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Functional group and aridity regulate impacts of climate change on plant phenology: a meta-analysis

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The interaction between temperature and precipitation greatly affects plant phenology. However, these effects can vary between additive, antagonistic, and synergistic, and it is not clear what determines these different outcomes. One hypothesis is that the effect on plant phenology varies with aridity and plant functional group. Here, we find support for this hypothesis using a global meta-analysis on the timing of leaf-out (2178 values from 55 experimental sites) and flowering (4027 values from 117 experimental sites). We find that, globally, the onset of leaf-out is more influenced by water availability than by temperature, while first flowering is more affected by temperature than by precipitation. On its own, warming advances leaf-out for all functional groups (except in semi-humid regions), whereas warming combined with decreased precipitation delays leaf-out in semi-arid regions. Warming also advances flowering across all functional groups, regardless of changes in precipitation and aridity. We observe synergistic effects of warming and precipitation on leaf-out for forbs in semi-arid regions, while antagonistic effects occur for grasses and sedges except in arid regions. Our findings suggest that considering drought tolerance or resistance of plants across ambient climates is critical for improving our understanding and predictions of how plant phenology responds to climate change.

Shifts in phenology can significantly impact organism fitness, ecosystem function, and the provision of ecosystem goods and services[1–4]. Since the early 1980s, climate change has driven substantial changes in plant phenology (e.g., leaf-out and flowering) across natural terrestrial ecosystems globally[5–7]. Evidence suggests that warming generally advances phenology, as plants meet their accumulated heat requirements earlier in warming conditions[7–10]. However, warming can also induce soil drought, which may delay phenology[11,12]. Additionally, increased precipitation combined with warming tends to advance phenology, especially in arid and semi-arid zones[12–18]. These discrepancies in the effects of climate change on phenology may stem from the fact that manipulative experiments used to study climate change effects have been conducted in habitats with different ambient climate conditions, particularly different levels of aridity (i.e., arid,

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semi-arid, semi-humid, and humid regions). The effects of ambient climate on plant phenology are often greater than those of experimental treatments[19]. Yet, whether ambient climate modulates the responses of plant phenology to warming and its interaction with precipitation remains unclear.

A trade-off between temperature and precipitation might explain the different responses of plant spring phenology in different habitats[16,20,21]. Long-term monitoring and manipulative experiments reveal significant differences in plant phenology responses to warming across various regions (e.g., arid or humid sites) or climates[3,22,23]. For example, the response of flowering phenology in the perennial grass *Spiranthes sinensis* to warming was opposite in humid vs. non-humid regions[20], and the effects of warming on plant phenology differed based on drought conditions in grasslands[16]. However, most of these manipulative experiments have been conducted at single sites, leaving it unclear whether the effects of warming and its interaction with precipitation alterations on phenology depend on aridity. We hypothesized that in arid and semi-arid regions, decreased precipitation (DP) could delay plant phenology, while increased precipitation (IP) and temperature could advance phenology; the interaction between warming and DP could delay plant phenology, but the interaction between warming and IP could advances plant phenology (additive or synergistic effects) (Fig. 1a). In semi-humid regions, both DP and IP could advance plant phenology due to the limiting effect of water availability, and the interactions between warming and precipitation alterations could also advances plant phenology (additive or synergistic effects) (Fig. 1a). However, in humid regions, excessive precipitation could delay the accumulation of heat required, so DP could advance plant phenology, but IP could delay plant phenology; warming and its interaction with DP could advance phenology (additive effects or synergistic effects), however, the interaction between warming and IP could delay plant phenology (antagonistic effects) (Fig. 1a).

Additionally, the composition of plant species and functional groups in natural grasslands varies and can lead to different responses in phenology to warming and precipitation alterations due to differences in adaptability and growth characteristics[8,16,17,24–27]. Plants in arid and semi-arid regions generally exhibit higher drought tolerance or resistance, which may partially offset the negative effects of warming-induced reductions in soil water content on phenology[17,28]. Shallow-rooted plants with an annual life history (low drought resilient species) tend to be more vulnerable to warming and precipitation alterations than deep-rooted, perennial species (high drought tolerant species)[11,12,17,29]. For example, warming delayed the first flowering of some shallow-rooted early flowering species due to drought conditions in the Qinghai-Xizang Plateau (a semi-arid region)[11,30]. Other studies found that warming advanced the green-up of *Kobresia pygmaea* (sedge, a shallow-rooted species) in wet conditions[12,31], while it delayed its green-up in dry conditions[12]. These results suggest that the effects of climate change on plant phenology vary with ambient climate and functional groups, yet the extent of this pattern remains unclear.

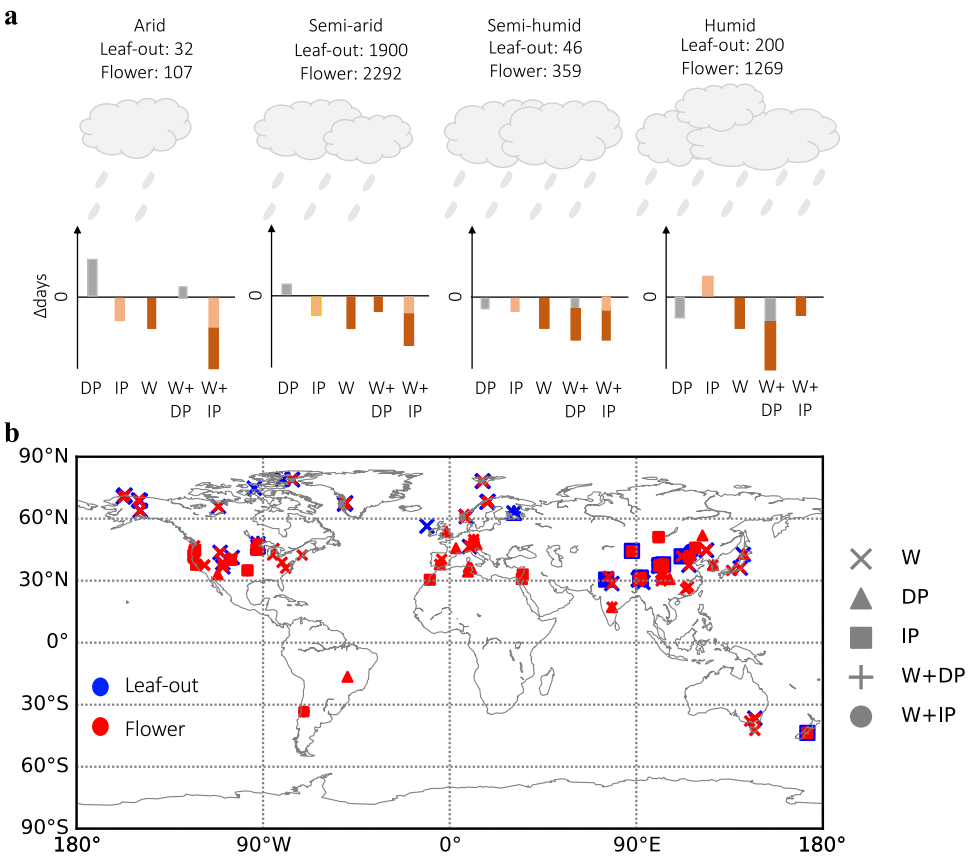

Fig. 1 | Conceptual diagram of how interactive effects between warming and precipitation alterations on plant phenology (DOY, day of year) depend on ambient climate. a Positive and negative values mean delay and advance in plant phenology, respectively. The bars mean the magnitudes of delay or advance. Gray, orange and red represent the responses of plant phenology to decreased precipitation (*DP*), increased precipitation (*IP*) and warming (*W*), respectively. The interactions sometimes occur, and they vary from additive (e.g., in semi-arid and semi-humid regions) to synergistic effects (e.g., in arid regions) and antagonistic effects (e.g., in humid regions) depending on aridity. The number of manipulative experiments for measurements of onset of leaf out and first flowering under different climatic zones are shown for each level of aridity. **b** Site location of the experiments with manipulative warming and precipitation alteration at global scale (The base map was created using the Matplotlib Basemap Toolkit in python 3.9). *W* warming; *DP*; decreased precipitation; *IP*; increased precipitation.

