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Influence of seed mass and shape on light plasticity of germination of alpine plants on the Tibetan Plateau: The role of photoblastic taxa, dispersal ability, and life history

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ABSTRACT

Responses of post-disposal germination to light play a crucial role in shaping germination niches and determining the success of seedling establishment, ultimately impacting species distribution and community composition. Seed traits are pivotal factors that influence species' germination, dispersal, and life history strategies. However, it remains unclear whether the relationship between seed traits and the light plasticity of germination is regulated by factors such as life history, photoblastic taxa, and dispersal ability.

We measured the seed shape and seed mass of 114 species on the grasslands of the Tibetan Plateau. Germination experiments were conducted under two light conditions: dark and light. We also classified species based on photoblastic taxa (photostimulation vs. photoinhibition), life history (annual vs. perennial), and dispersal ability (weak vs. strong). Phylogenetic structural equation models (SEM) were used to test the complex relationship between seed traits, life history, dispersal ability, and light plasticity.

We found that neither seed mass nor shape differed between the two photoblastic taxa. Species with photostimulation taxa exhibited a greater light plasticity of germination compared with photoinhibition taxa. Non-spherical seeds (elongated or flat) possessed low light plasticity of germination. The relationship between seed mass and germination light plasticity varied in different photoblastic taxa. Specifically, in photostimulation species, increased seed mass was associated with higher light plasticity of germination, whereas in photoinhibition species, an opposite relationship was evident. Moreover, dispersal ability and life history indirectly influenced the light plasticity of germination via seed shape.

Our results imply that different combinations of seed traits can shape germination strategies in response to light stimulation, which in turn may influence the germination niches differentiation and species persistence in soil. Furthermore, life history and dispersal ability can indirectly affect

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the light plasticity of germination, which implies that the reproductive strategy of species to adapt to the environment may be regulated by multi-faceted life history strategies.

1. Introduction

Germination strategies play a central role in breaking dormancy, maintaining seed banks, and establishing seedlings, which in turn influence population dynamics, community assembly, and habitat restoration on various spatiotemporal scales (Donohue et al., 2010; Baskin and Baskin, 2014; Jiménez-Alfaro et al., 2016; Saatkamp et al., 2019). Light signals emerge as a crucial regulator of germination, either promoting or inhibiting this process, thereby shaping the species composition of the soil seed bank (Baskin and Baskin, 2014; Fenner and Thompson, 2005). The light plasticity of germination, which refers to the differences in germination performance under different phenotypic circumstances, is an essential factor influencing a species' ability to respond to environmental changes (Zhang et al., 2022). Furthermore, the light plasticity and species composition of the seed bank can significantly affect the species composition and stability of aboveground communities, especially in disturbed environments (Donohue et al., 2010; Ma et al., 2021). It is undeniable that understanding the light plasticity of germination offers valuable insights into species coexistence and community stability. However, the intrinsic difficulty of measuring the light plasticity hinders the wide use of light plasticity in evaluating community stability. Therefore, exploring the relationship between the light plasticity of germination and other traits which are easier to measure (e.g., seed traits) not only offers valuable insights into the underlying mechanism of how light plasticity affect community stability, but also provides proxies of light plasticity for later studies and evaluations.

Seed traits are closely related to germination strategy and its light plasticity (Milberg et al., 2000; Bu et al., 2017; Wang et al., 2021; Zhang et al., 2022). Milberg et al. (2000) found that small seeds had greater photoplasticity of germination (Milberg et al., 2000). In alpine environments, small seeds exhibited a higher germination proportion and shorter germination time (Wang et al., 2021; Fernández-Pascual et al., 2021). Variations in light quality reaching the soil are influenced by the staggered cover between plants (Tester and Morris, 1987; Vázquez-Yanes & Orozco-Segovia 1993; Xia et al., 2016). Small seeds in the soil therefore sense external environmental conditions through light signals, influencing their decision to germinate (Batlla and Benech-Arnold, 2014). Consequently, prolonged dark soil conditions may favor species with small seeds and high light plasticity of germination. Regarding seed morphology, spherical seeds tend to show lower germination proportion, probably due to low water absorption. (Bu et al., 2016; Barak et al., 2018; Wang et al., 2021). Seed shape may potentially influence light plasticity of germination, as some studies indicated that Asteraceae seeds (which tend to be more elongated) have neutral or positive responses to light in the germination (Schütz et al., 2002; Mölken et al., 2005).

