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Meta-analysis

Contrasting responses of early- and late-season plant phenophases to altered precipitation

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Precipitation is a key driver of plant phenology in addition to temperature and photoperiod. Although a few studies have explored phenological responses to altered precipitation, the general patterns of sequential phenophase responses and their potential drivers remain elusive. Here, we conducted a meta-analysis of the responses of ten phenophases to altered precipitation from 63 manipulative experiments. We show that early-season (leaf out, first flowering, last flowering and first fruiting) and late-season phenophases (last fruiting and leaf colouring) shifted in opposite directions with precipitation changes. Advanced early-season phenophases and delayed late-season phenophases led to extensions of the reproductive phase and growing season with precipitation increases. Similarly, delayed leaf out and advanced leaf colouring resulted in a shorter length of the growing season with precipitation decreases. We further found that the responses of phenophases were less pronounced in wetter regions than in drier regions, regardless of the precipitation increase or decrease treatments. In addition, the phenophase responses were mediated by the seasons when the precipitation changes were imposed. For instance, early-season phenophases were more responsive to winter or spring precipitation increases, but late-season phenophases were only significantly affected by spring–autumn precipitation increases. These findings will help improve the forecasts of plant phenological responses to precipitation changes and will assist in the incorporation of precipitation representations into next-generation phenological models.

Synthesis

Most phenological studies have focused on how individual phenological event responds to climate change. However, our current understanding of how the entire phenological sequence, from leaf out to leaf coloring, responds to altered precipitation remains incomplete. Synthesizing 63 manipulative precipitation experimental studies worldwide, we found that early- and late-season phenological events shifted in opposite directions in response to precipitation changes. Additionally, plant phenology responded more significantly to altered precipitation in drier regions than in wetter ones. These findings will help incorporate precipitation representations into next-generation phenological models.

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Keywords: climate change, phenological responses, seasons of precipitation change, sequential phenophases

Introduction

Global precipitation patterns are expected to change significantly by the end of this century, including changes in the annual amount and seasonal precipitation patterns (IPCC 2021). Such changes in precipitation patterns have an impact on the annually recurring sequence of plant developmental stages, i.e. phenology (Lieth 1974, Cleland et al. 2007), thus affecting plant productivity and ecosystem carbon cycling (Peñuelas et al. 2009, Keenan et al. 2014, Wang et al. 2020). However, in comparison to those to climate warming, the responses of plant phenology to altered precipitation have been understudied (Peñuelas et al. 2004, Piao et al. 2019). Furthermore, most of the current phenological models have considered the roles of temperature and photoperiod, but the representation of precipitation is still largely neglected (Chuine and Régnière 2017, Piao et al. 2019). Improving the understanding of plant phenological responses to altered precipitation is urgently needed to better predict future vegetation dynamics.

Altered precipitation often produces diverse phenological shifts at different life stages of plants (Peñuelas et al. 2004, Sherry et al. 2007). Plant phenophases in early and late seasons may differ in their responses to precipitation changes, which are associated with water demand and water availability to plants at different stages (Eggemeyer et al. 2008). On the one hand, precipitation changes should affect early- and late-season phenophases in different directions because plants could extend/compress their edges in improved/deteriorated environments. In addition, compared to late-season phenophases, early-season phenophases, which are closely associated with plant morphogenesis and organogenesis (e.g. leaf and flower), should be susceptible to precipitation changes because of their immature tissue and high production rate (Andrés and Coupland 2012, Hahn et al. 2021, Stuble et al. 2021). On the other hand, precipitation changes may shift early- and late-season phenophases in the same direction because of the cascading effects between different phenophases (Li et al. 2016, Piao et al. 2019). To date, whether early- versus late-season phenophases show different responses to altered precipitation remains unclear at a global scale.

Complex phenological shifts under precipitation changes have been reported, with advanced/delayed timing or shortened/lengthened duration observed among different ecosystems (Peñuelas et al. 2004, Shen et al. 2015). The discrepancy could be attributed to the fact that the studied phenophase responses were dependent on climate conditions, experimental factors and plant characteristics (Suonan et al. 2019, Wang et al. 2021). For instance, plants in arid ecosystems will experience more severe water limitation than those in humid ecosystems; thus, plants are more sensitive to altered precipitation (Reynolds et al. 2004, Collins et al. 2014, Post and Knapp 2020). Additionally, the responses of plant phenophases may vary depending on the seasons when the experimental manipulation occurs, as decreased precipitation in summer may shift plant phenology to a larger extent because of the water stress caused by high evaporation levels (De Boeck et al. 2011). Plant characteristics, such as functional groups, may also lead to diverse phenological shifts due to their differences in morphological and physiological traits (Wang and Tang 2019). For example, it has been reported that deeper-rooted species gain more water and nutrients from deep soil to resist drought than shallower-rooted species (Liu et al. 2018). To date, we still know little about potential factors that drive the contrasting responses of plant phenology to altered precipitation.

