表型可塑性差异，突显了光周期在评估物种应对气候变化能力中的关键作用。

关键词：干旱，野草莓(*Fragaria vesca*)，生长积温，开花起始时间，光周期，植物物候

INTRODUCTION

Plant phenology is the study of periodically recurring patterns of plant growth and development throughout the year (Lieth 1974). Climate change, involving increasing temperatures and extreme precipitation events, can affect plant phenology because these climatic variables influence developmental timing, both independently and through interactions with other cues, such as photoperiod (Cleland *et al.* 2007). The onset of flowering—the specific timing of the first appearance of flowers in a plant's lifecycle—has been identified as a particularly sensitive phenological response to climate change (Büntgen *et al.* 2022; Collins *et al.* 2024; Levy and Dean 1998; Prevéy *et al.* 2017). Several studies have shown that climate change can either delay or advance flowering onset, with varying consequences—both positive and negative—for plant fitness (Cleland *et al.* 2007; Collins *et al.* 2024; Franks *et al.* 2007). Thus, exposing plants to varying environmental conditions, such as changes in precipitation and/or temperature, can provide valuable insights into how they adjust their phenological events, such as the onset of flowering, in response to the shifting environmental conditions predicted under climate change (De Frenne *et al.* 2013).

Outdoor common garden experiments replicated along a latitudinal gradient offer a powerful approach to investigate, under natural conditions, how flowering onset responds to environmental variation (i.e. genotype-by-environment interactions; De-la-Cruz *et al.* 2022; de Villemereuil *et al.* 2016). Moreover, such experiments can provide insights into how flowering phenology may shift in response to novel environmental conditions expected under climate change (Blois *et al.* 2013; De Frenne *et al.* 2013). For example, one can assess the onset of flowering in genotypes from higher European latitudes (e.g. Nordic countries) when they are translocated to warmer, lower latitudes, where current temperatures resemble those projected for higher latitudes by the end of this century (Blois *et al.* 2013; De Frenne *et al.* 2013). This is relevant because it has been reported that subarctic and arctic environments are warming at four times the rate of the global average (Rantanen *et al.* 2022). It is equally relevant to study the onset of flowering in genotypes from lower latitudes under the environmental conditions of higher latitudes. Plant populations from lower latitudes in Europe are consistently spreading to higher latitudes, escaping the increasingly warmer conditions in their original range (Bradley *et al.* 2024; Pecl *et al.* 2017; Zhang *et al.* 2023). Nevertheless, the notably shorter autumn season at higher latitudes (e.g. boreal, subarctic and arctic regions) characterized by a rapidly shortening photoperiod compared to lower latitudes (Ettinger *et al.* 2021; Mølmann *et al.* 2021) may present ecological and physiological challenges for perennial plants from lower latitudes that are adapted to initiate and develop vegetative and floral buds during longer autumns (Blackman 2017; Heide and Sønsteby 2007; Hytönen and Kurokura 2020). Consequently, plants from lower latitudes may not have sufficient time to complete autumn bud development at higher latitudes, potentially leading to a delayed flowering onset in the following spring compared to plants native to higher latitudes.

If plants from lower latitudes are unable to spread to higher latitudes to escape rising temperatures, they will only persist in their current habitats if they can acclimate to the predicted warmer conditions through phenotypic plasticity and/or adaptation (Anderson and Wadgymar 2020; De Frenne *et al.* 2013; Rauschkolb *et al.* 2023). Similarly, plants from higher latitudes will also need to adjust to the predicted temperature increases in their native habitats via plasticity and/or adaptive evolution (IPCC 2021; Rantanen *et al.* 2022; Rauschkolb *et al.* 2023). Climate change models for subarctic and arctic regions have predicted 3–5 °C of warming in spring and 7–13 °C in autumn by the end of the century (IPCC 2021; Overland *et al.* 2014). However, climate change involves both rising temperatures and shifts in precipitation patterns (Mirza 2003; Wang *et al.* 2022). For instance, reduced precipitation can lead to more frequent and severe droughts (Dai *et al.* 2018). Several studies have found that advancing the onset of flowering is a common response of plants to cope with drought and/or warming, enabling them to escape ensuing drought by completing reproduction before conditions become too severe (Collins *et al.* 2024; Rauschkolb *et al.* 2023; Roiloa and Retuerto 2006). Nonetheless, a delayed onset of flowering under drought conditions has also been found (e.g. Shavrukov *et al.* 2017). Thus, investigating flowering onset along a latitudinal gradient (which includes variation in temperature regimes) and under drought conditions is crucial for understanding plant responses to novel environments predicted under climate change. A latitudinal gradient also facilitates the assessment of how spatial variation in photoperiod influences flowering phenology (Faehn *et al.* 2023; Hytönen and Kurokura 2020). It has been shown that photoperiod is a major abiotic driver of phenological variation across geographic ranges (Rauschkolb *et al.* 2024).

In this study, we used the woodland strawberry, *Fragaria vesca*, to investigate the role of different environments at different latitudes, reduced precipitation and the latitudinal origin of the genotypes (which serves as a proxy for plants being adapted to different photoperiods and temperature conditions), in determining the flowering phenology of genotypes collected along a latitudinal gradient in Europe. To this end, genotypes from the southern, central and northern latitudes of Europe were translocated to four separate experimental sites, ranging from 40° N to 70° N across the European continent. As plant populations from specific latitudes have evolved distinct flowering onset patterns as responses to abiotic factors, such as differences in temperature, precipitation and photoperiod (e.g. a specific onset of flowering; Blackman 2017), we hypothesized that (1) when *F. vesca* genotypes originating from a specific latitude are translocated to a new latitude, they will exhibit altered flowering onset (e.g. accelerated or delayed), and a lower proportion of flowering individuals compared to their flowering pattern at their latitude of origin and to genotypes native to the new latitude. This is because non-native genotypes are not adapted to the environmental conditions of the new latitude to initiate flowering timely or even flowering at all. (2) If genotypes, irrespective of their latitude of origin, can adjust their developmental cycles to the environmental conditions of new latitudes through phenotypic plasticity, they would show uniform onset of flowering within the same location. (3) All genotypes are expected to exhibit an earlier onset of flowering (as previously reported in other perennial species; see above) under reduced precipitation compared to control conditions.

