Phenological mismatches between above- and below-ground plant responses to climate warming: a global synthesis

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Running head: Response of below-ground phenology to warming

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Abstract

Climate warming is changing above-ground phenology of plants around the world[1, 2]. However, warming effects on below-ground phenology of plants are unclear despite that roots play a vital role in carbon cycling[3]. By conducting a global meta-analysis, we show a phenological mismatch between above- and below-ground plant responses to climate warming. Herbaceous plants advanced both the start and end of the growing season based on their above-ground responses, resulting into a shorter growing season. Below-ground phenophases did not exhibit any obvious changes in herbaceous plants. In contrast, climate warming did not affect the length of above-ground growing season but extended the below-ground growing season of woody plants. These results highlight that climate warming can differentially affect above- and below-ground plant phenology with mismatches arising in herbaceous plants *via* less responsive below-ground phenology whereas mismatches in woody plants *via* more responsive below-ground phenology. Mismatches in above- and below-ground plant phenology imply that terrestrial carbon cycling models exclusively based on above-ground responses are less accurate, which highlight the urgent need to incorporate below-ground plant phenology into future Earth system models.

Introduction

The timing of life-history events of organisms (e.g., phenology) is crucial for their fitness and survival[4]. There is an increasing consensus that anthropogenic climate change has shifted the phenology of several organisms often with detrimental consequences for ecosystem functioning[5]. Our current understanding of plant phenological shifts to climate warming heavily relies on the above-ground part of plants[6], and the terrestrial biosphere models accordingly use above-ground plant phenology as a surrogate of whole plant phenology[3]. Yet, how below-ground phenology responds to climate warming and whether those responses match with shifts in above-ground plant phenology remain little understood[7, 8].

Climate warming typically shifts above-ground phenology of plants by advancing the start of the growing season and delaying the end of the growing season[9, 10]. The warming effects on the start of growing season have been well documented[6, 11]. However, the mechanisms of how the end of the growing season respond to warming remains less clear, despite that the shifts at the start of growing season would have cascading effects on the end of the growing season[12, 13]. Based on functional equilibrium theory, symmetric shifts in above- and below-ground plant phenology should be observed because of their physiological coupling[14]. However, recent experimental evidence suggests that above- and below-ground plant phenology may respond differently to warming[8, 15]. While the underlying reasons for such a mismatch is less known, it could likely depend on how various functional groups of plant compete for limited resources, and how climate warming could alter those resources.

For instance, woody plants face stronger above-ground competition for light availability and herbaceous plants face stronger below-ground competition for soil nutrients[16]. Moreover, given our limited understanding of below-ground phenological responses to warming, we suspect that our current predictions of ecosystem processes (e.g., soil carbon dynamics) under climate change scenario merely using above-ground phenology could be lesser reliable.

Here we aim to unravel how climate warming alters both above- and below-ground plant phenology and whether these responses match each other. We do so for woody and herbaceous plants and investigate what may underlie match or mismatch in responses between above- and below-ground plant phenology. Towards this end, we performed a global meta-analysis of 75 independent studies to find general patterns of phenological responses of herbaceous and woody plants to experimental warming (Figure 1). Our results provide a compelling evidence for mismatches between above- and below-ground plant phenology, but also differences in phenological responses between herbaceous and woody plants to climate warming.

Results

Warming effects on above- and below-ground phenology

Climate warming significantly advanced the start and the end of the growing season by 2.88 (95% CI: -1.85~-3.91) and 5.1 days (95% CI: -2.84~-7.11) based on above-ground herbaceous plant responses (Fig. 2A and C; Table S1), respectively. The stronger advancement of the end of growing season resulted in a shorter growing season (Fig. 2E, $P < 0.05$). In contrast, warming did not affect any below-ground phenophases including the start, the end and the length of the growing season of herbaceous plants (Fig. 2A, C and E, all $P > 0.05$).