Here, we conducted a meta-analysis of ten phenophases by compiling information on 218 terrestrial plant species from 63 experimental studies to assess the overall effect of altered precipitation on plant phenology and to identify its sources of variation (Fig. 1a–b). We used a metric of shift days induced by precipitation changes to represent phenological responses (Arft et al. 1999). The following hypotheses were tested: 1) increased precipitation will advance the early-season phenophases and delay the late-season phenophases and lead to extensions in the reproductive phase and growing season length, while decreased precipitation will have the opposite effects; 2) the responses of plant phenology to altered precipitation will be mediated by an array of experimental and ecological factors; for instance, the responses of phenophases will weaken with increases in the wetness of experimental sites.

Material and methods

Data compilation

We collected publications that focused on how the timing and duration of plant phenophases respond to altered precipitation in terrestrial ecosystems by searching the Web of Science and China's National Knowledge Infrastructure. Here, we focused on how changes in precipitation amounts affected plant phenophases, including increased precipitation, decreased precipitation and both. The following search terms were used to find papers published before June 2022: (drought OR dry OR decreased precipitation OR water reduction OR increased precipitation OR water addition OR wet OR altered precipitation OR water treatment*) AND (bud* OR leaf-out OR leaf flushing OR leaf unfold* OR onset OR flowering OR anthesis OR fruiting OR ripen* OR seed OR maturity OR senescence OR leaf colour OR leaf colour OR brown OR yellow OR growing season OR reproducti* OR phenolog*) AND (experiment* OR control* OR treatment*). We then browsed these papers and selected studies meeting the following criteria: 1) At least one plant phenophase was considered; 2) initial

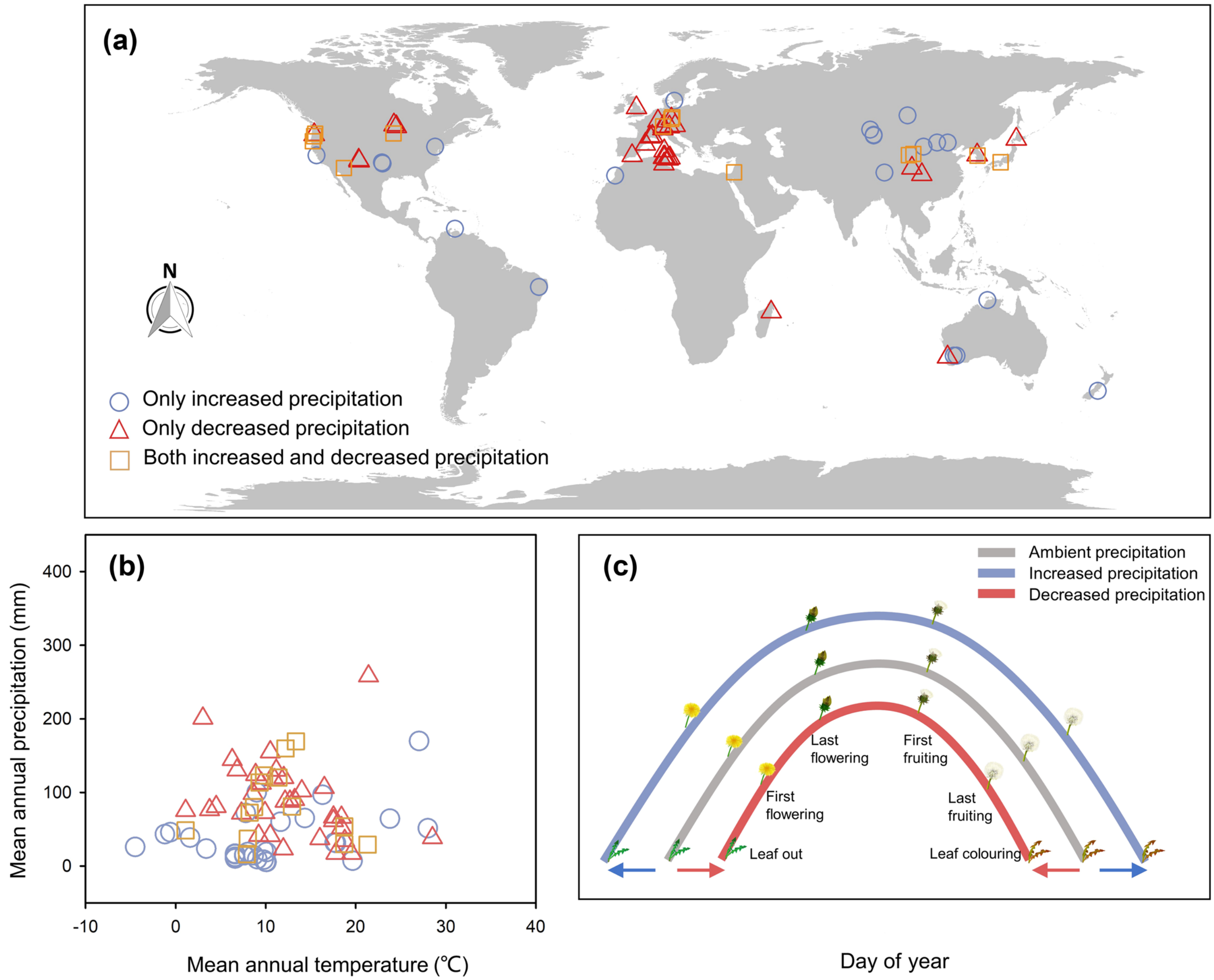

Figure 1. Global distribution and climatic conditions of experimental sites selected in the meta-analysis (a, b) and hypotheses tested in this study (c). In (a), the blue circle, red triangle and orange rectangle indicate sites subjected to increased precipitation, decreased precipitation and both, respectively. In (c), we hypothesize that increased precipitation would prolong plant phenophases but decreased precipitation would shorten plant phenophases. Here, our hypotheses obscure the sequence of first flowering and leaf out.