MATERIALS AND METHODS

Study system

The woodland strawberry, *F. vesca* (Rosaceae), is a perennial plant species distributed throughout the Northern Hemisphere and its ease of vegetative propagation via stolon cloning, makes it an excellent model system for studying flowering phenology to different environmental conditions (Hilmarsson *et al.* 2017). *Fragaria vesca* grows in semi-open habitats such as forest clearings, forest edges, roadsides, and paths (Hancock and Luby 1993). Its flowering period varies, extending from April to September at lower European latitudes, while lasting only from June to August at northern European latitudes (Hancock and Luby 1993; Heide and Sønsteby 2007). *Fragaria*

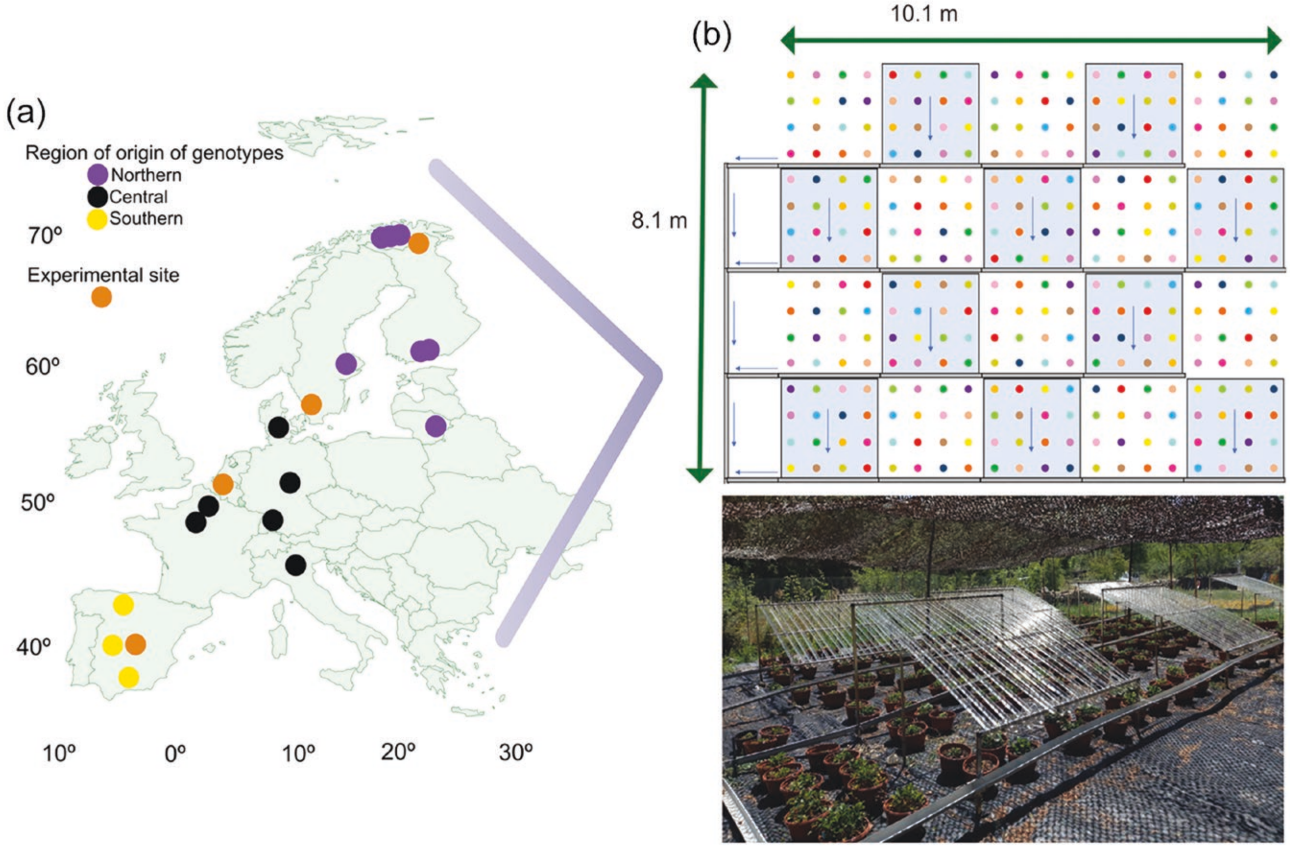

Figure 1: (a) A map showing the distribution of the experimental sites (orange dots) along the south–north latitudinal gradient across Europe: Spain (Rascafría), Belgium (Gontrode), southern Sweden (Alnarp) and northern Finland (Kevo). The exact coordinates of the experimental sites are provided in Methods. The yellow, black and purple dots indicate the southern, central and northern origin, respectively, of each of the 16 *Fragaria vesca* genotypes used in the study. The region of origin for each genotype was determined based on a clustering analysis using latitude coordinates as the grouping factor (see Methods and Supplementary Fig. S1). (b) A sketch of the experimental design. The colors of the circles represent each of the 16 *F. vesca* genotypes exposed to control (white squares) and reduced precipitation (blue squares) treatments. Arrows indicate the direction of the rain flow in the shelters. Shelters excluded 50% of incoming precipitation. More detailed information for temperature, precipitation, soil moisture and proxies of the length of growing and flowering season for each site can be found in Supplementary Table S1.

vesca initiates and develops flower buds in autumn, followed by a winter dormancy, and then blooms in the subsequent spring (Faehn *et al.* 2023; Heide and Sønsteby 2007; Hytönen and Kurokura 2020).