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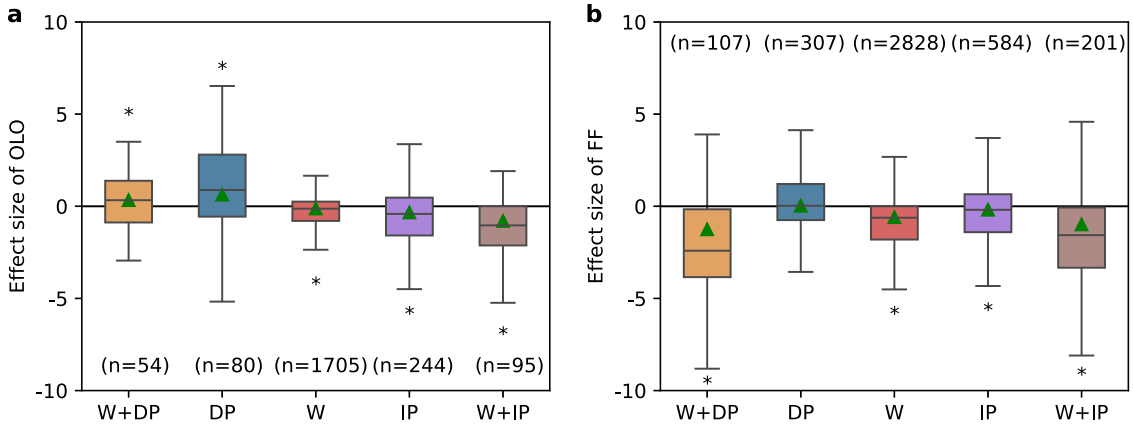

Fig. 2 | Effects of warming and precipitation manipulations on the early spring phenology. The responses of (**a**) onset of leaf out (OLO) and (**b**) first flowering date (FF) to warming combined with precipitation manipulations (*W*: warming; *DP*: decreased precipitation; *IP*: increased precipitation). Negative values of effect size indicate a phenological advances, and positive values of effect size indicate phenological delays. The two-tailed test was used to monitor whether the treatment effect was significant. Asterisks represent significant treatment effects ($p < 0.05$). Box plots also display the 25th and 75th percentiles (box edges), minima and maxima (whiskers). Asterisks represents that the treatment effects are significant. The numbers of n represent the sample sizes in the figure. Source data are provided as a Source Data file.

To test whether the effect of interactions between temperature and precipitation on plant phenology varies with aridity and plant functional groups and explore the underlying mechanisms, we construct a global dataset and conduct a synthetic-analysis (see Methods). We collect 2,178 values for the onset of leaf-out from 55 experimental sites and 4,027 values for first flowering from 117 experimental sites across arid, semi-arid, semi-humid, and humid zones worldwide (Fig. 1), and include the following functional groups: grass, sedge, forb, and legume. Our study addresses three key questions: (1) How do precipitation changes modulate the effects of temperature on first leaf-out and flowering across natural grasslands globally (i.e., independent of ambient climate and functional group)? (2) Do the interactive effects between temperature and precipitation vary with aridity (arid, semi-arid, semi-humid, and humid)? (3) How do the interactions of warming, precipitation, and aridity depend on functional groups?

Results

Responses of onset of leaf-out and first flowering to climate manipulations

Phenological data for the date of onset of leaf out (hereafter leaf-out) and first flowering (hereafter flowering) was collected globally based on climate manipulation experiments, including warming, decreased precipitation (DP), increased precipitation (IP), warming + DP, and warming + IP. Overall, precipitation alterations significantly affected leaf-out and flowering, temperature alone also affected flowering but its interaction with aridity affected leaf-out (Table S1). Considering overall effect sizes for each treatment across all functional groups and aridity regions, warming on its own advanced the leaf-out date (Hedges' g = −0.12, 95% CI: −0.15 to −0.10) (Fig. 2a), with 62.3% of cases showing an advance and 37.8% showing a delay (Fig. S1a). IP also advanced leaf-out (Hedges' g = −0.34, 95% CI: −0.44 to −0.23). Conversely, DP delayed leaf-out (Hedges' g = 0.63, 95% CI: 0.46 to 0.81), independent of warming (Fig. 2a). Warming advanced the flowering date (Hedges' g = −0.59, 95% CI: −0.61 to −0.57) (Fig. 2b), with 76.1% advancing and 23.9% delaying (Fig. S1b). IP also advanced flowering (Hedges' g = −0.19, 95% CI: −0.24 to −0.13), regardless of warming. Conversely, DP did not affect flowering, although flowering advanced when DP was combined with warming (Fig. 2b). In summary, warming and IP generally advance leaf-out and flowering, whereas DP delays leaf-out.

Segmented regression analysis revealed that there might be drought thresholds in the response of leaf-out to increased aridity index (i.e., higher humid) under the treatment of warming (0.36) (Fig. 3c; Table S2), and there might be drought thresholds in the response of flowering to increased aridity index under the treatment of DP (0.33), warming (0.16) and coupled warming-IP (0.46) (Figs. 3f, h and j; and Table S2). Moreover, only warming significantly delayed leaf-out and flowering under drought before breakpoint due to reduction in soil water content induced by warming, whereas it significantly advanced leaf-out and marginally advanced flowering after breakpoint (i.e., along increase in precipitation) (Figs. 3c, h). Warming-IP interaction significantly advanced flowering with aridity before the breakpoint, and it first advanced and then delayed flowering when aridity index was > 0.7 (Fig. 3j). However, the responses of leaf-out to DP and flowering to warming-DP interaction advanced with the increasing of aridity index (Figs. 3a, i). These results suggested that the precipitation alteration regulated the response of flowering to warming depending on aridity, and there was a synergistic effect between warming and IP along aridity and an antagonistic effect between warming and IP when aridity index was > 0.7 (i.e., humid regions).

Furthermore, negative relationships were observed between both the changes in dates of leaf-out and flowering and warming magnitude (both $p < 0.001$) (Table S3), suggesting that leaf-out and first flowering occur earlier with higher warming magnitudes. However, positive relationships between these dates and warming duration were also found (both $p < 0.001$) (Table S3), suggesting that longer warming episodes could reduce the rate of advancement in leaf-out and flowering.

In addition, warming method and the intensity of precipitation changes may affect the response degree of leaf-out and flowering to warming. For instance, infrared heater warming had larger effects on leaf-out and flowering than the method of chamber and cable; and the date of leaf-out was significantly advanced with increasing precipitation intensity. However, neither warming method nor precipitation intensity altered the response direction or trend of different phenophases (Figs. S2 and S3).