environmental conditions including soil, vegetation, microclimate in controls were the same as in treatment plots; 3) number of days phenophases shifted were provided at the species level or could be calculated by comparing controls with treatments; 4) the methods used to alter precipitation in experiments were described; and 5) sample size was reported.

The phenophase data were directly extracted from tables or texts in the literature or indirectly extracted from illustrations using GetData Graph Digitizer ver. 2.20 (GetData Software Company). In this study, we defined phenophases as follows (Supporting information): 1) leaf out: the start of growing season, leaf burst or leaf unfolding or needle emergence; 2) first flowering: the start of reproduction, time to first flower or 25% of flowers opening; 3) last flowering: the time to all flowers or 75% of flowers open; 4) first fruiting, the time to first fruit or 25% of fruits occur or first immature pod; 5) last fruiting, the time to all fruits or 75% of fruits occur or start of seed maturity; 6) leaf colouring, the end of growing season, leaf browning or leaf withering; 7) flowering duration, the interval of time between first flowering and last flowering; 8) fruiting duration, the interval of time between first fruiting and last fruiting; 9) reproductive duration, the interval time between first flowering and last fruiting; and 10) growing season length, the interval time between leaf out and leaf colouring. Finally, we grouped the six phenophases into early-season phenophases and late-season phenophases according to the characteristics of plant development (Stuble et al. 2021). The early-season phenophases associated with plant morphogenesis and organogenesis included leaf out, first flowering, last flowering and first fruiting, and the late-season phenophases included last fruiting and leaf colouring in this analysis.

Other variables, including longitude, latitude, mean annual temperature (MAT), mean annual precipitation (MAP), intensity and season of experimental treatment and functional group of plant species, were also collected (Supporting information). In several studies, MAT and MAP were not reported, and thus, we obtained them from the data bank at www.worldclim.org according to the latitude and longitude of the research site. In total, we selected 63 peer-reviewed articles in the study (Supporting information).

Statistical analysis

We used a meta-analytical method to assess the phenophase responses of terrestrial plant species to altered precipitation. Following previous studies (Arft et al. 1999, Stuble et al. 2021), we calculated the shift in days induced by treatment to compare phenophase responses to increased and decreased precipitation treatments (Eq. 1):

$$\text{Shift in days} = \bar{x}_t - \bar{x}_C$$

where $\bar{x}_t$ and $\bar{x}_C$ are the average values of plant phenological parameters from the treatment and control groups, respectively.

We used the sample size (N) to weigh individual cases, which was consistent with other studies (Adams et al. 1997, Peng et al. 2017)(Eq. 2):

$$w_i = \frac{N_c N_t}{N_c + N_t}$$

where N_c and N_t are the sample sizes in the treatment and control groups, respectively. W_i is a weighing factor, and a higher value gives a greater weight to cases whose estimate has a higher precision.

The weighted responses across all cases were calculated (Hedges et al. 1999)(Eq. 3):

$$\text{Shift in days}_{++} = \frac{\sum_{i=1}^{k} w_i \left(\text{Shift in days}\right)}{\sum_{i=1}^{k} w_i}$$

where k is the total number of cases and i represents the number of individual cases.

The 95% confidence intervals (cis) were obtained by the bootstrapping method based on 999 iterations using METAWIN ver. 2.1 (Sinauer Associates Inc.) (Adams et al. 1997). The bootstrap method for meta-analysis is more efficient when the sample sizes are small because bootstrapping estimates the parameter and confidence interval by simulating a number of samples, which would avoid bias caused by small sample sizes (Van Den Noortgate and Onghena 2005). If the 95% cis did not overlap with zero, then the effects of altered precipitation were considered significant. A positive weighted effect indicates a delayed timing or an extended duration of phenophases, and a negative value represents an advanced timing or a shorter duration.

We used meta-regression to examine the relationships between phenophase responses and climate conditions (MAT, MAP and wetness index), experimental factors (experimental season and intensity of treatment) and plant characteristics (plant functional group, longevity and pollination type). The experimental season was divided into four types (winter, spring, summer and spring to autumn). We separated plant species into different functional groups (woody versus herbaceous plants), longevity (annual/biennial versus perennial plants) and pollination type (wind versus insect-pollinated plants). The range of other continuous variables are in the Supporting information. The wetness index was calculated as follows in Eq. 4 (De Martonne 1926):

$$\text{wetness index} = \frac{\text{MAP}}{\text{MAT} + 10}$$

After separating the case studies into different groups, we employed homogeneity tests to examine whether different groups responded differently to altered precipitation (Gurevitch and Hedges 1999, Harrison 2011). Total heterogeneity (Q_t) was divided into within-group (Q_w) and between-group (Q_b) heterogeneity. Responses were considered to be statistically significant among groups when the p value of Q_b was less than 0.05. In addition, we tested the publication bias of ten phenophase responses by Egger's regression and fail-safe analysis (Supporting information).