In addition to seed traits, which are widely recognized as primary influencers of light plasticity, various factors that directly or indirectly affect light plasticity have been highlighted in previous studies. These factors include life history traits, dispersal abilities, and photoblastic characteristics (Bu et al., 2007; Baskin and Baskin, 2014; Zhang et al., 2021). Species strategically allocate resources for offspring based on their life history, with annual species producing numerous small seeds to counterbalance the establishment disadvantage associated with low seed mass (Henery and Westoby, 2001; Jakobsson and Eriksson, 2000). Typically, small seeds exhibit higher germination percentages and shorter germination times compared to larger seeds (Bu et al., 2007; Norden et al., 2009; Zhang et al., 2014). This germination strategy suggests that small seeds can occupy the germination niche through rapid germination, enhancing seedling growth advantages (Donohue et al., 2010). It has also been observed that the trade-off between dispersal and dormancy is mediated by life history via its impact on seed mass (Chen et al., 2020).

Species' dispersal abilities are intricately linked to seed mass and shape (Albert et al., 2015; Moles, 2018; Saatkamp et al., 2019; Wang et al., 2024). For example, wind-dispersed pioneer species generally cover long dispersal distances, facilitating rapid germination and colonization of new ecological niches, such as bare ground, under tree canopies, or within soil cracks (Foster and Janson, 1985; Pearson et al., 2003; Augspurger et al., 2017). In pioneer tree species, small seeds have been found to rely more on light for germination than large ones (Pearson et al., 2003; Xia et al., 2016), suggesting that species with enhanced dispersal abilities may exhibit lower sensitivity to light during germination.

Species display different germination strategies when exposed to varying levels of light stimulation. Baskin and Baskin (2014) categorized photoblastic taxa into three groups: photostimulation (light stimulates germination), photoinhibition (light inhibits germination), and photoneutral (light has no effect on germination). For example, in Australian grassland and forest communities, studies revealed that after light stimulation, 21 species experienced an increase in the germination proportion, while the germination proportion of 9 species decreased (Clarke et al., 2000). Besides, high germination proportion occurred under dark conditions for 105 Australian desert plant species (Jurado and Westoby, 1992). Furthermore, Carta et al. (2017) reported that the seed mass of 301 species belonging to the photoinhibition taxon was relatively large compared to the global average seed mass. In contrast, Silva Dias et al. (2020) found no differences in seed mass and shape among different photoblastic taxa across 222 species. Therefore, differences in seed traits, light plasticity capabilities of germination, and their interactions among different photoblastic taxa are still controversial.

While previous studies have explored the factors influencing the light plasticity of germination, a comprehensive understanding of the intricate relationships and interactions among seed traits, life history, dispersal ability, and light plasticity is still lacking. Particularly, there is a notable gap in research focusing on how life history, dispersal ability, and photoblastic characteristics regulate the interplay between seed traits and light plasticity. Therefore, in this study, we aim to investigate the relationship between seed mass, seed shape, and light plasticity in germination, with a particular focus on the potential influences of photoblastic taxa, life history, and

dispersal ability on the relationship between seed traits and light plasticity. We conducted our analysis on 114 species inhabiting the grasslands of the Tibetan Plateau and addressed the following questions: 1) Do seed mass and shape influence light plasticity in germination? 2) Do photoblastic taxa, life history, and dispersal ability directly or indirectly affect light plasticity in germination by influencing seed traits? We hypothesize that: 1) Spherical and smaller seeds may exhibit higher light plasticity during germination; 2) Plant life history affects the relationship between seed traits and light plasticity in germination; and 3) Species dispersal indirectly affects light plasticity of germination through seed traits.

2. Materials and methods

2.1. Study region and sites

The study area is the Gannan area located on the eastern of Tibetan Plateau in China (101°06'104°33'E, 32°22'-35°24'N, covering about 40,000 km²). The elevation spans from 1200 to 4800 m a.s.l. with a mean annual precipitation range of 450–780 mm and a mean annual temperature of 1.2 °C (ranging from –11 °C in January to 12 °C in July). There are an average of 270 frost days a year in our study region, and the growing season generally ranges from late April to early November.

2.2. Seed morphology data collection

We collected seeds from 114 herbaceous species (Table S1) representing 29 different families in Gannan area on the eastern Tibetan Plateau. Each species was randomly sampled from an altitude in ungrazed grassland or winter pastures with minimal disturbance. Only species with widely distributed populations in local communities were collected to ensure sufficient seeds. In total, more than 10,000 seeds of each species were collected, representing at least 50 individual plants during the natural dispersal season, which extended from summer to late autumn in 2015. Collection areas for each species covered at least 60,000 m². Seeds with appendages, primarily pappus, were carefully treated and stored in paper bags. They were then air-dried at room temperature (approximately 15 °C) until reaching a constant mass. This storage process took place at the Gannan Grassland Ecosystem National Observation and Research Station (34°550 N, 102°530E, elevation 2950 m a.s.l.) on the eastern Tibetan Plateau. The seeds remained in storage from late summer and autumn 2015 until the start of the germination season in the study area in May 2016. Seeds stored for 9–12 months can effectively reduce the effects of primary dormancy (Holdsworth et al., 2008). And several months of storage can reduce dormancy and increase germination percentage in many alpine and subalpine species (Körner, 2003).