For above-ground phenology of woody plants, climate warming slightly advanced the start but did not affect the end and the length of the growing season (Fig. 2B, D, F). Compared to the above-ground responses, woody plants exhibited stronger below-ground responses. Warming significantly advanced the start of the below-ground growing season by 6.47 days (95% CI: -2.36~-10.58) and accordingly extended the growing season length by 2.26 days (95% CI: -4.20~8.73), despite the end of the below-ground growing season was unresponsive (Table S1).

Environmental and ecological controls of above- and below-ground phenophases

For herbaceous plants, the start of the growing season was not significantly affected by any examined factors based on above-ground responses (Fig. 3A). However, the response of the end of the above-ground growing season was strongly affected by that of the start of the growing season (Fig. 3C), with positive relationships observed (Fig. 4A). Model selection showed that experimental duration was the most important driver for the start of the growing season based on the below-ground response (Fig. 3E), the advancement of the start of the growing season diminished and was further delayed after the initial 4 years (Fig. 4B). Despite our model selection identifying MAP as an important driver (Fig. 3C), meta-regression analysis did not detect any significant relationships (Fig. 4C; $P > 0.1$).

For woody plants, we found that the start of the growing season based on above-ground response was clearly affected by experimental duration (Fig. 3B), with a greater advancement observed over the experimental duration (Fig. 4D). However, the below-ground phenophases of woody plants were not influenced by any factors examined in our study (Fig. 3).

Discussion

Understanding of climate warming-induced phenological shifts in organisms is central for advancing climate change biology. Several recent studies have pointed the importance of how phenological mismatches across trophic groups can alter the balance of ecosystem functions[17, 18]. Here, two important findings emerged in our global quantitative synthesis. First, we found that below-ground phenology responds differently to warming among different functional groups, that is, below-ground phenology of herbaceous plants was less sensitive to warming than woody plants. Second, we demonstrate that even within the same trophic group (i.e., plants), phenological mismatches may occur due to climate warming. Such mismatches in plant above- and below-ground phenological responses can have far-reaching consequences for ecosystem stability and functioning.

For herbaceous plants, above-ground phenophases were more sensitive to climate warming than below-ground phenophases. The advanced start of above-ground growing season in herbaceous plants in our meta-analysis has been commonly reported, which often relates to warming-induced advancing of the accumulated temperature requirements in plants[6, 10, 19]. By contrast, the lesser sensitive below-ground phenophases in herbaceous plants are likely to be driven by more complex endogenous and exogenous factors such as photosynthate supply to roots, and soil moisture that would mediate the overall below-ground responses to warming[7]. As the above-ground growing season length advanced and thereby potentially exploited a large proportion of stored carbohydrates[20], we suspect that a relatively stable start of below-ground growing season could be a net effect of the positive effects of warming on root growth combined with the negative effects from the competition of photosynthesis with above-ground parts[7, 21]. This is purely a speculation and merits further examination in future experimental (plant) phenology studies.

The early termination of above-ground and unaltered end of below-ground growing season in herbaceous plants could further be due to different strategies to cope with warming effects between above- and below-ground plant organs. For instance, when warming advanced the start of the growing season, a plants' demand for nutrients and water also elevates earlier in the year[22]. As a result, soil nutrient pools may become further depleted by the end of the growing season in nutrient-limited ecosystems. In such cases, above-ground plant production slows down, or senescence starts earlier[23].

In contrast, warming may not slow down below-ground biomass production because plants tend to allocate more photosynthetic products to below-ground to utilize limiting resources during the growing season. In addtion, the earlier start of the growing season also resulted in an earlier end of the growing season because of the limited leaf longevity and programmed cell death in plants[24, 25].