Results

Responses of plant phenophases to altered precipitation

Increased precipitation advanced early-season phenophases, including leaf out (95% CI: −5.30 to −2.87 days), first flowering (95% CI: −2.83 to −0.98 days) and first fruiting (95% CI: −3.99 to −1.01 days) (Fig. 2a). However, it delayed leaf colouring (95% CI: 0.01–3.37 days). The timing shifts caused by increased precipitation led to an extension of the fruiting phase, reproductive phase and growing season (Fig. 2b). In contrast, decreased precipitation delayed leaf out (95% CI: 2.17–4.50 days) but advanced leaf colouring (95% CI: −11.21 to −5.01 days). The timing shifts with decreased precipitation led to a shorter growing season but an unchanged flowering phase.

Climate drivers of the plant phenophase responses

The responses of many phenophases to altered precipitation were regulated by climate conditions (Supporting information). In general, most plant phenophases exhibited stronger responses to altered precipitation at drier sites than at wetter sites (Fig. 3, Supporting information). Specifically, the delay of leaf colouring and the extension of flowering duration,

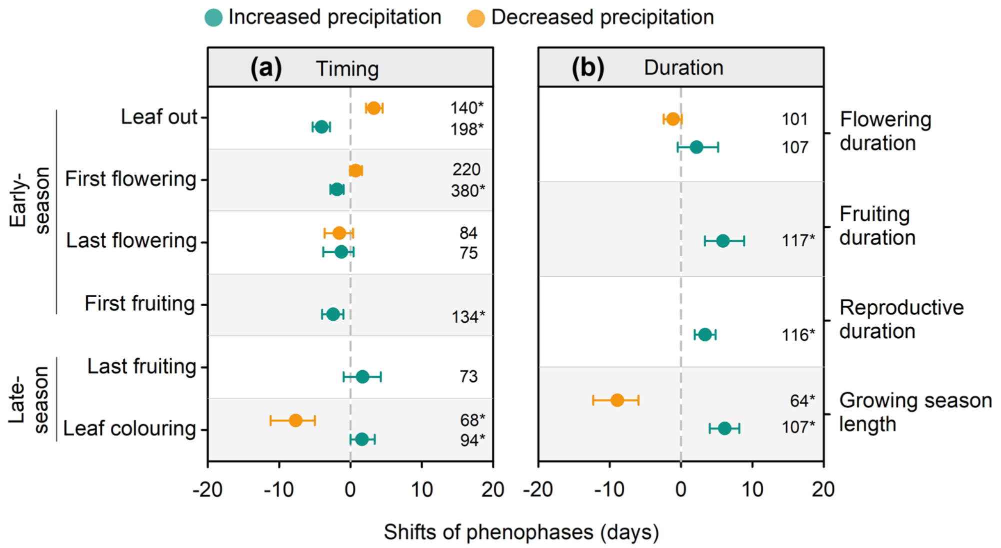

Figure 2. Responses of plant phenophases to experimental precipitation changes. In (a), six phenological timings. Four phenophases, leaf out, first flowering, last flowering and first fruiting, were considered early-season phenophases. Two phenophases, last fruiting and leaf colouring, were considered late-season phenophases. In (b), four phenological durations. The vertical dotted lines indicate that the shift in phenophases equals 0. The numbers on the right represent the number of observations. Error bars represent 95% bootstrap confidence intervals. The asterisks denote significant effects induced by precipitation changes ($p < 0.05$).

fruiting duration and reproductive duration with increased precipitation were attenuated with the increase in the wetness index (Fig. 3c–f). At the same time, the delay of leaf out, the advancement of last flowering, leaf colouring and the compression of flowering duration and growing season length under decreased precipitation became less pronounced at sites with a larger wetness index (Fig. 3g–k).

Leaf out and first flowering responded more to increased precipitation, but last fruiting and leaf colouring responded less to increased precipitation at sites with higher MATs (Supporting information). The responses of the last flowering and flowering duration to decreased precipitation became more pronounced at sites with higher MAT (Supporting information).

Experimental factors and plant characteristics that mediate the plant phenophase responses

The responses of most phenophases varied with seasons when precipitation change was applied (Supporting information). The responses of early-season phenophases to increased precipitation were stronger in winter or spring than in summer or spring–autumn (Fig. 4a–d). However, the late-season phenophases showed stronger responses to increased precipitation in spring–autumn than in winter (Fig. 4e, f). Thus, the extension of the growing season length was greater with increased precipitation in winter than in spring–autumn (Fig. 4g). In addition, increased precipitation in spring shortened the flowering duration, but increased precipitation in winter prolonged it (Fig. 4h). Decreased precipitation in spring–autumn delayed leaf out and advanced leaf colouring, thus shortening the growing season length. However, decreased precipitation in spring did not affect leaf out and delayed leaf colouring, which led to prolonged growing season (Fig. 4i, l, m). In addition, the flowering phenophases responded less to decreased precipitation in summer than in the other seasons (Fig. 4i–k).