For seed shape measurements, digital vernier calipers were used to measure the height of ten randomly selected seeds from each species. Images of seeds from each species were analyzed using an Epson Expression 10000 XL scanner and WinSEEDLE 2011a software to measure seed length and width. Seed shape was quantified using the formula from Thompson et al. (1993):

$$\text{Seed shape} = \sum \frac{(x - \bar{x})^2}{2}$$

where x is length/length, width/length, and height/length, \bar{x} is their average. This metric assigned the lowest value of zero to the perfect spherical and the highest value of 0.333 to the elongated or flat seed. Measurements of seed shape were performed after the dispersing unit (flagella and villi) were removed.

To determine seed mass, three random samples of 100 seeds were weighed using an analytical balance for each species. The mean seed mass from these three measurements, divided by 100, was used for subsequent analyses.

2.3. Germination experiment

The germination experiment, conducted in May 2016, aimed to investigate the germination response under different light treatments. Two light treatments were employed: dark and light. For each species, 50 seeds were placed on a double layer of filter paper moistened with distilled water within Petri dishes (9 cm in diameter). Three replicate plates were prepared for each species, resulting in a total of 50 seeds x 3 replicate Petri dishes x 2 light treatments. The Petri dishes were then positioned in temperature chambers, simulating diurnal temperature fluctuations and relative humidity of approximately 70%. The temperature fluctuated between 25 °C during the day (for 12 hours) and 5 °C at night (for 12 hours) both the dark and light treatment. These temperature ranges closely resemble the soil surface temperatures in May and June, corresponding to the early growth season (Wang et al., 2021). The percentage of germinating seeds (radicles protruding from the seed coat) was recorded daily and then removed from the Petri dishes. Seeds in the dark treatment were observed under green safe light (Baskin et al., 2006). Distilled water was added to the filter paper as needed. The germination experiment continued for 40 days, after which minimal additional germination was observed. To verify the viability of un-germinated seeds, the triphenyltetrazolium chloride test (TTC) was performed (Ruf and Brunner, 2003). The germination proportion was calculated using only viable seeds and measured as:

Germination proportion (GP) was measured as: $GP = n/N$.

where n = the total number of germinated seeds in a plate and N = total number of viable seeds in the plate.

Light plasticity of germination (LPG) is calculated (Milberg et al., 2000) as:

$$LPG = |GP_{\text{light}} - GP_{\text{dark}}| / (GP_{\text{light}} + GP_{\text{dark}})$$

where: GP_{light} = the germination proportion in light treatment; GP_{dark} = the germination proportion in dark treatment. LPG represents a range of values varying from 0 to 1. Species will be ignored if the germination proportion of less than 5% both light and dark treatment to reduce the effect of non-light effects on the dormancy mechanism (Milberg et al., 2000). We used the average values of GP and LPG for further analyses.

2.4. Photoblastic taxa, life history and dispersal ability

Phooblastic taxa were categorized as either photostimulation species (with a higher germination proportion under light treatment than under dark conditions) or photoinhibition species (with a higher germination proportion under dark treatment than under light conditions).

The life history of herbaceous plants was classified into two categories: annual and perennial.

The dispersal ability of herbaceous plants was classified into two groups: weak and strong dispersal, based on the species' dispersal modes (Thomson et al., 2011). The strong dispersal category encompassed wind and attachment dispersal modes, while other dispersal modes fell under the weak dispersal category. Dispersal modes were determined by examining the morphological characteristics of the seeds (Westoby et al., 1996; Lengyel et al., 2010), including unassisted (seeds lacking obvious dispersal morphological structures, 78 species), ant (7 species), wind (seeds possessing hairs, wings, or pappus, 24 species), and attachment (seeds with thorns, hooks, or barbs, 6 species).