For woody plants, the below-ground phenophases were more sensitive to climate warming than above-ground phenophases. Comapred to the herbaceous plants which distributed in more arid regions, woody plants in our study were from the more humid regions (average of annual precipitation was 1026 mm for woody plants and 901 mm for herabceous plants). The abundant soil water could make woody plants extend both above- and below-ground growing season under warming. The greater extension of below-ground phenology of woody plants indicated plants allocate more nutrients to below-ground rather than above-ground organs under warming, which may relate to the fact that the growth of the whole plants require more nutrients.. Interestingly, we found that the response of the start of the below-ground growing season for woody plants became stronger over experimental duration. On one hand, soil's ability to buffer high temperature could result in a lagged response of below-ground phenology[26]. On the other hand, the longer below-gournd growing season of woody plants could accumulate an increasing larger nutrient reseviors over years, including nonstructural carbohydrates, which may promote a more positive responses of plant phenology to warming through nutrient and carbohydrate supply[20]. In addition, based on the “transient maxima hypothesis”, the short-term reponse of plant phenology to warming may be due to the transient increase under the non-equilibrium condition[27].

Understanding the (a)synchrony between above- and below-ground phenology under climate warming is crucial for predicting the whole ecosystem responses in a changing world. Our meta-analysis provides a compelling evidence of mismatches between above- and below-ground plant phenology and further the differences in those mismatches between herbaceous and woody plants. These results therefore suggest that above-ground phenology is a poor proxy for below-ground phenology. Most of the contemporary Earth system models still either use above-ground phenology as a proxy of below-ground phenology or do not take below-ground phenology into account at all[28]. Our results accordingly encourage next-generation Earth system models to explicitly incorporate below-ground plant phenology but also to consider the differences between woody and non-woody plants to make predictions with greater accuracy for carbon dynamics in terrestrial ecosystems in response to anthropogenic climate change.

Methods

Data compilation

We used meta-analysis to assess the effect of experimental warming on above- and below-ground plant phenology. We searched for journal articles using ISI Web of Science and China National Knowledge Infrastructure, with the following keyword combinations: (warming OR heat* OR increas* temperature OR elevate* temperature) AND (effect* OR respon* OR affect* OR impact* OR increas* OR decreas* OR alter*) AND (below-ground phenology OR root phenology OR root allocation OR root growth) AND (shoot phenology OR growth OR above-ground biomass) from 1980 to 2020. We also included literature cited in the papers we found. Papers had to meet the following criteria to be included in our dataset: (i) warming experiments were conducted in terrestrial ecosystems; (ii) initial environmental conditions including climate, soil type and species composition in control plots were the same as in warming plots; (iii) at least two temperature regimes were included in a given experiment. To fulfill the criteria of independence of observations, we only considered treatment effects from the latest reported year. We acquired data regarding plant growth dynamics directly from text or tables in original papers or extracted data indirectly from figures by using GetData software (version 2.22). In total, our dataset included 272 paired observations from 75 studies. Among these observations, there were 182 pairs of above-ground phenological observations and 90 pairs of below-ground phenological observations (Figure 1; Figure S1: PRISMA diagram; Table S3).

Ancillary site information including latitude, longitude, annual mean air temperature, and mean annual precipitation were also compiled. Annual mean air temperature and annual precipitation were taken directly from original papers or from the cited papers. If these data were not presented, we extracted them from the “worldclim” database (www.worldclim.com).

Phenological parameters extraction

Similar to previous studies[29, 30], the start and the end of the above-ground growing season were defined as the Julian days at which 10% and 90% of annual growth in above-ground dry matter, stem height, stem diameter or leaf biomass were accumulated, while those of the below-ground growing season were defined as the Julian days when 10% and 90% of annual growth in root dry matter or root length were accumulated. Here, we used the production between the first sampling time and the last sampling time within a year as the annual production. Before extracting the phenological parameters, we standardized the production at the sampling dates by subtracting the production at the first experimental time to remove the effects of pre-year production.