Effects of aridity on the responses of plant phenology to climate change depend on functional group

Aridity modulated the effects of climate change on mean leaf-out and mean flowering, depending on functional group (Fig. 4 and Table S1). Warming significantly advanced leaf-out across climate regions, except in semi-humid regions, where it had no effect on leaf-out (Fig. 4a). However, this effect of warming depended on functional

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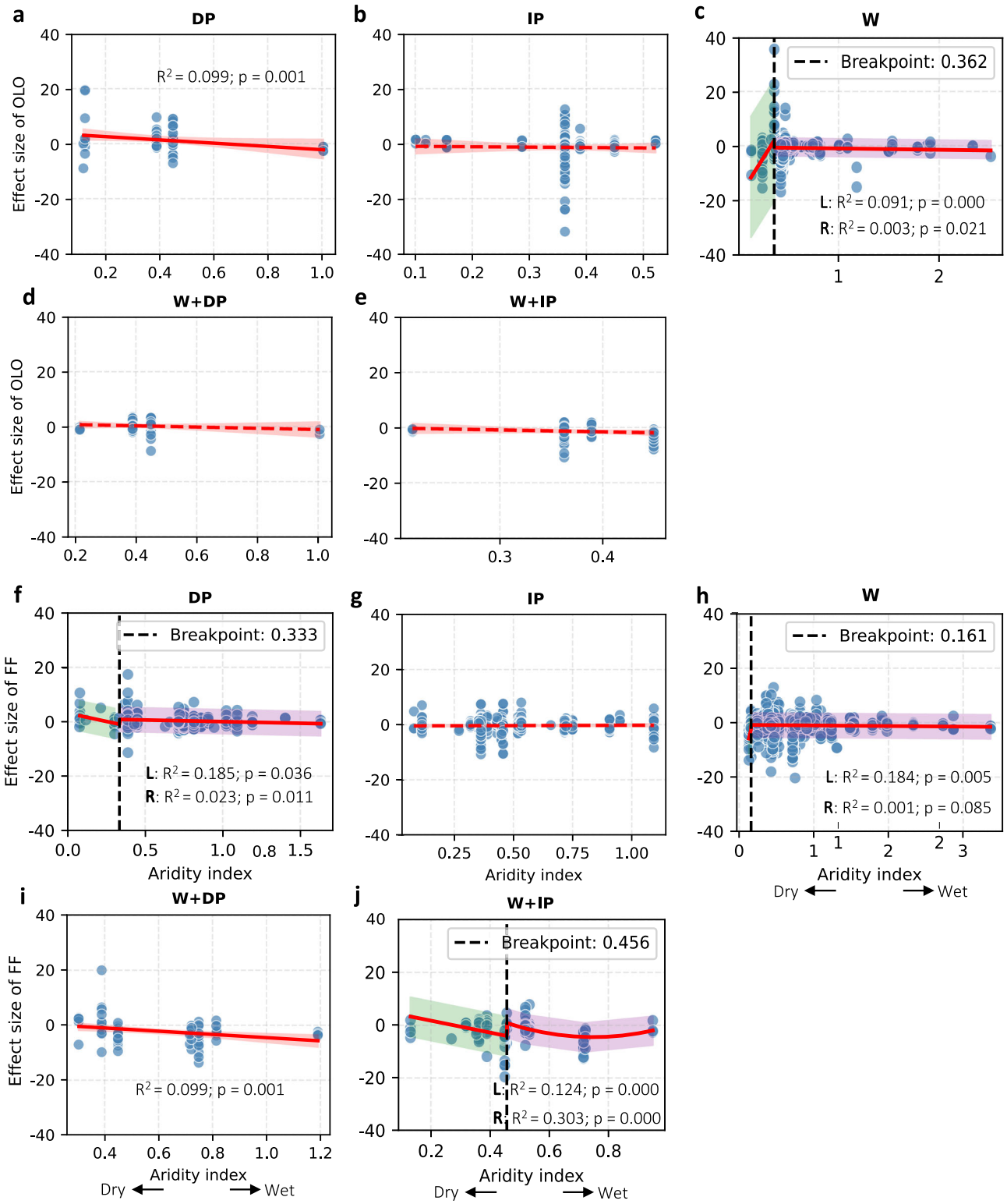

Fig. 3 | Responses of the early spring phenology to increased aridity index under the treatment of warming and precipitation changes. a–e Onset of leaf-out (OLO) and (**f–j**) first flowering (FF). The dashed line indicates that there is no significant relationship between the aridity index and the phenological response ($p > 0.1$). The shaded area represents the 95% confidence interval. *W* warming; *DP* decreased precipitation; *IP* increased precipitation; *L* the regression results of the left segment; *R* the regression results of the right segment. Regression equations were shown in Table S2. Source data are provided as a Source Data file.

group: warming only advanced the leaf-out of grasses in arid regions; forbs, sedges, and legumes in semi-arid regions; and forbs and grasses in humid regions (Fig. 4a). Warming also significantly advanced flowering for all functional groups, regardless of climate region (Fig. 4b). These results suggest that the effect of warming on leaf-out is influenced by both climate region (i.e., aridity) and functional group, whereas flowering is primarily determined by temperature, independent of aridity and functional group.

Findings from the decreased precipitation (DP) treatments indicate that water may not be a limiting factor for leaf-out in grasses in

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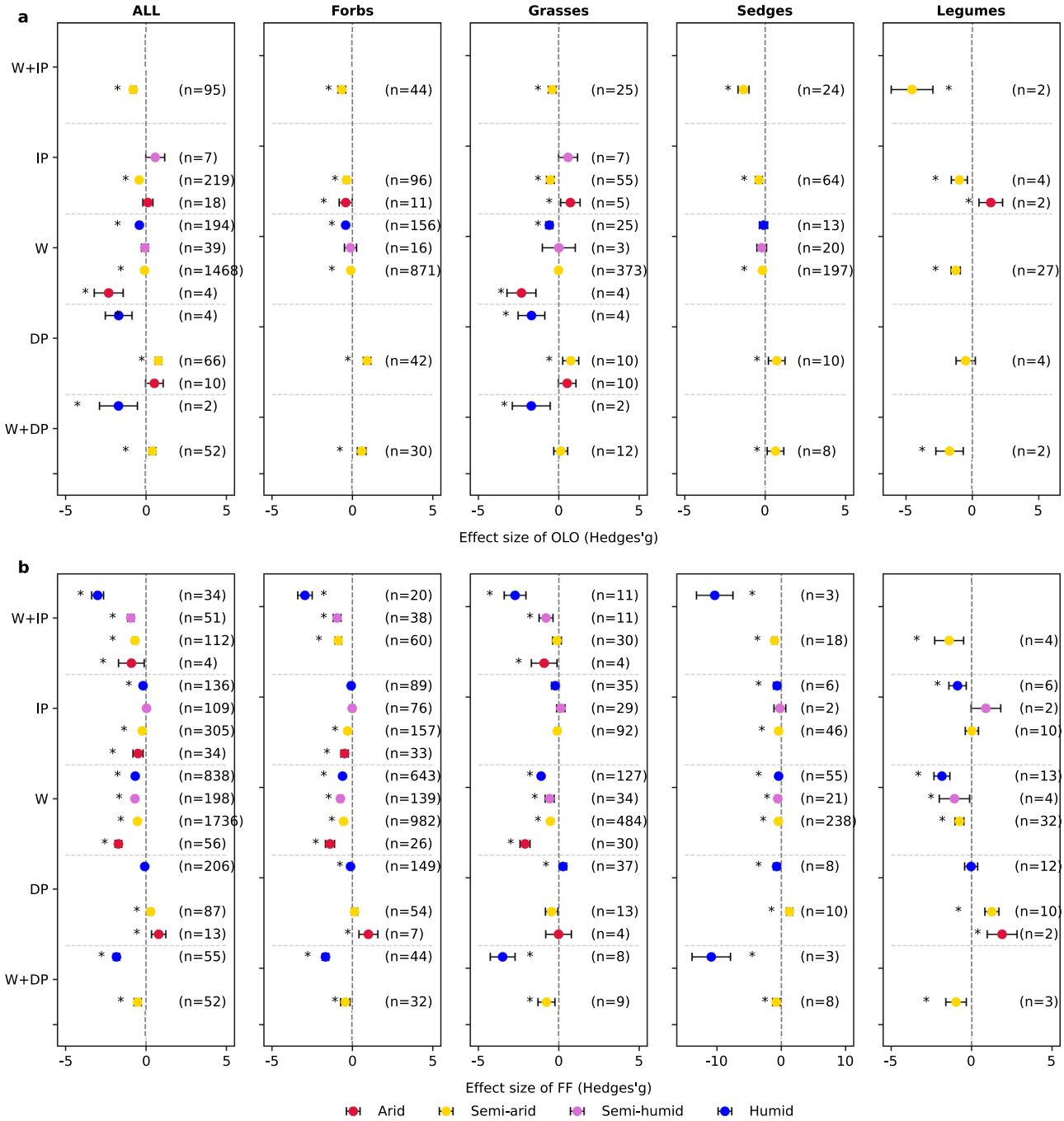