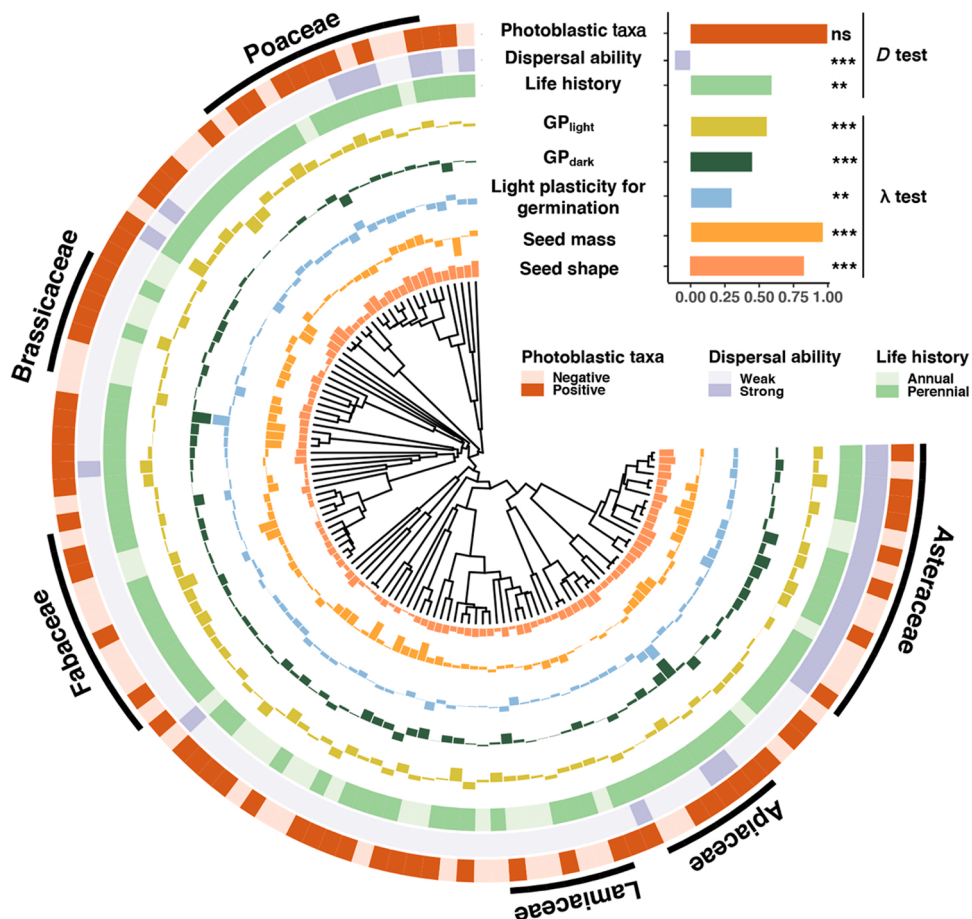


Fig. 1. Visualization of the phylogram and phylogenetic signal of 114 species, including the seed mass, seed shape, light plasticity for germination, germination proportion under full light (GP_{light}) and dark (GP_{dark}), photoblastic species taxa (photostimulation vs. photoinhibition), dispersal ability (weak vs strong) and life history (annual vs perennial). Phylogenetic signal was tested using the Pagel's λ statistics in continuous variable (seed mass, seed shape, light plasticity for germination, GP_{light} and GP_{dark}), while using the D test in binary variables (photoblastic species, dispersal ability and life history). D values close or less than zero indicate a strong phylogenetic signal (highly conserved), and near one indicate a weak phylogenetic signal (overdispersed). λ values close to zero indicate a weak phylogenetic signal, and close to one indicate strong phylogenetic signals. Phylogenetic family containing most species are named. Seed mass was \log_{10} -transformed. Light plasticity for germination was logit-transformed. The shape value of the perfect spherical seed is zero and seeds with larger shape values are non-spherical (flat or elongated). ** $P < 0.01$; *** $P < 0.001$; ns $P > 0.05$.