The responses of several phenophases increased as the intensity of the treatment increased. Specifically, the advancement of first fruiting accelerated with increasing intensity of precipitation increases, and the compression of the growing season became more pronounced with increasing intensity of precipitation decreases (Fig. 4n, p). In addition, the last fruiting tended to be delayed with slight precipitation increases but to be advanced with high intensity precipitation increases (Fig. 4o).

The last flowering, leaf colouring and reproductive duration of woody plants were more sensitive to increased precipitation than those of herbaceous plants (Fig. 5, Supporting information). In addition, in comparison to that of annual plants, the fruiting duration of perennial plants was more sensitive to increased precipitation (Fig. 5, Supporting information).

Discussion

Ecologists have spent substantial effort on elucidating how global climate changes affect terrestrial plant phenology. However, less attention has been devoted to their responses to precipitation changes in comparison with those to climate warming (Piao et al. 2019). We identified general patterns of plant phenophase responses to precipitation across terrestrial species. Our results showed diverse responses of plant phenophases to precipitation changes between early- versus late-season phenophases, which led to changes in phenological durations. We found that phenological responses were greatly affected by the experimental seasons of precipitation change. Increased winter or spring precipitation had greater effects

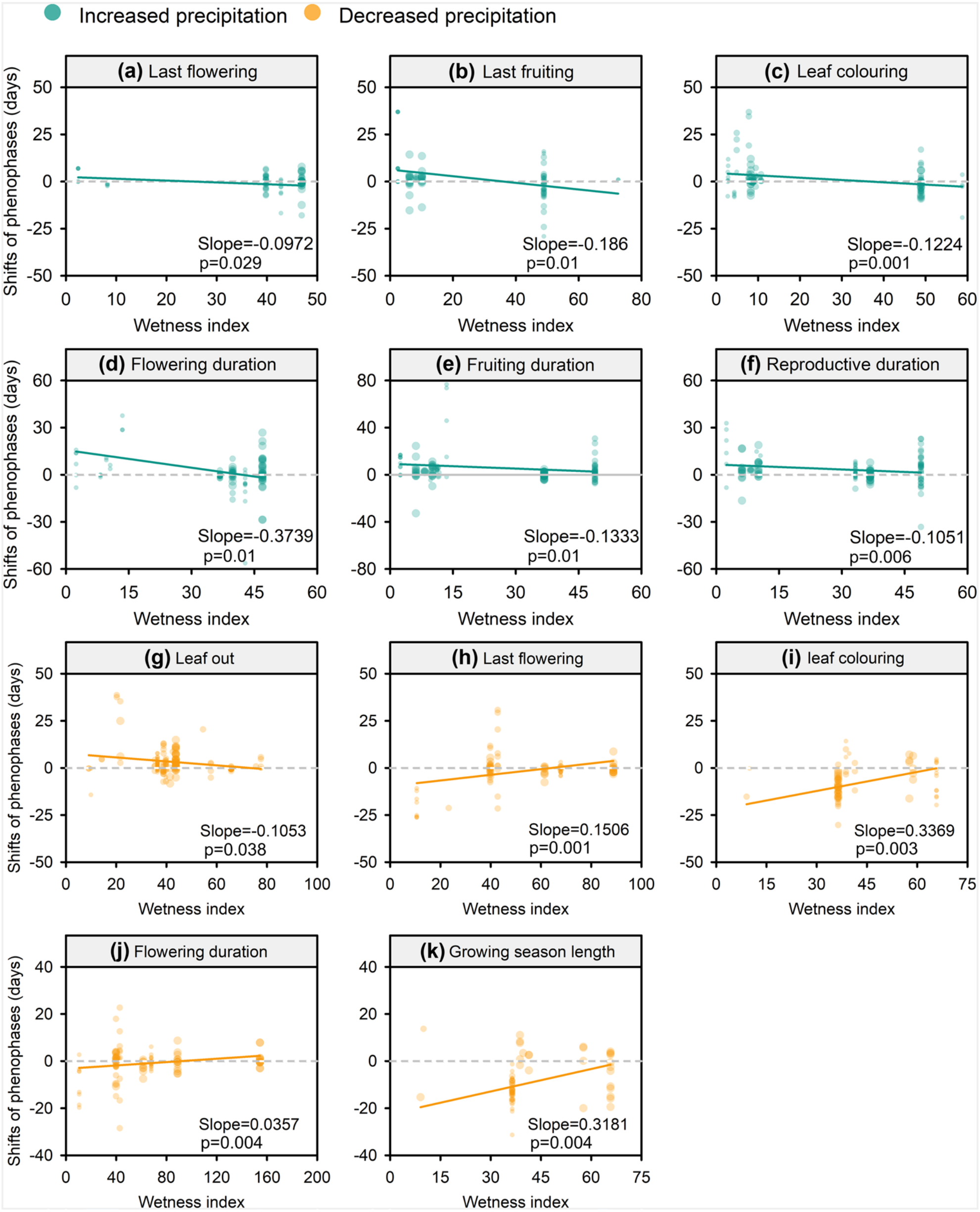

Figure 3. Relationships between phenological responses to precipitation change and the wetness index. In (a–f), phenological responses to increased precipitation. In (g–k), phenological responses to decreased precipitation. Here, leaf out, first flowering, last flowering and first fruiting were considered early-season phenophases. Last fruiting and leaf colouring were considered late-season phenophases. The horizontal dashed lines indicate that the shift in phenophases equals zero. Circle sizes are proportional to the weights used in the meta-regression.