Study sites

The four study sites (Fig. 1a; Supplementary Table S1) were chosen to capture a south–north gradient across the distribution area of *F. vesca* in continental Europe. The study sites were Rascafría in central Spain (40°54′17.941″ N, 3°52′46.31″ W), Gontrode in Belgium (50°59′0.581″ N, 3°47′50.248″ E), Alnarp in southern Sweden (55°38′59.99″ N, 13°03′60.00″ E) and Kevo in northern Finland (69°34′51″ N, 26°42′56″ E). This selection ensured a diverse range of precipitation regimes, photoperiod, humidity levels and temperatures across the species' potential range (Fig. 1a; Supplementary Table S1). It is important to highlight that the site in Spain is situated at a higher elevation—1200 m a.s.l.—compared to the other selected sites (Supplementary Table S1). This higher elevation is characterized by mean annual temperatures similar to those at Alnarp in southern Sweden during the growing season of *F. vesca*, thereby not aligning with the expected temperature–latitude gradient (i.e. temperature decreases toward higher latitudes). As a result, some genotypes (e.g. southern Swedish genotypes) may experience similar temperatures when translocated to Spain as in their native sites, rather than encountering markedly warmer conditions. However, other key environmental factors—particularly photoperiod, which plays a critical role in flowering development (Rauschkolb *et al.* 2024)—vary consistently along the latitudinal gradient in Europe, shifting from approximately 14 h/9.5 h (summer/winter) at the Mediterranean margin to 24 h/0 h (summer/winter) at and north of the Arctic Circle (Faehn *et al.* 2023). Thus, exposing *F. vesca* genotypes from higher to lower latitudes and vice versa provides an opportunity to investigate how photoperiod variation influences the onset of flowering. Likewise, although the Spanish genotypes were originally collected from lower elevations than the Spanish experimental site—and therefore not necessarily experiencing the same temperatures as in their native habitats—this site was selected to align with their latitudinal origin and associated environmental conditions, particularly photoperiod.

Plant materials

The 16 plant genotypes used in this study originated from distinct wild populations along the continental European south–north gradient and were collected from elevations below 1200 m a.s.l. (Fig. 1a). The plant material was propagated clonally via stolon production in a greenhouse at the Ruissalo Botanical Garden, University of Turku, Turku, Finland, at 20 °C, with a 16:8-h light:dark cycle. The resulting plantlets (i.e. the vegetative propagules) from the stolons were planted into 0.05-L pots filled with a commercial potting substrate (Kylvö-ja Taimimulta, product code 34647, Kekkilä Garden) during December 2020 and January 2021. To minimize potential transgenerational effects from the maternal plants originally collected in their native habitats, it is important to note that these plants were maintained under uniform controlled environmental conditions in the greenhouse for approximately 3 years. During this period, they underwent multiple vegetative generations of clonal propagation, including the generation used in this study. Therefore, any transgenerational effects are expected to have been effectively removed over time.

The plantlets were transported to the study sites between late March and mid-June 2021, matching with the start of the growing season at each site (Supplementary Table S1), and planted directly into 6-L (27-cm diameter) pots filled with Kekkilä Rough Potting Mixture (FBM 640 Airboost R8421). Twenty clonally propagated plantlets per genotype were planted at each site, each in a separate pot, except for one genotype, which had only 10 replicate plants per site. Likewise, one genotype from northern Europe was not planted in northern Finland because the plants died in the greenhouse due to a technical error prior to their translocation to this site.

At three sites (Spain, Belgium and southern Sweden), the plants were established within 1 week of the spring equinox (*c.* 20 March 2021). At the Finnish site, the plants were established in mid-June after the temperature was above 5 °C for 10 consecutive days. As plants were exposed to outdoor conditions for establishment for almost a whole growing season at each site in 2021, we do not expect confounding effects related to differences in the timing of plant establishment between the sites (see also onset of flowering observations below). Plants were watered during an establishment period of four weeks (0.5 L per pot per watering) and, to avoid frost damage, they were covered with fleece if the weather forecast indicated night-time temperatures below 4 °C. The fleece was removed during the daytime. A camouflage net (14468020 w/l basic bulk net, Mil-Tec; Fig. 1b) was also placed at a height of 2 m above the experimental area at each site to decrease direct sunlight exposure during summer (i.e. wild strawberries grow best in partial shade; Hancock and Luby 1993). This particular camouflage net with holes was selected because it facilitates free air circulation and minimally reduces rainfall, thereby maintaining environmental conditions as close to natural as possible (Fig. 1a). It is important to note that as both treatments were under the net, any intercepted rainfall affected them equally, with drought-treated plants still receiving only 50% via rainout shelters.

Experimental design

At the end of the establishment period (4 weeks), the plants (n = 310 in Spain, Belgium and southern Sweden and n = 290 in northern Finland due to one genotype not being planted at this site; see above) were divided into two treatments, reduced precipitation and control, and exposed to the sites' natural conditions (Fig. 1b). At each site, 10 plants from each of the 15 (14 in northern Finland) genotypes, and 5 from 1 genotype, from then onwards received a reduced precipitation treatment, while the other 10 plants per genotype (5 for one genotype) served as controls. A split-plot design was used with the genotype as a split-plot factor (one plant per genotype was planted within each block, arranged in a random design) and the reduced precipitation treatment applied to whole plots (blocks; Fig. 1b). Pots were spaced 50 cm apart in all directions in a regular grid formation (Fig. 1b). The reduced precipitation treatment consisted of rainout shelters that reduced the incoming precipitation by 50% (Fig. 1b; Yahdjian and Sala 2002). Plants for the control treatment were placed in blocks without shelters (Fig. 1b).