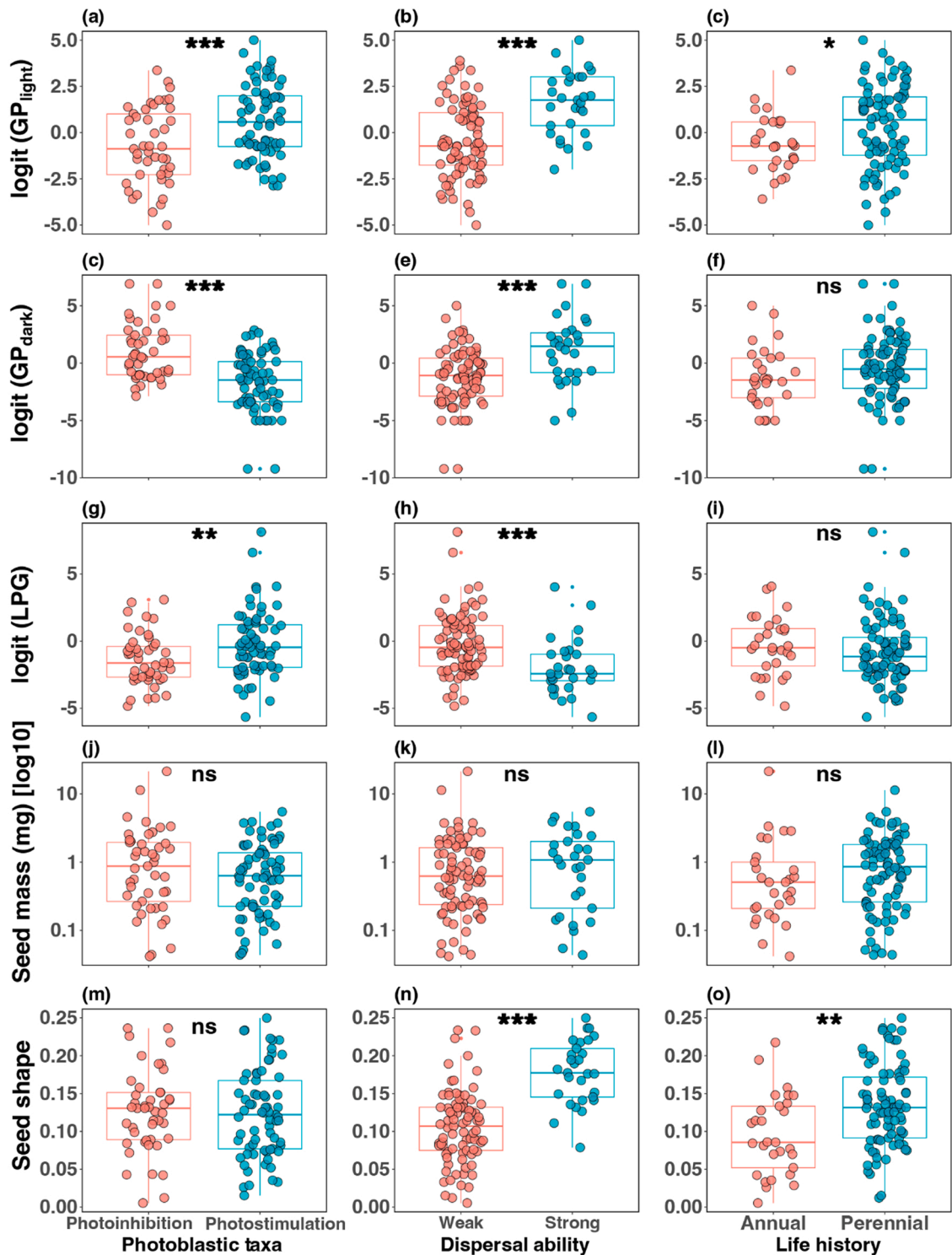


Fig. 2. Results of Analyses of Variance to test for photoblastic taxa, life history and dispersal distance differences in light plasticity for seed mass and shape, germination (LPG), germination proportion under full light (GP_{light}) and night (GP_{dark}). Significant results are highlighted in bold. * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; ns, $P > 0.05$. Mass was \log_{10} -transformed. GP_{light} , GP_{dark} and LPG were logit-transformed.

2.5. Data analysis

All statistical analyses were conducted with R v.4.2.1 (R Core Team, 2022). GP_{dark} , GP_{light} and light plasticity of germination (LPG) was logit-transformed to improve normality. Seed mass was \log_{10} -transformed to improve normality.

To test for phylogenetic signal (Table S2), we first generated the phylogenetic tree from the megatree of Zanne et al. (2014), using the 'phylo.maker' function in the V.PhylMaker R package (Jin and Qian, 2019) with branch lengths for the 114 species. Second, we