on early-season phenophases, and increased spring–autumn precipitation had greater effects on late-season phenophases. We also found that plant phenophases were more sensitive to altered precipitation at drier sites than at wetter sites, and these results may help us to better predict future ecosystem dynamics under climate change.

Diverse responses of plant phenophases to altered precipitation

Our results showed that the early- and late-season phenophases respond differently to precipitation increases. The advancement in early-season phenophases that we observed may have been related to increased precipitation relieving plant water stress and leading to plant growth (Seneviratne et al. 2010) and improving plant nitrogen availability by increasing soil physical fragmentation and nutrient diffusion (Santiago et al. 2005, Chang et al. 2014). Additionally, plant growth is characterized by turgor-driven expansion and differentiation of cells, which are mostly regulated by water content and availability (Coussement et al. 2021). In the early developmental stages of plants, increased precipitation is likely to promote leaf expansion and flower opening by increasing turgor pressure on cells (Beauzamy et al. 2014). In contrast,

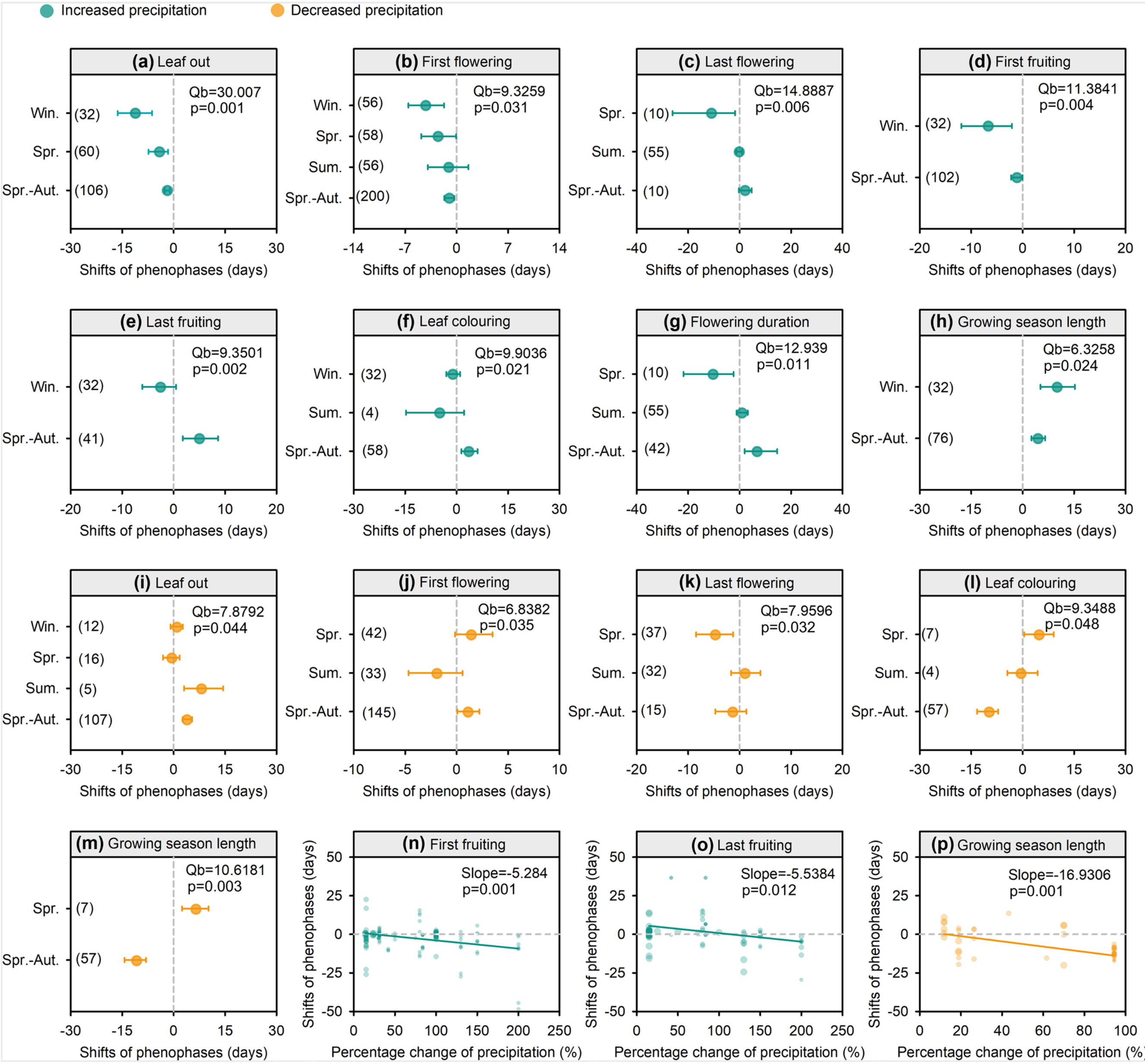

Figure 4. Impacts of experimental factors on the responses of plant phenophases to precipitation changes. (a–m) Comparisons of phenological responses among different seasons of precipitation change. In (n–p), relationships between phenological responses to precipitation change and intensity of treatment. Here, leaf out, first flowering, last flowering and first fruiting were considered early-season phenophases. Last fruiting and leaf colouring were considered late-season phenophases. Q_b denotes the heterogeneity in the sensitivity explained by experimental seasons. The numbers on the left represent the number of observations, and the vertical dashed lines indicate that the shift in the phenophases equals 0. 'Spr.', 'Sum.', 'Aut.' and 'Spr.–Aut.' are abbreviations for spring, summer, autumn and spring to autumn, respectively.