The entire experimental area was covered with polypropene groundcover (MyPex, Don and Low Ltd) to prevent weed growth and fenced with fine-mesh chicken wire (also dug into the soil) to prevent mammalian herbivory. In all sites, during the summer (June–August), the soil moisture was measured after 6–8 days without rain (or after 3 days without rain if the maximum daily temperatures were +30 °C or above) with a soil moisture meter (Fieldscout TDR 150, Spectrum Technologies, Inc.). If the average soil moisture of 20 randomly chosen pots (10 per treatment) was lower than 10% of the volumetric water content, additional water was supplied: 1 and 0.5 L to plants under control and reduced precipitation conditions, respectively. Thus, plants in the reduced precipitation treatment always received 50% of the amount of water compared to the control plants. Furthermore, soil moisture was also measured at two opposite sides of each pot at two different time points during the growing season of *F. vesca* at each site in 2022 (Supplementary Table S1). Mean soil moisture for each plant's pot was then calculated and used for subsequent analyses (see Statistical Analysis and Results).

Onset of flowering observations

As plants were exposed to natural environmental conditions in 2021 at each site, they were able to initiate flower buds under field conditions at each experimental site in the autumn of that year without confounding effects (see above). Thus, any potential influence of the establishment period on flowering was mitigated. In the subsequent year (2022), the onset of flowering was monitored every second day by recording the Julian date of the first open flower on each plant at each site.

Temperature measurements

Temperature data were obtained from the nearest public and national weather station for each site (Supplementary Table S1). In the case of Spain and North Finland, the weather station was situated adjacent to the experimental site. For the Belgian site, the weather station was located within 1 km of the experimental site, and in southern Sweden within 15 km. We extracted the average, minimum, and maximum temperatures for each day from 1 June 2021, until the plants flowered the following year. The setup and conditions of these stations follow standard protocols (Dumas *et al.* 2021), enabling us to compare data across different locations.

Estimation of growing degree days to flowering

In addition to Julian days to the onset of flowering, we quantified the heat units leading to the onset of flowering using growing degree days (GDDs), a metric frequently employed to delineate the precise timing of key biological processes (McMaster and Wilhelm 1997). We computed GDDs necessary for the beginning of flowering for the year 2022 using the formula:

$$\mathrm{GDD} = \frac{T\mathrm{min} + T\mathrm{max}}{2} - T\mathrm{base} \tag{1}$$

where Tmin and Tmax were the lowest and highest temperatures, respectively, recorded daily from January 1 to September 30 at each site. The calculation of daily GDDs was extended through September, allowing for the possibility that some plants would produce their first flower by this time. Tbase was the base temperature under which no significant plant development is expected (McMaster and Wilhelm 1997). A generally accepted Tbase value of 5 °C was used for GDD calculations (Hatfield and Prueger 2015; Körner 2008), and accumulated GDD values until the observation of the first open flower were calculated for each plant.

Flower-inductive conditions and chilling accumulation

To estimate flower initiation and winter chilling periods at each site, we collected photoperiod and temperature data from summer to autumn 2021 through winter 2022. Flower induction was defined using criteria from previous studies—either a photoperiod <14 h with a weekly mean temperature <18 °C, or a weekly mean temperature <10 °C—and was considered to persist until weekly mean temperatures dropped below 5 °C (Heide and Sønsteby 2007; Hytönen and Kurokura 2020). Chilling accumulation was quantified as the number of days with mean temperatures <5 °C between October 2021 and April 2022 (Bigey 2002).

Statistical Analysis

All statistical analyses were carried out and plots generated using JMP PRO version 18.0 (SAS Institute).

To evaluate the impact of the latitudinal region of origin of the genotypes on the onset of flowering or

GDDs to flowering across the four different sites, the 16 genotypes were grouped by the latitude coordinates of their locations of origin using the Ward hierarchical clustering method (Ward 1963). The groups were identified following the ‘elbow’ method from a scree plot. A further validation of the groups from the clustering analysis was carried out using a discriminant analysis. The 16 genotypes were classified into three groups (Supplementary Fig. S1), which correspond to three latitudinal ranges: southern, central and northern Europe (Wilks’ Lambda$_{4/24}$ = 0.0001; Approx. $F = 21.25$; Supplementary Fig. S1). Thus, this new variable is henceforth referred to as “region of origin” of the genotypes. We then refer to southern, central and northern genotypes as those originating from southern, central and northern latitudes in Europe (Supplementary Fig. S1).

We first analyzed the mean differences in soil moisture across treatments and sites for 2022 using a linear mixed model (LMM). To this end, the mean soil moisture per pot calculated during the growing season (see above) was used as the response variable, with treatment, site and their interaction included as predictors. Block was used as a random effect to adjust for spatial heterogeneity in soil moisture across the area of each site. We then carried out Student’s *t*-tests as multiple comparison tests. *P*-alues of the multiple comparisons were adjusted using the Benjamini–Hochberg false discovery rate (Benjamini and Hochberg 1995).

We constructed a contingency table to observe differences in the proportions of flowering plants per region of origin across sites. In this table, site and region of origin of the genotypes were used as categorical variables to construct the contingency table, and the table cells contained the counts of the total number of plants that flowered per region of origin in each site. Calculations were carried out separately for both the control and reduced precipitation treatment.

Effect of reduced precipitation and region of origin on the onset of flowering across the sites

To evaluate the effect of the treatment (control versus reduced precipitation), site and region of origin of the genotypes on the onset of flowering and GDDs to flowering, we generated a Generalized linear mixed model (GLMM) and an LMM, respectively. The GLMM was generated using a Poisson error distribution with a Log link. In each model, we used site, treatment, region of origin, and all the possible interactions between them as predictors and the onset of flowering or GDDs to flowering as a response. Pearson and deviance goodness-of-fit of the models were checked to account for the dispersion of the variance, and we did not detect overdispersion. Pairwise comparisons used Student’s *t*-tests as post hoc tests. *P*-values of the pairwise comparisons were adjusted using the Benjamini–Hochberg False Discovery Rate (Benjamini and Hochberg 1995).

In each model, individual genotype (not clustered by latitude) nested within region of origin, block, as well as genotype nested within region of origin × treatment, genotype nested within region of origin × site, and genotype nested within region of origin × treatment × site interactions were included as random effects. *P*-values of the random effects were obtained using the Wald test (Wald 1943). Incorporating random effects into these GLMMs serves to account for genetic variation between plants and their influence on the response variables. For instance, considering interactions that involve the genotype nested within region of origin as a random effect allows for the recognition that the impacts of fixed effects (treatment, site, region of origin) may vary according to the plants’ genotypes (Harrison *et al.* 2018).