Statistical analysis

Because the response ratio changes depending on when the phenological event happened, it is not the most suitable metric for the date type variables (e.g., the difference between average value in control and warming is 10 in both cases, however, response ratios are different for 15/5 and 135/125)[11]. To address this issue, we used absolute value to assess warming effects for the date type variables (e.g., 2007/12/1). Effect size of start and end of growing season was then calculated as follows:

$$\text{Effect size } = X_w - X_c \quad \text{Eqn. 1}$$

where X_w and X_c are means values of plant phenological parameter at warming and control plots, respectively.

Estimates of response magnitudes from meta-analyses could be contingent on how individual studies are weighted. Thus, we weighted studies by the number of replicates as following[31]:

$$\mathrm{Wr} = (\mathrm{Nc} \times \mathrm{Nw})/(\mathrm{Nc} + \mathrm{Nw}) \quad \text{Eqn. 2}$$

where Wr is the weight assigned to each observation, weighting more the studies having higher sampling size, and Nc and Nw are the number of replicates for ambient and elevated temperature treatments, respectively.

We used “rma.mv” function in the “metafor” package in R software to calculate weighted effect sizes and their 95% bootstrapped confidence intervals. The meta-analysis model included the variable “publication” as a random factor as some studies resulted into more than one effect size. Warming effects on plant phenological parameters were considered to be statistically significant when the 95% confidence intervals of effect sizes did not overlap with 0.

Model selections were used to assess the relative importance of predictors to above- and below-ground phenological parameters using multi-level meta-analyses. Firstly, all the examined factors were combined in a mixed-effect meta-regression model by using the “glmulti” package in R software. We then computed a model sets based on delta (Δ) corrected Akaike information criterion < 2. The importance of each predictor was finally computed as the sum of Akaike weights for models including the given factor. A cutoff of 0.8 was set to distinguish the essential and nonessential predictors in current study^{32}. Here, we included mean annual temperature (MAT), mean annual precipitation (MAP), experimental duration, warming magnitude and warming method to predict the start of growing season for both above- and below-ground plant responses. As the start of growing season could affect the end of growing season, we also added the start of growing season as a predictor of the end of growing season. After the essential predictors were identified by using model selections, we further used a between-group Q statistical test to compare the heterogeneity of the warming-induced shifts in phenological events among different categories of the predictors. Egger's regression and Fail-Safe Analysis were used to test the publication bias (Table S2). All the statistical analysis was conducted by R 3.6.1.

Data accessibility

Should be manuscript be accepted, the data and the R scripts for data processing in this study will be archived in an appropriate public repository such as Figshare.

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Competing Interest Statement

All authors declare no conflicts of interest.

Author Contributions

H.Y.L and H.W. developed the idea, analyzed the data, and wrote the manuscript with substantial input from M.P.T. and X.H.Z. All authors contributed to the writing of the paper.