we observed a delayed effect of precipitation increases on the late phenophases. Improving soil water and nutrient conditions with increased precipitation is likely to retard a series of physiological processes related to foliar senescence, such as chlorophyll degradation, protein degradation and lipid peroxidation (Munné-Bosch et al. 2001, Munné-Bosch and Alegre 2004), thus delaying late-season phenophases.

In contract to increased precipitation, decreased precipitation led to a delay in leaf out, which may have been related to drought-induced water and nutrient limitation on plant growth (Hu and Schmidhalter 2005). However, our results showed that decreased precipitation tended to advance the last flowering. The premature end of flowering may have occurred because many species accumulate reactive oxygen radicals under drought stress, which accelerates the end of the reproductive phases (Van Breusegem and Dat 2006, Gechev and Petrov 2020). At the same time, an advancement in leaf colouring under decreased precipitation may reduce water losses from leaf transpiration and stimulate nutrient redistribution to other younger tissues; thus, plants will adopt this

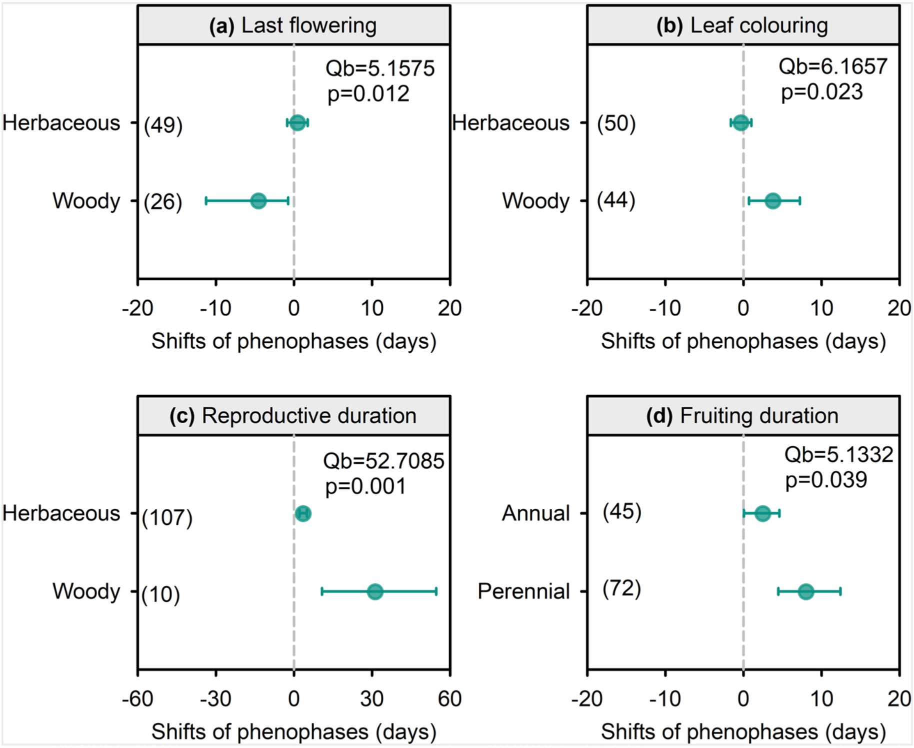

Figure 5. Comparisons of phenological responses to increased precipitation among functional groups and longevity. Q_b denotes the heterogeneity in responses explained by the functional groups and longevity, and $p < 0.05$ indicates significant differences between groups. The numbers on the left represent the number of observations, and the vertical dashed lines indicate that the shift in the phenophases equals 0.

strategy to survive severe drought stress (Munné-Bosch and Alegre 2004).

Such timing shifts of phenophases under altered precipitation led to changes in phenological duration in our study, and this impact may further affect some ecosystem processes. The prolonged growing season that occurred with increased precipitation could lead to increased carbon uptake, as an extra one day increases gross primary productivity by 5.8 g C m^{-2} in the Northern Hemisphere (Piao et al. 2007). The slightly compressed flowering phase that occurred with decreased precipitation may reduce pollinator visit duration and success of plant reproduction and even cause phenological mismatch between flowering and pollinators (Rafferty and Ives 2012, Thackeray et al. 2016).