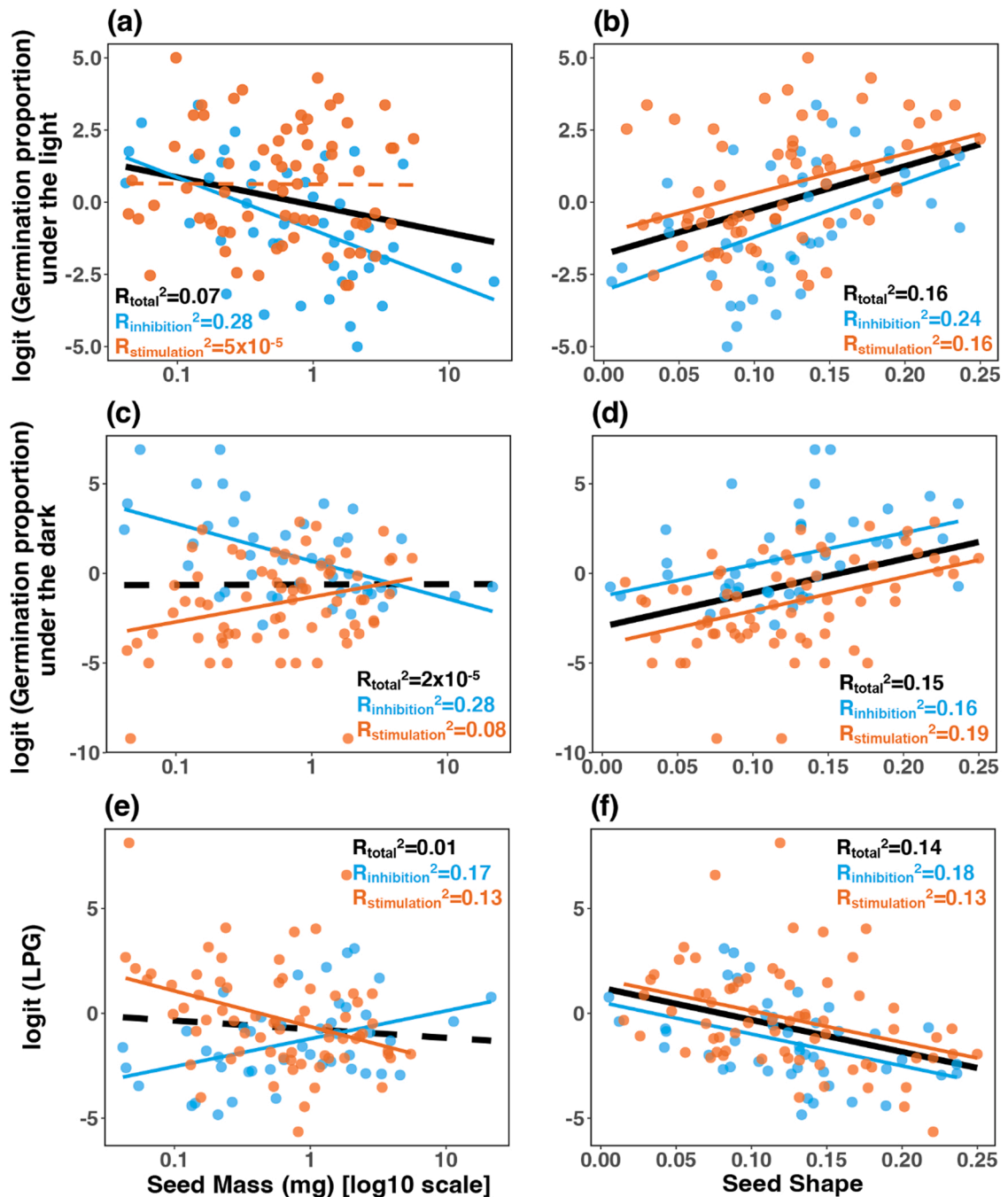


Fig. 3. General liner regression analysis of the relationship between seed mass, shape and light plasticity for germination (LPG) and germination proportion under full light (GP_{light}) and night (GP_{dark}) of all species, photostimulation and photoinhibition taxa. Black lines show the result of all species. Orange lines and points show the result of photostimulation species. Blue lines and points show the result of photoinhibition species. The solid and dotted lines show significant and non-significant relationships respectively. The shape value of the perfect spherical seed is zero and seeds with larger shape values are non-spherical (flat or elongated).

tested for phylogenetic signal of continue factors (seed mass, shape, GP_{dark} , GP_{light} , LPG) by estimating Pagel’s λ for 10,000 randomization simulations tests with the ‘phylosig’ function from the R package ‘phytools’ v.0.6–99 (Revell, 2012). Phylogenetic signals for bivariate factors (life history, dispersal ability and photoblastic taxa) were tested using the ‘phylo.d’ function from the R package ‘caper’ package (Orme et al., 2013).

In order to explore the differences in seed traits, germination rate and germination light plasticity under different categories (life history, dispersal ability and photoblastic taxa), we conducted an ANOVA analysis using the “ANOVA” function in the “car” package.

To examine the relationship between seed traits (seed mass and shape) and germination and light plasticity of germination, general linear regression models were constructed using ‘lm’ function in the ‘stats’ package across all species and different photoblastic taxa. Germination proportion and light plasticity of germination were the dependent variables with seed mass and shape as predictor variables respectively.

To explore how traits and life history strategies mediate the relationship between seed traits the light plasticity of germination, we constructed phylogenetic structural equations using the ‘piecewiseSEM’ package (Lefcheck, 2016). And compared analysis using non-phylogenetic SEM. In the phylogenetic SEM, the predictors were GP_{dark} , GP_{light} and LPG, respectively. The predictors were seed mass, seed shape, life history, dispersal ability and photoblastic taxa. According to previous findings, we considered direct effects of seed traits, life histories, and dispersal abilities, as well as indirect effects of life histories and dispersal abilities via seed traits. Specifically, to further elucidate the effect of photoblastic taxa, we conducted SEM analysis in different photoblastic taxa groups, respectively. Continuous factors were standardized by scale to ensure the comparability of effect size. Submodels in phylogenetic SEM were obtained using the ‘ppls’ function from the ‘caper’ package (Orme et al., 2013). Submodels of the non-phylogenetic SEM package