RESULTS

Variation in soil moisture across sites

Belgium experienced the highest mean rainfall during the growing season of *F. vesca*, whereas Spain was the driest site (Supplementary Table S1). The average soil moisture (%) for both treatments across all sites was as follows: control = 28.40 ± 0.48 (standard error), reduced precipitation = 12.08 ± 0.37 (see Supplementary Table S1 for the average soil moisture for each site). In each site, the reduced precipitation treatment significantly reduced soil moisture compared to the control treatment (Supplementary Tables S1 and S2). This reduction corresponded to 1.74- to 4.23-fold higher soil moisture in the control treatment compared to the reduced precipitation treatment (Supplementary Table S2). The highest soil moisture level was found in Belgium under the control treatment, while the lowest level was recorded in southern Sweden under reduced precipitation (Supplementary Fig. S2). These measurements confirmed the effectiveness of the reduced precipitation treatment (Supplementary Fig. S2).

Differences in the proportion of plants that flowered per region of origin across sites

Across both treatments, the proportion of southern-origin plants that flowered was higher in Spain than in Belgium and northern Finland, but similar to that in

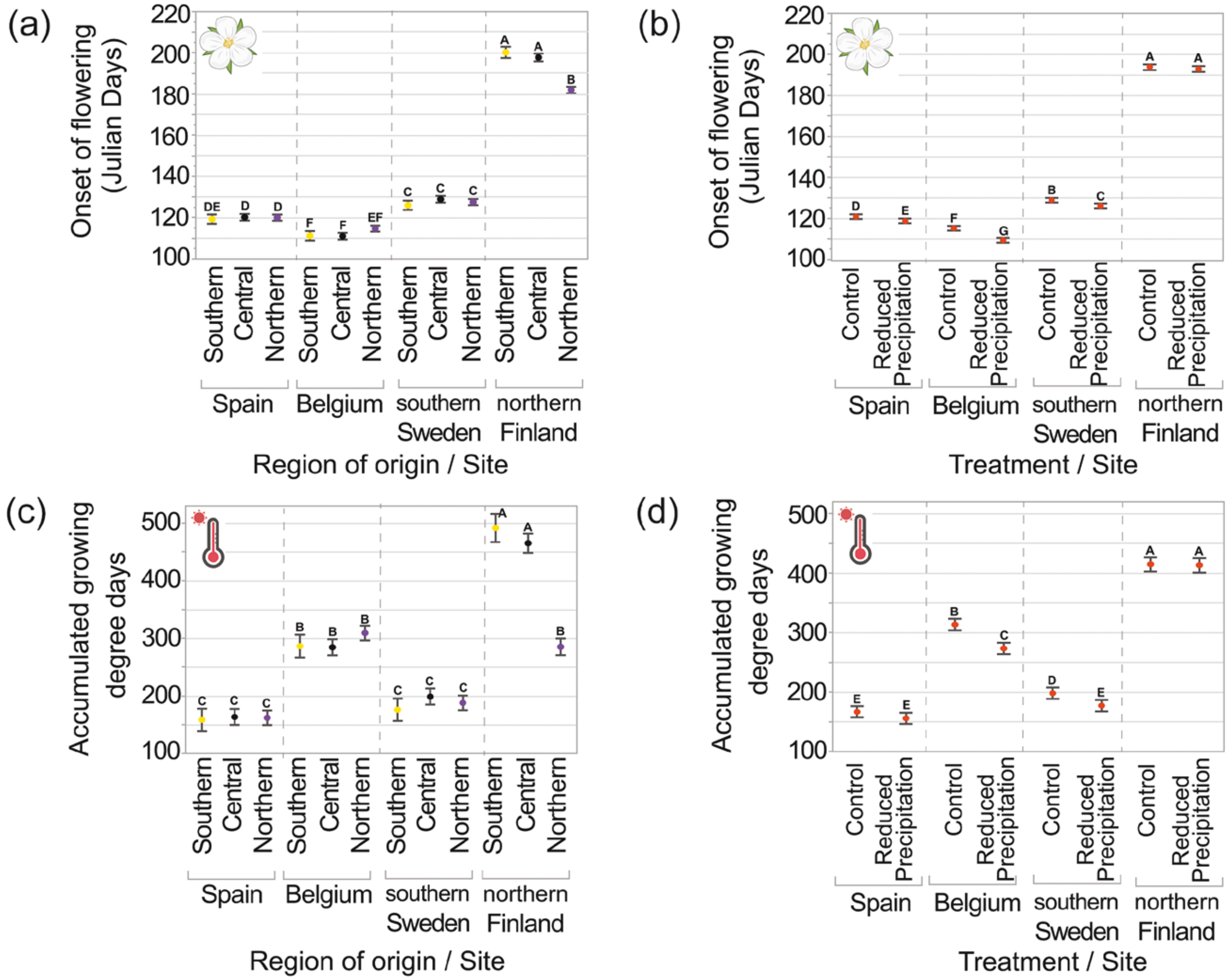

Figure 2: (a) Least square mean ± standard errors of onset of flowering (Julian days) for genotypes grouped by their region of origin (southern, central, northern Europe) across the four study sites (site × region of origin interaction). (b) Least square mean ± standard errors of onset of flowering (Julian days) in reduced precipitation and control treatments across the four study sites (site × treatment interaction). (c) Least square mean ± standard errors of growing degree days for genotypes grouped by their latitudinal region across the four study sites (site × region of origin interaction). (d) Least square mean ± standard errors of growing degree days in reduced precipitation and control treatments across the four study sites (site × treatment interaction). Colors of the circles in panels (a) and (c) represent the mean flowering onset and GDDs, respectively, for genotypes grouped by their region of origin (Yellow = southern, Dark = central, Purple = northern European genotypes; see Fig. 1 and Supplementary Fig. S1). Letters above error bars indicate the multiple comparison analyses. Different letters indicate statistical difference ($P < 0.05$) after correcting for false discovery rate (FDR) of these multiple comparisons. See also Supplemental material S4–S13. Icons in the panels of the figures were created in BioRender.