Fig. 4 | Effects of warming and precipitation treatments on the early spring phenology for different plant functional groups in various aridity. a Onset of leaf-out (OLO) and (**b**) first flowering (FF). Negative Hedges'g indicates the advance of OLO and FF, and positive Hedges'g indicates the delay of OLO and FF. *OLO* onset of leaf-out; *FF* first flowering; *PFGs* plant function groups. *DP* decreased precipitation; *IP* increased precipitation; *W* warming. Asterisks represent that the treatment effects are significant (95%CIs not overlapping with the zero lines). The numbers of *n* represent the sample sizes in the figure. Source data are provided as a Source Data file.

arid or humid regions and legumes in semi-arid regions, with warming effects overriding precipitation effects on leaf-out in legumes in semi-arid regions. DP significantly delayed leaf-out for all functional groups except legumes, which were unaffected in semi-arid regions (Fig. 4a). DP advanced leaf-out for grasses in humid regions but did not affect leaf-out for grasses in arid regions. The combination of warming and DP advanced leaf-out for grasses in humid regions and legumes in semi-arid regions but delayed leaf-out for forbs, grasses, and sedges in semi-arid regions. Conversely, increased precipitation (IP) advanced leaf-out for all functional groups in semi-arid regions (Fig. 4a). IP advanced leaf-out for forbs, but delayed leaf-out for grasses and legumes in arid regions, and had no effect on leaf-out for grasses in semi-humid regions. Warming with IP advanced leaf-out for all functional groups in semi-arid regions.

Although temperature seems to be the primary determinant of first flowering, water availability can inhibit the flowering of forbs, sedges, and legumes in certain climate regions. DP significantly delayed flowering for forbs and legumes in arid regions, of sedges and legumes in semi-arid regions, and of grasses in humid regions (Fig. 4b). However, DP advanced flowering for forbs and sedges in humid

regions and did not affect flowering for grasses and legumes in semi-arid regions, nor for forbs in semi-arid regions. Warming combined with DP advanced flowering for all functional groups in semi-arid and humid regions. In contrast, IP advanced the flowering for forbs in arid and semi-arid regions, for sedges in semi-arid regions, and for sedges and legumes in humid regions (Fig. 4b). IP did not affect flowering for grasses and legumes in semi-arid regions, for any functional groups in semi-humid regions, and for forbs and grasses in humid regions. Warming combined with IP advanced flowering for all functional groups across all climate regions, except for grasses in semi-arid regions, which displayed no effect (Fig. 4b).

In addition, the results of segmented regression analysis showed that both leaf-out and flowering across different plant functional groups exhibited nonlinear or linear responses trends with increasing aridity index under warming treatment. We found that warming significantly advanced the leaf-out and first flowering of forbs with increase in aridity index under both sides of breakpoints (Figs. 5a, j). However, warming delayed first flowering of grasses before aridity breakpoint (0.16), but advanced leaf-out and first flowering after aridity breakpoint (0.24 and 0.16, respectively) (Figs. 5b, k). Warming advanced leaf-out and first flowering of sedges with increased aridity index (Figs. 5c and 5i). However, the effects of DP and IP on leaf-out and first flowering did not vary with aridity index except the effects of DP on the first flowering of forbs and sedges, which advanced their first flowering with increase in aridity index (Fig. S4; Table S4). Moreover, warming + DP and warming + IP advanced first flowering across all plant functional groups with increased aridity index (Figs. 5m-5r). These results showed that the responses of plant phenology to warming and its interactions with precipitation alteration varied with aridity depending on plant functional groups.

Synergistic and antagonistic effects of temperature and precipitation on the early spring phenology depending on functional group

We further explored whether additive, synergistic or antagonistic interactions of temperature and precipitation alteration depended on aridity and functional groups (Figs. 6; and S5). We found that there was a significant synergistic effect of warming and DP on leaf-out of forbs, whereas an antagonistic effect was observed for sedges and legumes in semi-arid regions, and an additive effect for grasses in semi-arid and humid regions (Figs. 6a and S5a). Warming and IP showed synergistic effects on leaf-out for forbs, grasses, and sedges, and an additive effect was noted for legumes in semi-arid regions. These interactions of warming and precipitation alteration affected the summed individual effects on the leaf-out by −444% to 104% in Hedges' g across all study regions, with average changes of 274% observed (Fig. 7a).

Similarly, there was a significant synergistic effect of warming and DP on the flowering of legumes, with an antagonistic effect on flowering for grasses, and an additive effect on flowering for forbs in semi-arid regions (Figs. 6b and S5b). Warming combined with IP had a significant synergistic effect on the flowering for forbs, sedges, and legumes, but produced antagonistic effects for grasses in semi-arid, semi-humid, and humid regions, along with additive effects for forbs in semi-humid and humid regions. These interactions of warming and precipitation alteration affected the summed individual effects on flowering by 53% to 125% in Hedges' g across all study regions, with average changes of 80% observed, respectively (Fig. 7b).

Discussion

Our study provides insights into the changing patterns of plant phenology globally and its underlying mechanisms driving these changes in two key ways. First, we found that precipitation primarily determined shifts in leaf-out, while first flowering was more determined by temperature than by precipitation changes across the global scale, across most levels of aridity and functional groups combined (Fig. 2 and Table S1). Second, there were significant synergistic and antagonistic effects of temperature and precipitation alterations on plant phenology depending on aridity and functional group, suggesting that how aridity modulates the effects of warming on plant phenology varies with functional group (Figs. 4–7 and Table S1). Therefore, our findings highlight that understanding the regulations of aridity and functional group on the effects of climate change on plant phenology could be critical for understanding the underlying mechanisms of the responses of plant phenology to future climate change.