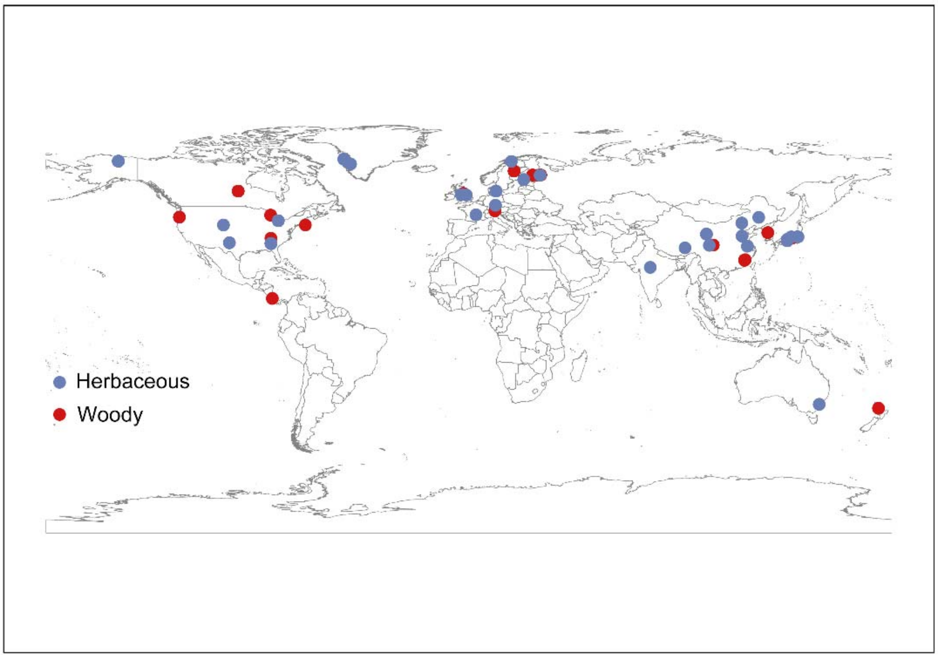

Figure 1 The global distribution of warming experiments selected in this meta-analysis. The blue and red circles indicate which experiment provided seasonality data of herbaceous and woody plants, respectively.

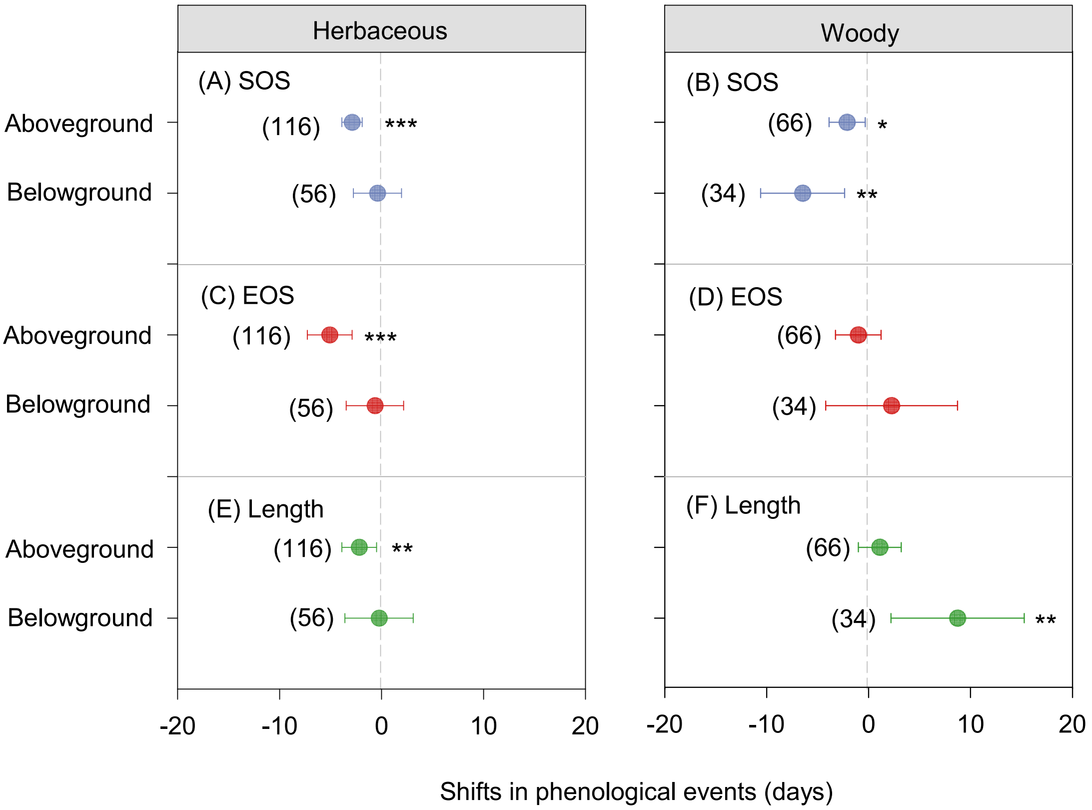

Figure 2 Response of above- and below-ground phenological events to warming in herbaceous (A, C, E) and woody (B, D, F) plants. SOS, EOS and length represent start, end and length of growing season, respectively. Error bars indicate 95% bootstrapped confidence intervals (CI). The vertical dotted lines are drawn at effect size equals 0. The warming effect was considered significant if the 95% CI of the effect size did not overlap with zero. The observation numbers were shown in brackets. *, $P < 0.05$; **, $P < 0.01$; ***, $P<0.001$.