southern Sweden (Supplementary Table S3 and Fig. S3). However, in Spain, northern-origin plants showed the highest flowering proportions, surpassing central and southern genotypes (Supplementary Table S3 and Fig. S3). Central-origin plants flowered consistently across sites, except in northern Finland, where the proportion of flowering plants was reduced (Supplementary Table S3 and Fig. S3). Higher proportion of northern-origin plants flowered in Spain, Belgium and southern Sweden than in northern Finland, but still more flowering plants were found among northern than central and southern genotypes at northern Finland (Supplementary Table S3 and Fig. S3).

Effect of reduced precipitation and region of origin on onset of flowering across sites

The onset of flowering measured in Julian days to the first open flower was generally delayed with increasing latitude of the experimental site, except in Belgium, where flowering occurred earlier than at the other sites (Fig. 2a). The onset of flowering of genotypes originating from southern and central latitudes exhibited a delay as compared to their northern counterparts in northern Finland, as well as relative to more southerly locations (site × region of origin; Table 1; Fig. 2a; Supplementary Tables S4 and S5). No significant differences in flowering onset were found between the region of origin of the genotypes at the experimental sites in Spain, Belgium and southern Sweden (Fig. 2a; Supplementary Tables S4 and S5). Plants under the reduced precipitation treatment produced their first open flower 2, 6 and 3 days earlier in Spain, Belgium and southern Sweden, respectively, compared to the control (Table 1; Fig. 2b; Supplementary Tables S6 and S7). The only significant random effect in the model for the onset of flowering was the genotype nested within region of origin × site interaction (Supplementary Table S8).

Effects of reduced precipitation and region of origin on GDDs to flowering across sites

Southern and central genotypes had higher GDD values than northern genotypes in northern Finland, and their GDD values were higher in northern Finland compared to sites located further south (site × region of origin interaction; Table 1; Fig. 2c; Supplementary Tables S9 and S10). Furthermore, no significant differences in GDDs were found between the region of origin of the genotypes at the experimental sites in Spain, Belgium and southern Sweden (Fig. 2c; Supplementary Tables S9 and S10).

Under control conditions, genotypes of southern, central and northern origin required 10, 40 and 21 more GDDs to flower than under reduced precipitation in Spain, Belgium and southern Sweden, respectively (site × treatment interaction; Table 1; Fig. 2d; Supplementary Tables S11 and S12). However, in northern Finland, there was no difference in GDDs to flowering between control and reduced precipitation treatments (site × treatment interaction; Fig. 2d; Supplementary Tables S11 and S12). The significant random effects in the model for GDDs were genotype nested within region of origin × site and genotype nested within region of origin × site × treatment interactions (Supplementary Table S13).

Flower initiation and chilling period

At the three southernmost sites, conditions were suitable for flower bud initiation and development for roughly three months, whereas in northern Finland, this period was 4–6 weeks shorter (Supplementary Table S14). The number of chilling days was the lowest in Belgium ($N = 53$) and extremely high in northern Finland ($N = 220$; Supplementary Table S14).

DISCUSSION

This study provides new insights into the onset of flowering in *F. vesca* genotypes translocated from southern Europe to subarctic latitudes and vice versa under a climate change scenario. Overall, we identified both plastic responses and signals of local

Table 1: Mixed models testing the effects of treatment (control vs. reduced precipitation), site (Spain, Belgium, southern Sweden, northern Finland), region of origin (genotypes from southern, central and northern Europe) and their interactions on (a) onset of flowering (Julian days) and (b) growing degree days.

	Onset of Flowering (Julian days)				Growing degree days			
Effects	**d.f.Num**	**d.f.Den**	***F***	***P***	**d.f.Num**	**d.f.Den**	***F***	***P***
Site	3	24.8	1151.34	**0.0001**	3	22.5	150.03	**0.0001**
Treatment	1	19.9	24.28	**0.0001**	1	17.0	18.50	**0.0005**
Region of origin	2	13.1	3.33	0.0676	2	12.9	7.67	**0.0064**
Site × Treatment	3	35.6	5.32	**0.0039**	3	30.8	5.95	**0.0025**
Site × Region of origin	6	23.7	10.65	**0.0001**	6	21.8	15.32	**0.0001**
Treatment × Region of origin	2	16.8	0.08	0.9211	2	19.3	0.12	0.8917
Site × Treatment × Region of origin	6	31.9	1.32	0.2761	6	30.6	2.01	0.0945

d.f.Num = degree of freedom; d.f.Den = denominator degrees of freedom; *F* = ratio of the variation explained by the model (Mean Square Model) and the unexplained variation (Mean Square Error), significant *P*-values (*P*) are in bold. For more detailed information on the multiple comparison tests carried out for Site × Treatment and Site × Region of origin, see Supplementary Figs S4–S13 and Fig. 2a–d.

adaptation in the onset of flowering among different genotypes of *F. vesca* across a latitudinal gradient in Europe. Our findings revealed no significant differences in flowering onset among genotypes when they were translocated to Spain, Belgium and southern Sweden. In alignment with Hypothesis No. 2, this suggests that plant genotypes, irrespective of their latitudinal origin, were able to adjust their flowering onset in response to local environmental stimuli when translocated to new latitudes, allowing them to flower simultaneously with genotypes from nearby latitudes. Several studies have shown that plasticity enables plants to sense and adjust to changes in environmental cues such as day length and temperature across both space and time (reviewed in Blackman 2017). These studies have demonstrated that information from environmental cycles is integrated at the molecular level, ensuring that key transitions, such as germination and flowering, occur during periods favorable for growth, reproduction and seed set (Blackman 2017; Ehrlén *et al.* 2023). However, plasticity may be insufficient when species or populations encounter environmental conditions outside the range of historical variability to which they are adapted (Anderson and Wadgymar 2020). This insufficient plasticity was found in southern and central genotypes translocated to the northernmost site, where they exhibited a delayed onset of flowering. These southern and central plants needed to accumulate, on average, 256 additional GDDs to flower compared to plants of these same genotypes growing in Spain and Belgium. These results also suggest the existence of a latitudinal threshold in environmental conditions below which plasticity remains effective for southern and central genotypes. For the case of *F. vesca*, flowering onset plasticity appears to be sufficient in a latitudinal range from the middle of Spain to southern Sweden to enable non-native genotypes to adjust their onset of flowering in response to local cues and ensure timely flowering relative to more local genotypes.