Our results imply that water availability primarily determines leaf-out timing[11,12,17], whereas temperature is the primary driver of flowering[32]. When combining all functional groups and aridity levels, we observed that decreased precipitation significantly delayed mean leaf-out, regardless of warming; in contrast, warming consistently advanced mean first flowering, regardless of precipitation alterations. The unexpected response of leaf-out may be partially attributed to the fact that most of the data originated from semi-arid regions (Fig. 1). Leaf-out may be delayed for some species in response to increased warming for many reasons. Preseason water deficiencies induced by warming likely restrict plant growth and delay leaf-out, even when heat accumulation requirements are met[11,30]. Additionally, warming advances the timing of spring snowmelt in alpine ecosystems[33–36], increasing soil exposure prior to leaf-out, therefore potentially intensifying preseason drought stress through evapotranspiration[37,38], and increasing the risk of frost damage[39,40]. Previous studies had also indicated that precipitation played a dominant role in the changes of early phenology in semi-arid regions[12,18,41]. These results suggested that the timing of leaf-out is not only affected by chilling requirements and accumulated temperature, but soil moisture is also a key factor for plants to break dormancy, bud differentiation or stem germination, especially in arid and semi-arid grassland ecosystems.

Effects of warming and precipitation on timing of leaf-out are more nuanced once functional groups and aridity are considered. The diverse interaction types (e.g., synergistic or antagonistic effects) between warming and precipitation across different climatic regions emphasize that the regulatory role of water availability on leaf-out depends on the ambient climate. Specifically, water availability has a greater impact on leaf-out in semi-arid regions compared to humid regions (Fig. 4), presumably because water is a more critical constraint on plant growth in semi-arid environments[20,42]. Indeed, studies conducted in dry ecosystems with mean annual precipitation below 300 mm reported delayed effects of experimental warming on spring phenology, while studies in wetter conditions with over 800 mm of annual precipitation typically detected advances[9,43,44], which further support our findings that there may be aridity index thresholds in the response of plant spring phenology to warming at global scale (Fig. 3). Thus, phenological responses to warming are more pronounced when water availability is not an additional limiting factor[7,32,45]. The synergistic effects of warming and decreased precipitation in arid and semi-arid regions and the antagonistic effects of warming and increased precipitation in humid regions on the plant phenology also support this interpretation (Figs. 3, 6 and 7).

Our study also revealed differences in the responses of plant phenology to warming and precipitation alterations among functional groups in different habitats (Table S1), and the treatment effects may be spatially dependent (Table S3). For example, contrary to our hypothesis, we found that warming advanced leaf-out of grasses in arid regions, but did not affect leaf-out for any functional groups in semi-humid regions (Fig. 4a). Furthermore, the phenological responses of plant functional groups to warming showed different nonlinear patterns with increasing aridity index (Fig. 5). This result might reflect the fact that shallow-rooted grasses in arid regions, which make more use of upper soil water and nutrients[46,47], might be primarily influenced by winter precipitation or pre-season precipitation[17]. Consequently, the advance effects of warming on leaf-out may not be limited by water

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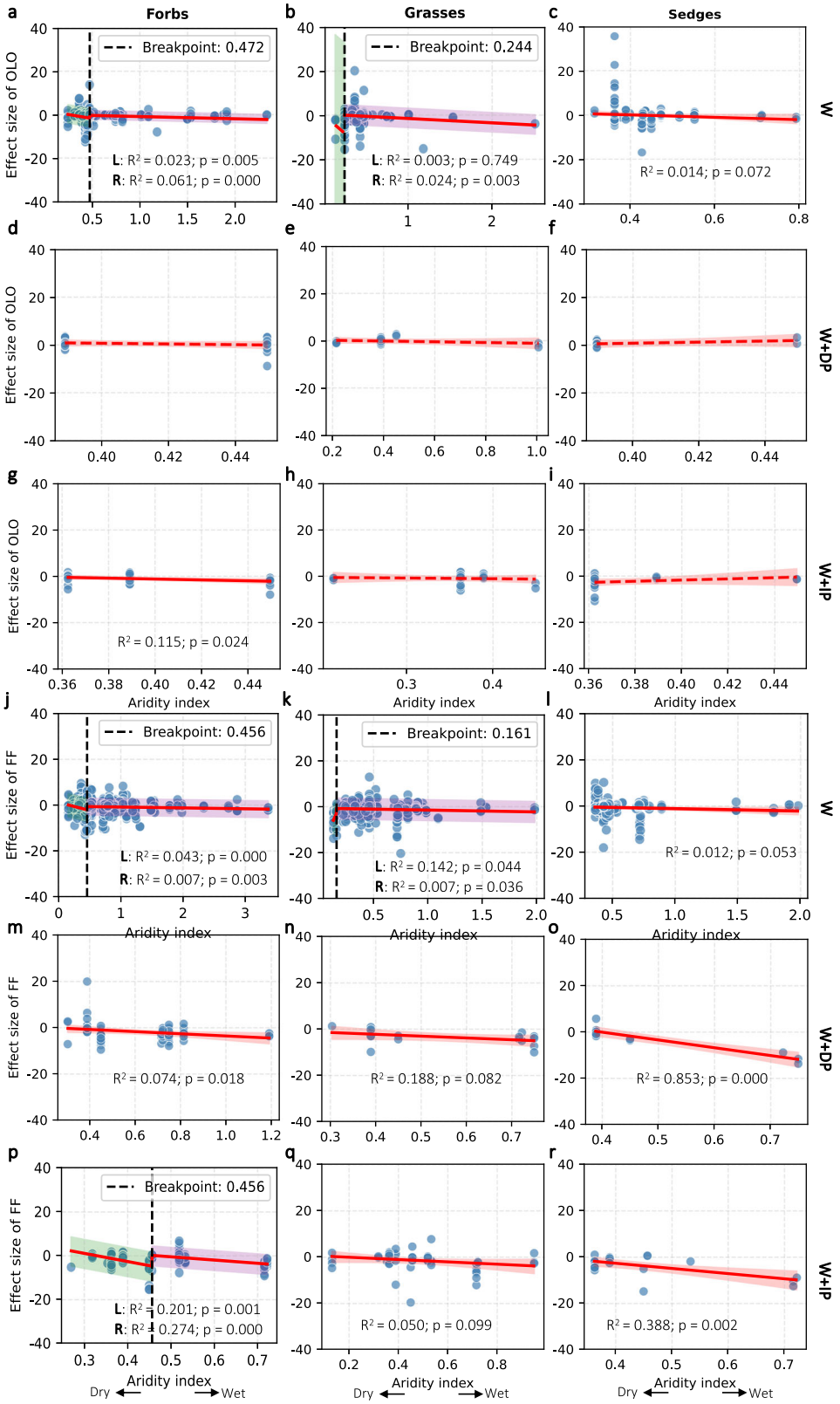

Fig. 5 | Responses of the early spring phenology to increased aridity index in different plant functional groups under warming and coupled warming-precipitation changes. a–i Onset of leaf-out (OLO) and (**j–r**) first flowering (FF). The dashed line indicates that there is no significant relationship between the aridity index and the phenological response ($p > 0.1$). The shaded area represents the 95% confidence interval. *W* warming; *DP* decreased precipitation; *IP* increased precipitation; *L* the regression results of the left segment; *R* the regression results of the right segment. Regression equations were shown in Table S4. Source data are provided as a Source Data file.