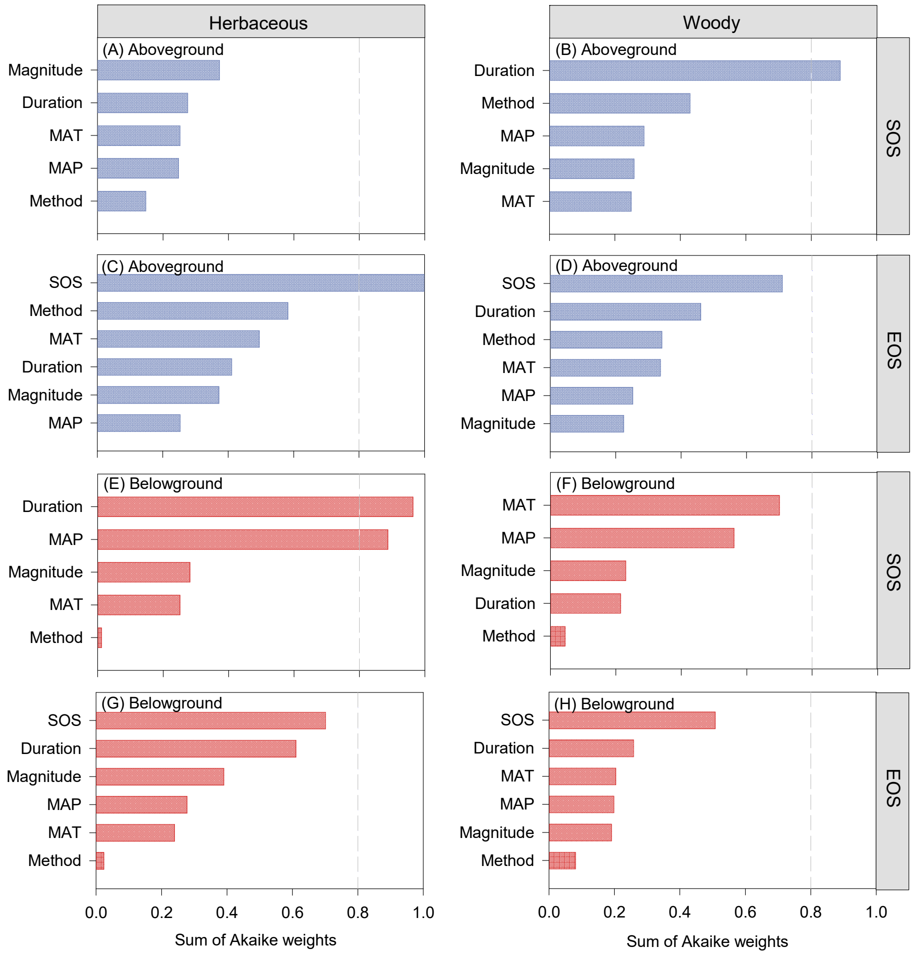

Figure 3 Model-averaged importance of the predictors of the warming-induced shifts in the above- and below-ground phenophases in herbaceous (A, C, E, G) and woody (B, D, F, H) plants. Model-averaged importance was calculated by the sum of the Akaike weights based on the model selection method using corrected Akaike's information criteria. The cutoff 0.8 was shown to determine the essential and nonessential predictors. MAP, mean annual precipitation; MAT, mean annual temperature; Magnitude, warming magnitude; Duration, experimental duration; Method, warming method; SOS, start of growing season; EOS, end of growing season.