The insufficient plasticity of southern and central genotypes in adjusting to the environmental conditions in northern Finland can be attributed to the significantly shorter period for flower bud initiation and development during autumn at this site compared to more southern locations. Previous studies have similarly found shorter growing seasons at Arctic latitudes compared to southern latitudes (Ettinger *et al.* 2021; Faehn *et al.* 2023). Moreover, studies have found that in the Arctic, perennials capable of forming flower buds in the shorter autumn and flowering rapidly after snowmelt in spring are predominant (Mølmann *et al.* 2021). For instance, 92% of the 169 flowering plant species in northeast Greenland produced overwintering flower primordia (Sørensen 1941). Therefore, genotypes from southern and central latitudes, which typically experience longer periods for flower bud initiation and development, may not have had sufficient time to complete their flower bud development during the much shorter autumn typical for higher latitudes. These southern genotypes likely completed their flower bud development during the following spring, resulting in the delayed onset of flowering. This same pattern has been previously observed in cultivated strawberries in northern Norway (Opstad *et al.* 2011). In other words, the earlier flowering found in northern genotypes at the northernmost site, compared to southern genotypes, can be interpreted as an adaptation to complete their reproductive cycle within the shorter growing season typical of these regions, as proposed in Hypothesis No. 1. Indeed, in this study, the proportion of flowering plants from northern latitudes in northern Finland was higher than that of southern and central latitudes. Moreover, a parallel analysis to assess signals of local adaptation using data from the same experiments of this study revealed that northern genotypes produced more fruits in northern Finland than southern and central genotypes (De-la-Cruz *et al.* 2025). Together, the findings from this study and De-la-Cruz *et al.* (2025) support the idea of local adaptation in northern genotypes to the shorter growing season. These findings may extend to southern populations of other annual and perennial species distributed from southern to higher latitudes in Europe. As southern populations expand northward in response to rising temperatures in their native southern ranges, they are likely to encounter more extreme environmental conditions—such as shorter growing seasons—that may constrain their capacity for phenological adjustment and successful establishment at higher latitudes (Bradley *et al.* 2024; Zhang *et al.* 2023).

As temperatures rise at northern latitudes (Anderson and Wadgymar 2020; IPCC 2021; Rantanen *et al.* 2022), it is likely that northern genotypes will exhibit an earlier onset of flowering compared to their historical onset of flowering. This is confirmed by our findings, which revealed that northern genotypes exhibited an earlier onset of flowering when translocated to the warmer sites of Spain, Belgium and southern Sweden compared to northern Finland. A recent study on 12 tundra plant species in the Canadian Arctic found that warming, particularly increased spring temperatures that have accelerated snowmelt, has extended the duration of spring, resulting in earlier flowering (Collins *et al.* 2024). Similarly, in this study, it is possible that northern genotypes experienced an earlier and longer spring at the three southernmost sites, compared to northern Finland, which enabled them to flower earlier. Since daily temperatures at these southernmost sites were higher than in northern Finland, it appears that northern genotypes accumulated heat more quickly (i.e. fewer GDDs) before the onset of flowering. For example, in Spain, northern plants required approximately 62 fewer days (~123 fewer GDDs) to flower compared to northern Finland. Moreover, northern genotypes exhibited a higher number of flowering plants in Spain, Belgium and southern Sweden than in northern Finland, demonstrating their capacity to flower in hotter and drier climates. However, a recent parallel analysis with data from the experiments of this study revealed that northern genotypes produced fewer fruits than southern ones in Spain, similar amounts in Belgium, and more than both southern and central genotypes in southern Sweden (De-la-Cruz *et al.* 2025). Thus, it appears that increased flowering of northern genotypes at southern latitudes, particularly in Spain and Belgium, does not necessarily lead to higher fruit production.

Under reduced precipitation, flowering onset advanced at almost all sites—by 2–3 days in Spain and southern Sweden and by 6 days in Belgium. A recent analysis for other traits measured in these same experiments revealed that under reduced precipitation, genotypes from nearly all latitudes formed larger rosettes at all three sites, and in Belgium, most genotypes also increased fruit and stolon production relative to controls (De-la-Cruz *et al.* 2025). Such shifts—earlier flowering, increased reproduction, and growth—are hallmarks of a drought-escape strategy (Collins *et al.* 2024; Rauschkolb *et al.* 2023; Roiloa and Retuerto 2006; Shavrukov *et al.* 2017). Belgium was the warmest site and also had the highest precipitation. This elevated precipitation likely enhanced water availability across both treatments, thereby promoting greater nutrient uptake and energy acquisition (De-la-Cruz *et al.* 2025). Consequently, even under reduced precipitation, plants in Belgium may have allocated resources more rapidly to earlier flowering and produced more fruits and stolons than those at drier sites (De-la-Cruz *et al.* 2025). However, further research is needed to better understand the ecological and evolutionary consequences of early flowering under drought. For example, it remains unclear to what extent advanced flowering onset may lead to temporal mismatches with pollinator activity and consequently disrupt plant–pollinator interactions (Glenny *et al.* 2018; Jaworski *et al.* 2022; Kuppler and Kotowska 2021).