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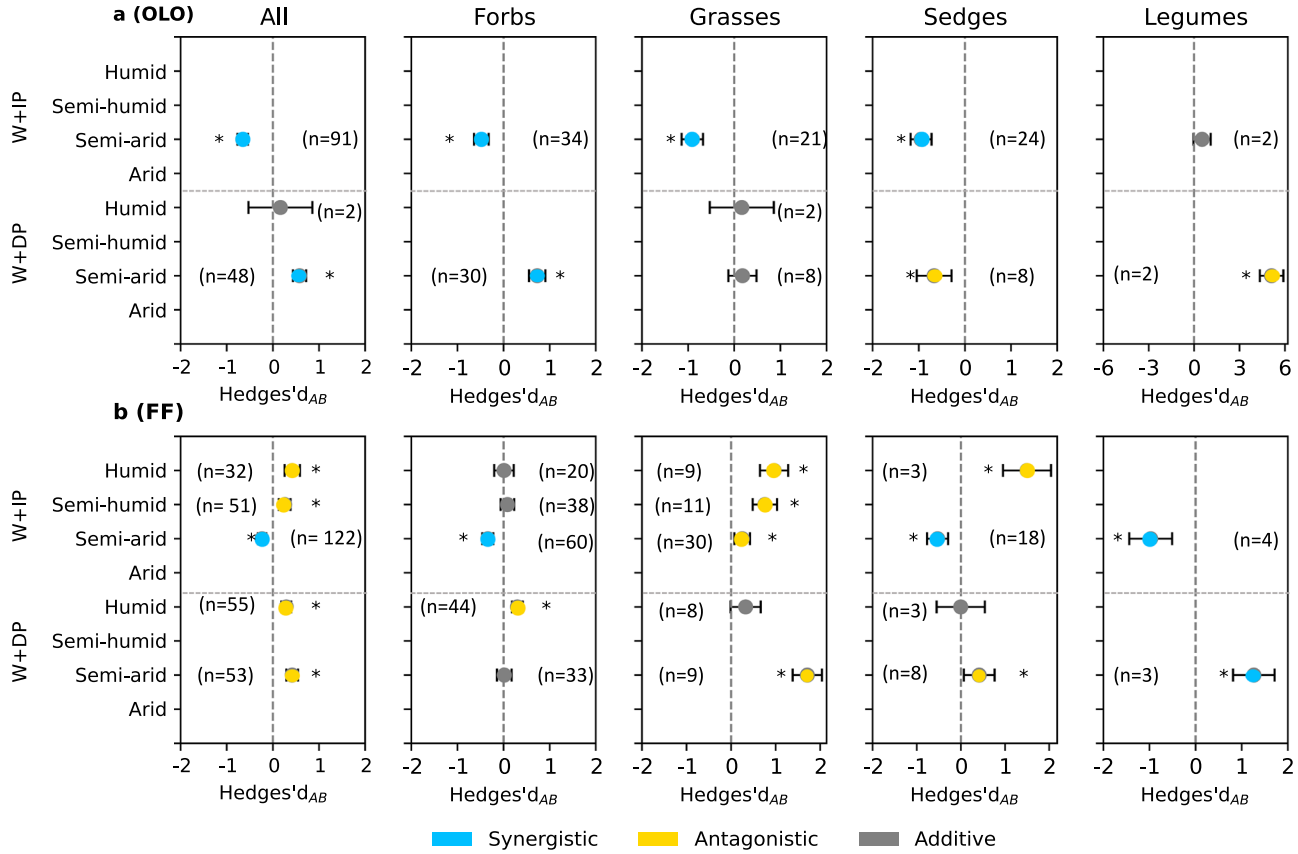

Fig. 6 | Interaction types between warming and precipitation alteration on the early spring phenology across different aridity and functional groups at global scale. a Onset of leaf-out (OLO) and (**b**) first flowering (FF). Asterisks represents that the treatment effects are significant (95%CIs not overlapping with the zero lines). The numbers of n represent the sample sizes in the figure. *DP* decreased precipitation; *IP* increased precipitation; *W* warming. Source data are provided as a Source Data file.

availability[14,17]. Providing further support, decreased precipitation had no significant effect on leaf-out of grasses in arid regions (Fig. 4a). In addition, inconsistent with our hypothesis, decreased precipitation and its interaction with warming advanced leaf-out of legumes in semi-arid regions (Fig. 4a). This probably occurred because the legumes (deep axial rooted plants) might be more affected by minimum temperatures and deeper soil water[11,29] and have long-term adaptation mechanisms – a water-saving or "phenological escape" strategy – to avoid water limitation[42,48]. Additionally the difference in photosynthetic pathways among different plants (e.g., C_3 or C_4 plants) may also cause different responses of phenology to climate change[49,50]. Therefore, root functional group (e.g., shallow vs deep rooted plants), photosynthetic pathway, and traits of drought-tolerant or resistance all likely regulates the direction of response of leaf-out to warming.

Inconsistent with our hypothesis (Fig. 1a), we found that warming and its interaction with precipitation alterations tended to advance the flowering of most PFGs in different habitats (Fig. 4b). A possible explanation is that grasslands in the Northern Hemisphere predominantly experience monsoon climates. In most regions, first flowering occurs after June, coinciding with the arrival of the rainy season when soil moisture constraints are typically reduced. Warming increases soil temperature and accelerates the accumulation of growing degree days (GDD) required for flowering, thereby advancing the date of first flowering. In addition, this is consistent with what is known about the expression of flowering genes, as warmer temperatures and photoperiod can trigger the physiological expression of flowering genes (e.g., *FT* genes) by regulating the synthesis of hormones or photoperiodic sensitivity[51–53]. And warmer conditions will promote the onset of reproduction across all ecosystems regardless of precipitation alteration, consistent with global trends[54,55]. However, we found that warming and increased precipitation had antagonistic effects on first flowering in humid regions (Figs. 3 and 7), which resulted in the coupling effects of warming and increased precipitation being lower than or opposite to that of warming alone[34,56]. These results suggested that when soil water availability was sufficient in wet ecosystems, increased precipitation could delay first flowering by reducing the diffusion rate of oxygen[57], photosynthetic efficiency[58] and nutrient cycling[59,60], thus offset the earlier effects of warming on the first flowering. Moreover, warming with decreased precipitation advanced the flowering of all PFGs in semi-arid and humid regions, indicating that the warming effect on flowering overrides the water effect.

Implications

Our study has two key implications. First, more studies are needed in arid regions to improve our understanding and prediction of responses of plant phenology to climate change. Few studies have examined how plant phenology responds to warming and decreased precipitation in arid regions[17] (Fig. 1b). This is important because drylands cover ~45% of the Earth's land surface[61], and drylands are facing severe impacts from aridification, such as reduced plant productivity, soil fertility, and plant cover and richness[62]. Moreover, the frequency of warming coupled with dry conditions is increasing in drylands due to climate change[63]. Our results showed that, inconsistent with our hypothesis, warming and its interaction with decreased precipitation advanced first flower timing in arid regions (Fig. 3b), implying that drought-tolerance or resistance of these plants might be critical for understanding and predicting these responses to climate change.