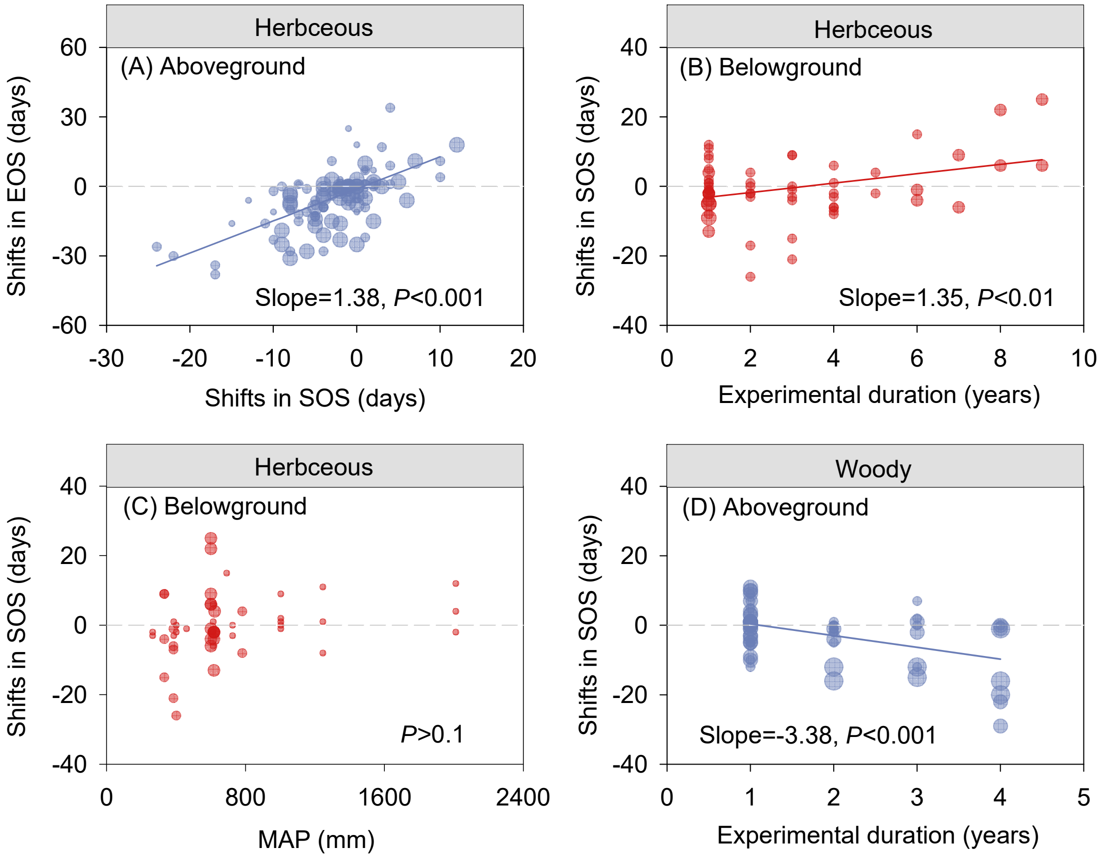

Figure 4 Contributors identified from model selection for the warming-induced shifts in above- and below-ground phenophases in herbaceous (A-C) and woody (D) plants. The size of the circles was proportional to the weights of the observation. The relationships between the warming-induced shifts in the start of above-ground growing season and warming-induced shifts in the end of above-ground growing season in herbaceous plants (A). The relationships between experimental duration and warming-induced shifts in start of below-ground growing season (B). The relationships between MAP and warming-induced shifts in start of below-ground growing season (C). The relationships between experimental duration and warming-induced shifts in start of above-ground growing season (D). SOS, start of the growing season; EOS, end of the growing season.

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