Responses of phenophases regulated by background climate

Our results showed that the responses of most plant phenophases were stronger at drier sites than at wetter sites, which was consistent with previous findings showing that plant productivity responded more to precipitation changes with a lower background level of precipitation (Wilcox et al. 2017). This result was likely due to the increasing water limitation of plant growth and decreasing biogeochemical limitations as the sites became drier (Knapp et al. 2017, Gherardi and Sala 2019). In addition, species will shift their strategies from slow to fast resource acquisition as the environment becomes drier because of higher selection pressure, thus displaying maximum photosynthesis rates and growth rates when water is available and benefitting more from increased precipitation (Santiago et al. 2004, Carvajal et al. 2019). In addition, the high level of competition for soil resources that occurs among species at wetter sites, caused by greater cover and density of plants, is likely to limit the positive effect of increased precipitation (Vinton and Burke 1997, Hänel and Tielbörger 2015).

We found that the early-season phenophases (i.e. leaf out and first fruiting) were more responsive to increased precipitation at colder sites than at warmer sites. This result is in contrast to our expectation because more precipitation usually reduces soil temperature and exacerbates temperature limitations for plants at colder sites. We speculated that the opposite results may have occurred because the colder sites often had lower precipitation amounts (Fig. 1c), and the plants at drier sites usually exhibited sensitive responses to altered precipitation (Shen et al. 2015). In addition, increased precipitation would lead to higher snowfall at colder sites during the pregrowing season, which could keep the soil warm, increase thaw depth and stimulate soil mineralization (Blanc-Betes et al. 2016, Semenova et al. 2016). The higher snow amount may make the plants at colder sites respond more to increased precipitation than those at warmer sites. We also found that the advancement of last flowering with decreased precipitation became stronger with increasing MAT, which could have been related to plant reproduction being more likely limited by available water as ecosystems became warmer (Huxman et al. 2004, Shen et al. 2015).

Divergent responses of phenophases with seasons and plant functional group treatments

The advancement of early-season phenophases with increased precipitation was greater in winter or spring than in the other seasons in our study. Such divergent responses may have occurred due to several possible reasons. First, increased precipitation in winter/spring likely transferred water to deeper soil profiles with the water staying longer because of low evaporation rates in cold seasons, which may have had greater effects on plant phenology (Li et al. 2020). Second, precipitation in winter or early spring often occurs as snow over the soil surface at mid and high latitudes, which would be beneficial for keeping the soil warm during the cold season and stimulating root growth (Blanc-Betes et al. 2016, Semenova et al. 2016). This phenomenon is supported by several studies showing that the growth of trees is mostly controlled by the amount of precipitation in winter compared to that in other seasons (Pellizzari et al. 2014, Allen et al. 2019).

Our results showed that increased precipitation in spring–autumn significantly delayed late-season phenophases, whereas increased precipitation in winter or summer tended to advance those phenophases. The delayed late-season phenophases may have occurred because increased precipitation in autumn would directly alleviate soil water limitation. The advanced late-season phenophases may have occurred because increased precipitation in winter would increase early-season productivity, which could result in plants finishing their seasonal cycles more rapidly (Zani et al. 2020).

In addition, we found that in comparison to the herbaceous plant phenophases, the woody plant phenophases were more responsive to increased precipitation. The stronger responses of woody plants may be attributed to their relatively high evapotranspiration rates and water demand (Joffre and Rambal 1993). Additionally, woody plants have a deeper root distribution than herbaceous plants and may benefit more from increased deep soil moisture (Jackson et al. 1996). In contrast, the overall stable phenophases of the herbaceous plants that occurred with the altered precipitation regimes were also likely related to their flexible morphology and diverse survival strategies (Šímová et al. 2018).

Conclusion

Understanding plant phenology in response to altered precipitation is key for predicting ecosystem dynamics under global climate change. Our study demonstrates that terrestrial plant species have diverse phenological responses to precipitation changes at different life stages, which are strongly regulated by climate contexts and the season during which precipitation changes occur. These findings will help with incorporating the role of precipitation into next-generation phenological models to improve the prediction accuracy.

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Conflict of interest – The authors declare no competing interests.

Author contributions

Chunyan Lu: Data curation (lead); Writing – original draft (lead). **Juanjuan Zhang**: Data curation (equal). **Xueting Min**: Data curation (equal). **Jianghui Chen**: Data curation (supporting). **Yixuan Huang**: Data curation (supporting). **Hongfang Zhao**: Writing – review and editing (equal). **Tao Yan**: Writing – review and editing (equal). **Xiang Liu**: Writing – review and editing (equal). **Hao Wang**: Writing – review and editing (equal). **Huiying Liu**: Writing – review and editing (lead).

Data availability statement

The data used in our study are available in the Figshare repository: https://figshare.com/s/6336c33cac0f83fb24ed.

Supporting information

The Supporting information associated with this article is available with the online version.

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