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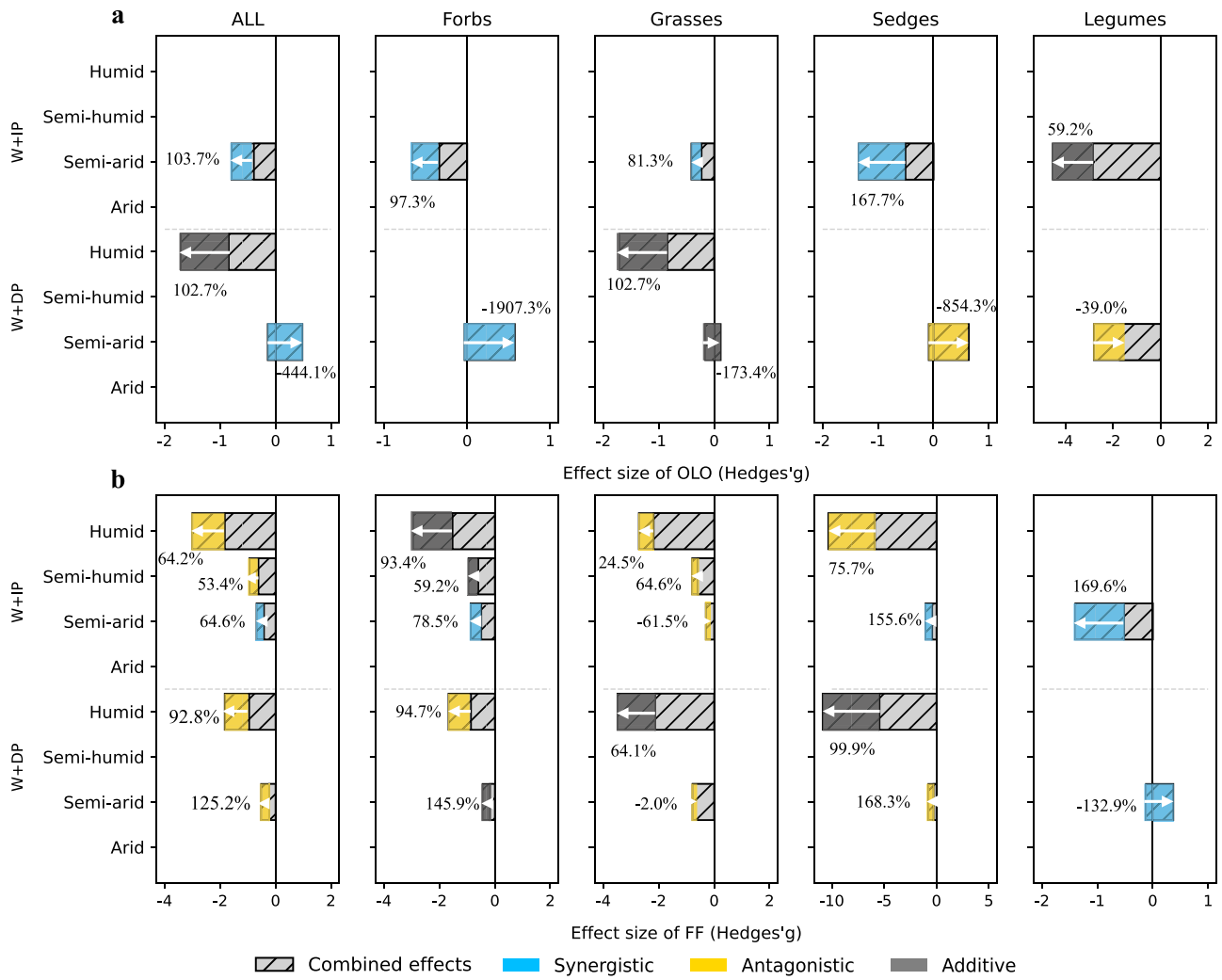

Fig. 7 | Importance of warming interacting with precipitation alteration on the early spring phenology across different aridity and functional groups at global scale. a Onset of leaf out (OLO) and (**b**) first flowering (FF). The importance is calculated as (combined effects − summed effects) ×100%/summed effects. Source data are provided as a Source Data file.

Second, the influence of ambient climate on the contrasting responses of plant phenology to warming depends on functional groups. Previous studies showed that the shift of plant phenology might affect species population growth or reproduction, and therefore potentially community composition[64–66], and warming can change the composition of plant species or functional groups, such as increasing the dominance of grasses and legumes while decreasing forbs in alpine grasslands[29,67–69], which may be caused by phenological changes under climate changes or by direct effects of warming. Ecosystem attributes are highly interconnected[70], so changes in one attribute (e.g., plant phenology) may trigger sequential changes in others (e.g., plant productivity and carbon sequestration) under climate change[71]. Understanding whether there are antagonistic effects between temperature and drought on plant phenology across a global scale is crucial for improving predictions of grassland ecosystem functions and for the conservation of biodiversity in the future.

In summary, our findings indicate that onset of leaf-out was primarily determined by precipitation, while first flowering was more determined by temperature than by precipitation changes across the global scale. Additionally, the responses of plant spring phenology to warming and precipitation depended on both aridity and plant functional groups. However, most of the previous experiments on warming and precipitation changes were conducted in semi-arid regions, and phenological data based on coupling manipulated experiments of warming and precipitation changes are still limited. More experiments are needed to improve our mechanistic understanding of plant phenology in the context of climate change, especially in arid environments. Overall, our research emphasizes the importance of drought and plant species or functional groups in regulating plant phenological responses to climate change, which is crucial to understand the feedback of grassland communities to fluctuating climate change and improve predictive models of phenology at the global scale.

Methods

Data collection from literature or networks of phenological observations

Data for this study were compiled from a recent meta-analysis and additional manipulative field experiments. The literature searches in the meta-analysis from Web of Science and China National Knowledge Infrastructure, the keywords about warming experiments included: (warming OR heat* OR increase* temperature OR elevate* temperature OR climate change) AND (bud* OR "bud burst" OR leaf-out OR "leaf

unfold*" OR "growing season" OR phenolog* OR reproducti* OR flowering OR senescence OR anthesis OR "leaf color" OR "leaf colour") AND (experiment* OR treatment* OR control*), and the keywords about precipitation changes experiments included: (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 "bud burst" OR leaf-out OR "leaf unfold*" OR phenolog* OR "first flowering" OR senescence OR anthesis OR "leaf color" OR "leaf colour") AND (experiment* OR treatment* OR control*) (Fig. S6)[32]. Firstly, phenological data on the onset of leaf-out date (hereafter referred to as leaf-out) and first flowering date (referred to as flowering) under warming, increased precipitation, decreased precipitation and their interactions treatments were extracted from Zhou et al.[32]. And we screened and only retained the phenological data of herbaceous plants. Then, we also screened and supplemented data on herbaceous plants from prior experiments, including an experiment in Nagqu, China (which included warming, increased precipitation, decreased precipitation, and the interaction between warming and either increased or decreased precipitation), a warming experiment in Haibei, China (warming only)[72], and the International Tundra Experiment (ITEX) (warming only, https://doi.org/10.21963/13215). All the phenological data of herbaceous plants based on the manipulative experiments were included, regardless of whether they are understory plants (<1%) or others. Finally, a new database was compiled containing data from 55 experimental sites for leaf-out (Supplementary data 1) and 117 sites for flowering (Supplementary data 2), resulting in 2178 values for leaf-out and 4027 values for flowering (Figs. 1 and S7).