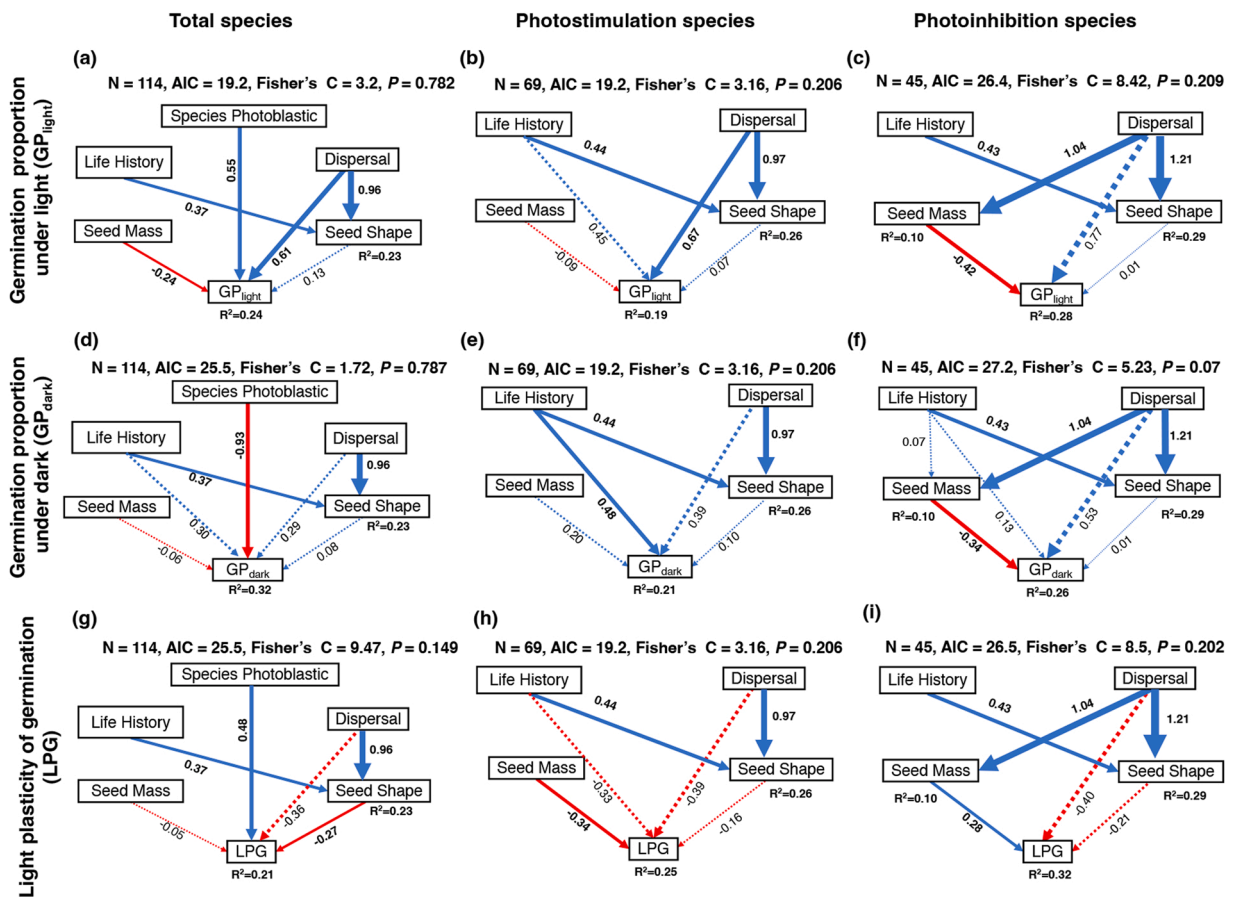


Fig. 4. Phylogenetic structure equation model showing the direct and indirect effects of see mass, seed shape, species photoblastic taxa, life history and dispersal ability on the light plasticity for germination (LPG) and germination proportion under full light (GP_{light}) and night (GP_{dark}). Annual, weak dispersal ability, photoinhibition species were used as references in the bivariate factors (life history, dispersal ability and photoblastic taxa) of the SEM model. Blue and red arrows indicate significantly positive and negative effects respectively. The thickness of solid and dashed arrows indicates the size of significant and no-significant effect. Pathway coefficients follows the side of arrows. R^2 indicates the explanatory power of the dependent variable (LPG, seed shape and mass). N indicates the species number, and AIC indicates the fit of the structure equation model. Fisher’s C indicates an adequate overall fit of structure equation model, and P must be greater than 0.05. The continuous variables (GP_{light} , GP_{dark} , LPG, seed mass and shape) in the model were scale-transformed, before which the seed mass was log10-transformed and GP_{light} , GP_{dark} and LPG were logit-transformed. The shape value of the perfect spherical seed is zero and seeds with larger shape values are no-spherical (flat or elongated).

use general linear models (Fig. S1). To evaluate the impact of elevation on phylogenetic SEM results, we constructed the phylogenetic SEM included elevation, LPG as predictor, seed mass, seed shape, life history, dispersal ability and photoblastic taxa and elevation as predictors (Fig. S2).