CONCLUSIONS

In summary, we found that the region of origin of the genotypes affected the onset of flowering. In particular, genotypes from southern and central latitudes were not well adapted to northern conditions, resulting in delayed flowering. However, plasticity enabled these same genotypes to adjust their flowering onset when translocated to other latitudes south of the northernmost site. In contrast, northern genotypes adjusted their flowering onset in response to the environmental conditions at southern and central European sites and had a higher number of flowering plants compared to southern and central genotypes, as well as at the northern site. Experimental sites in southern and central Europe are characterized by warmer temperatures with less extreme seasonal fluctuations in the photoperiod compared to northern sites. This suggests that, in terms of flowering onset regulation, the northern genotypes are capable of coping, at least temporarily, with the rising temperatures projected by climate change models for northern latitudes (IPCC 2021). Our findings highlight the role of latitudinal adaptation and phenotypic plasticity in shaping the onset of flowering.

Supplementary Material

Supplementary material is available at *Journal of Plant Ecology* online.

Figure S1: (a) Dendrogram of the cluster analysis carried out with the 16 *Fragaria vesca* genotypes using their latitude coordinates. (b) Discriminant analysis showing the significant separation of the three groups (southern, central and northern European *F. vesca* genotypes).

Figure S2: Least square mean ± confidence intervals (95%) of soil moisture across treatments (control and reduced precipitation) and experimental sites (Spain, Belgium, southern Sweden, northern Finland) in 2022.

Figure S3: Figures based on data from the contingency table to evaluate the differences in the number of plants of *Fragaria vesca* that flowered at least once among latitudinal regions (based on the clusters constructed according to the region of origin of the *F. vesca* genotypes in Europe) and experimental sites for the control (a) and reduced precipitation treatments (b).

Table S1: Main abiotic environmental conditions occurring at the four experimental sites

Table S2: (a) The results of the mixed model testing the mean differences in soil moisture across treatments and experimental sites in 2022 (onset of flowering was measured during this year). (b) Least square means of soil moisture across treatments and sites. (c) Pairwise comparisons using Student's t tests as post hoc tests.

Table S3: Contingency analysis table to evaluate the differences in the proportion of plants of *Fragaria vesca* that flowered at least once among latitudinal regions and experimental sites for the control and reduced precipitation treatments.

Table S4: Least square means estimates from the multiple comparison analysis for the significant experimental site × region of origin interaction from the generalized linear mixed model testing the effect of experimental site, treatment and region of origin on the onset of flowering of *Fragaria vesca*.

Table S5: Multiple comparison for the experimental site × region of origin interaction from the generalized linear mixed model testing the effect of experimental site, treatment and region of origin on the onset of flowering of *Fragaria vesca*.

Table S6: Least square means estimates from the multiple comparison analysis for the significant experimental site × treatment interaction from the generalized linear mixed model testing the effect of experimental site, treatment and region of origin on the onset of flowering of *Fragaria vesca*.

Table S7: Multiple comparison for the experimental site × treatment interaction from the generalized linear mixed model testing the effect of experimental site, treatment and regions of origin on the onset of flowering of *Fragaria vesca*.

Table S8: Random effects variance parameter estimates for the model testing the effects of experimental site, treatment, genotype nested within region of origin, and their interaction on onset of flowering of *Fragaria vesca*.

Table S9: Least square means estimates from the multiple comparison analysis for the significant experimental site × region of origin interaction from the linear mixed model testing the effect of experimental site, treatment and region of origin on growing degree days of *Fragaria vesca*.

Table S10: Multiple comparison for the experimental site × region of origin interaction from the linear mixed model testing the effect of experimental site, treatment and region of origin on growing degree days.

Table S11: Least square means estimates from the multiple comparison analysis for the significant experimental site × treatment interaction from the linear mixed model testing the effect of experimental site, treatment and region of origin on growing degree days of *Fragaria vesca*.

Table S12: Multiple comparison for the experimental site × treatment interaction from the linear mixed model testing the effect of experimental site, treatment and region of origin on growing degree days.

Table S13: Random effects variance parameter estimates for the model testing the effects of experimental site, treatment, genotype nested within region of origin, and their interaction on growing degree days.

Table S14: Number of days suitable for flower initiation and winter chilling at each experimental site.

Authors' Contributions

The study was conceived by I.M.D.C., T.H., J.A.S., A.M., M.L.V., D.B., S.O., D.P. The experiments were carried out by I.M.D.C., C.D., F.B., M.L.V., A.M., J.A.S., J.L.I., S.S., A.R., and T.H. The data were analyzed by I.M.D.C. and M.L.V. The draft manuscript was written by I.M.D.C. with considerable input from all the authors.

Funding

This project was funded by the European Commission (BiodivERsA project PlantCline: Adapting plant genetic diversity to climate change along a continental latitudinal gradient, project ID BiodivClim-177), Formas (the Swedish Research Council for Sustainable Development, grant no. 2020–02376), the Academy of Finland (grant no. 344726), the Research Foundation – Flanders (grant no. FWO ERANET G0H6520N and FWO KAN 1506619N), Ministerio de Ciencia, Inovación y Universidades (grant no. PCI2020-120719-2).

Acknowledgements

We thank Juan Antonio Vielva Juez, Director of the Centro de Investigación, Seguimiento y Evaluación del Parque Nacional de la Sierra de Guadarrama, Madrid, Spain, and Kevo Subarctic Research Institute, University of Turku, Finland, for hosting the southernmost (Rascafría/Spain) and northernmost (Kevo/northern Finland) study sites as well as for logistic support during the experiment. We thank Hans Matheve for helping with fieldwork and data digitalization, and also thank other field assistants who helped us with fieldwork. We also deeply appreciate the time, feedback and corrections made to this manuscript from the Associate Editor and two anonymous reviewers of the *Journal of Plant Ecology*.

Conflict of interest statement. The authors declare that they have no conflict of interest.

Data Availability

All data supporting the analyses of this manuscript can be found in DOI: 10.6084/m9.figshare.29302358.

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