Classification of aridity

Aridity was classified using the aridity index (AI), defined as the ratio of total annual precipitation to potential evapotranspiration (PET). AI value at global scale were extracted from the database of global AI published by Zomer et al. (2022), and the spatial resolution for these classifications is ~1 km[73]. Then, the AI value of each experimental site was obtained based on its longitude and latitude. Finally, regions were categorized as arid ($0.03 \le AI < 0.2$), semi-arid ($0.2 \le AI < 0.5$), semi-humid ($0.5 \le AI < 0.65$), and humid ($AI \ge 0.65$)[73].

Meta-analysis

Individual and combined effects of climate manipulations (i.e., no interactions). The effect sizes for individual and combined effects under warming, increased precipitation, or decreased precipitation (warming + increased precipitation or warming + decreased precipitation) were calculated using a bias-corrected method[32,74–76]. The effect size was calculated using the following equation:

$$g = \frac{(X_T - X_{CK})}{s} J \tag{1}$$

Where X_T and X_{CK} are the mean values of the treatments and control, respectively, and s and J are the standard deviation and the correction term for small sample bias, respectively. s and J were calculated as follows:

$$s = \sqrt{\frac{(n_{CK}-1)(s_{CK})^2 + (n_T-1)(s_T)^2}{n_{CK}+n_T-2}} \tag{2}$$

$$J = 1 - \frac{3}{4(n_{CK}+n_T-2)-1} \tag{3}$$

Where n_{CK} and n_T are the sample sizes of the control and treatments, and s_{CK} and s_T are the standard deviations of control and treatment, respectively.

The variance (v) of the observation i was calculated as:

$$v = \frac{n_{CK}+n_T}{n_{CK}n_T} + \frac{g_i^2}{2(n_{CK}+n_T)} \tag{4}$$

the weight mean effect size of all observations (total of m) (Hedges'g) was calculated by Eq. (5):

$$\text{Hedges'g} = \frac{\sum_{i=1}^{m} w_i g_i}{\sum_{i=1}^{m} w_i} \tag{5}$$

Where w_i is the reciprocal of the variance, as $w_i = 1/v_i$.

Interaction effects. For distinguishing the effect size of phenological responses to each or interactive treatment under the coupling treatments of warming and precipitation alteration, the main effects of warming (d_A) and precipitation changes (d_B) and their interactions (d_{AB}) were calculated by following equations, respectively:

$$d_A = \frac{(X_A - X_{CK}) + (X_{A+B} - X_{CK}) - (X_B - X_{CK})}{2s} J \tag{6}$$

$$d_B = \frac{(X_B - X_{CK}) + (X_{A+B} - X_{CK}) - (X_A - X_{CK})}{2s} J \tag{7}$$

$$d_{AB} = \frac{(X_{A+B} - X_{CK}) - (X_A - X_{CK}) - (X_B - X_{CK})}{s} J \tag{8}$$

Where X_A, X_B, X_{A+B} and X_{CK} are the mean values of the different treatments and control, respectively. And s and J are the standard deviation and the correction term for small sample bias, respectively. s and J were calculated as following equations, respectively:

$$s = \sqrt{\frac{(n_{CK}-1)(s_{CK})^2 + (n_A-1)(s_A)^2 + (n_B-1)(s_B)^2 + (n_{A+B}-1)(s_{A+B})^2}{n_{CK}+n_A+n_B+n_{A+B}-4}} \tag{9}$$

$$J = 1 - \frac{3}{4(n_{CK}+n_A+n_B+n_{A+B}-4)-1} \tag{10}$$

Where n_{CK} n_A, n_B and n_{A+B} are the sample sizes of the control and different treatments, s_{CK}, s_A, s_B and s_{A+B} are the standard deviations of control and treatments, respectively.

The variance (v) of the observation i under each treatment was calculated as:

$$v = \left[\frac{1}{n_{CK}} + \frac{1}{n_A} + \frac{1}{n_B} + \frac{1}{n_{A+B}} + \frac{d_i^2}{2(n_{CK}+n_A+n_B+n_{A+B})}\right] \times \frac{1}{4} \tag{11}$$

and the overall weighted mean (Hedges'd) were calculated according to Eq. (5). Results of funnel plots and Egger's regressions showed that publication bias in our meta-analysis was absence (Figure S8). The two-tailed critical value of the standard normal distribution was used to calculate the 95% CI[77]. The 95% CIs of effect sizes based on small sample size ($n < 20$) were calculated by the bootstrapping method based on 500 iterations[78]. A negative value of Hedges'g indicates a phenological advance, and a positive value of Hedges'g indicates a phenological delay. In addition, we classified the interactions between warming and precipitation changes into three types (additive, antagonistic, and synergistic) according to the methods in Folt et al. [77] and Zhou et al. [32,76]. If the 95% CI overlapped with zero, the interaction effect was insignificant, we consider it as additive effect. In contrast, the interactive effect was significant when the 95% CI did not overlap with zero, in which case the interaction effect was considered as synergistic when d_{AB} had the same sign as the sum of

d_A and d_B and antagonistic when d_{AB} had the opposite sign as the sum of d_A and d_B.

Statistical analyses

We utilized linear mixed models (LMMs) to examine the effects of warming (W), precipitation alteration (P) (IP = increased precipitation and DP = decreased precipitation), aridity (A), and plant functional group (PFG) and their interactions on leaf-out and first flowering at the global scale, with warming, precipitation alteration, aridity, and functional groups as fixed factors, and duration of study (in years) and study ID nested within aridity category as random intercepts (model <- lmer (Effect_size ~ W * P * PFG * A + (1|Aridity/studyID) + (1|Duration), data = data)) (Table S1). The following interactions were included in the LMM: W × P, W × PFG, W × A, P × PFG, P × A, PFG × A, W × P × PFG, W × P × A, P × PFG × A, and W × P × PFG × A. The statistical analyses were performed with the function lmer() using the R package *lme4*. And Egger's regression was carried out to assess the publication bias.

Next, single sample *t* tests were used to detect whether the treatment effects, W, DP, IP, W + DP and W + IP from the meta-analysis effect size calculations, on plant phenology were significantly different from zero ($p < 0.05$). These tests were employed to examine the total effect of each treatment across all aridity regions and functional groups and also for each effect size within each aridity region and functional group. We further fitted the linear or segmented regression to determine the response of the phenophases of all species or different functional groups with increasing aridity index under different treatments. Mann-Whitney U-tests were employed to compare the significant differences in plant phenological responses among different warming methods or precipitation intensities.

Finally, we wanted to gain further insight into potential mechanisms of phenological responses. Therefore, to examine phenological changes in response to continuous climate factors, regression analyses were conducted to test how phenological responses to warming and precipitation alterations depended on experimental and climatic factors, including warming magnitude, experimental duration, mean annual temperature, mean annual precipitation, aridity index, latitude, and longitude (Table S2). These statistical analyses were performed using SPSS 22.0, and all figures were created using Python 3.9.

Reporting summary

Further information on research design is available in the Nature Portfolio Reporting Summary linked to this article.

Data availability

The data that support the findings of this study are available from the Figshare (https://doi.org/10.6084/m9.figshare.29362091)[79]. Source data are provided with this paper.

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Author contributions

J. S., W. L., and S. W. contributed equally to this work. S.W. designed the research. J.S., W.L., and S.W. performed data analysis. J.S., S.W., and W.L. wrote the first draft of the paper. J.S., S.W., W.L., A.I., F.M., B.L., Y.Z., J.L., F.Y., C.L., J.P., T.Y., and S.P. contributed to the interpretation of the results and to editing the text.

Competing interests

The authors declare no competing interests.

Additional information

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