3. Result

3.1. Distribution of traits and phylogenetic signals

Seed shape ranged from 0.005 (*Vicia angustifolia*) to 0.250 (*Stipa capillacea*). Seed mass ranged from 0.042 mg (*Androsace erecta*) to 21.44 mg (*Vicia angustifolia*). Photoinhibition species included 45 species, with seed mass ranging from 0.042 (*Androsace erecta*) to 21.44 mg (*Vicia angustifolia*) and seed shape from 0.005 (*Vicia angustifolia*) to 0.236 (*Lilium pumilum*). Photostimulation species include 69 species, with seed mass ranging from 0.044 (*Juncus thomsonii*) to 5.48 mg (*Stipa capillacea*), and seed shape from 0.015 (*Galium verum*) to 0.25 (*Stipa capillacea*).

Significant phylogenetic signals were found in seed mass, shape, light plasticity of germination (LPG), germination proportion under dark and light conditions, dispersal ability (weak vs strong dispersal) and life history (annual vs perennial) (Fig. 1, Table S2). However, the phylogenetic signal strength of LPG was relatively weak compared to other traits ($\lambda = 0.295$, Fig. 1, Table S2). Moreover, there was no significant phylogenetic signal in the photoblastic taxa (Fig. 1, Table S2).

All Asteraceae ($n = 16$) exhibited strong dispersal ability, with half ($n = 8$) being photoinhibition species. In Poaceae ($n = 13$), only five species belonged to the photoinhibition taxon, with only four species having strongly dispersal ability. All Fabaceae ($n = 12$) had weak dispersal ability, with 8 species belonging to photoinhibition taxon. Only two species in the Apiaceae ($n = 7$) had strong dispersal ability, and two were photoinhibition taxon. Brassicaceae ($n = 7$) were all weakly dispersing, with only two being photoinhibition taxon. Within Lamiaceae ($n = 7$), all species demonstrated weakly dispersal ability, with four being photoinhibition taxon.

3.2. Relationship among seed traits, photoblastic taxa, life history, dispersal ability and germination proportion

Perennial species exhibited non-spherical (elongated or flat) seed morphology and higher germination proportion under light conditions compared to annual species (Fig. 2c and o). Seed mass, low light plasticity of germination (LPG), and germination proportion in the dark were not significantly different between annual and perennial species (Fig. 2f, i, and l).

Strongly dispersing species had non-spherical (elongated or flat) seeds, high germination proportion (under dark and light), and lower LPG compared with weakly dispersing species (Fig. 2b, e, h, and n). Seed mass did not differ significantly between strongly dispersing and weakly dispersing species (Fig. 2k).

Neither seed mass nor shape differed between the two photoblastic taxa (Fig. 2j and m). Species with photostimulation taxon exhibited a greater LPG compared with photoinhibition taxon (Fig. 2g).

In germination experiments with light, species with small, non-spherical seeds, and strong dispersal ability, as well as photostimulation species, exhibited higher germination proportion (Figs. 3a, b, 4a). Moreover, photostimulation species, dispersal ability was the main factor affecting the germination proportion (slope = 0.67; Fig. 4b); for photoinhibition species, seed mass directly affected germination proportion (slope = -0.42; Fig. 4c) with dispersal ability indirectly affecting germination percentage through seed mass (Fig. 4c).

In germination experiments under full darkness condition, photoinhibition species had significantly higher germination proportion compared to photostimulation species (slope = -0.93; Fig. 4d). For photostimulation taxa, perennial species and species with large seeds exhibited a higher germination proportion (slope = 0.48; Fig. 4e; Fig. 3c). For photoinhibition taxa, species with small seeds had a higher germination proportion (Fig. 4f, slope = -0.34) with dispersal indirectly affecting germination proportion through seed mass.

3.3. Effect of seed traits, photoblastic taxa, life history, and dispersal ability on the light plasticity of germination

The light plasticity of germination was affected by the seed shape across all species and photoblastic taxa (Figs. 3f, 4g). More spherical seeds exhibited higher light plasticity of germination, whereas elongated and flattened seeds had lower light plasticity of germination (Figs. 3f, 4g). Life history and dispersal ability indirectly affected the light plasticity of germination by influencing seed shape (Fig. 4g).

For all species, there was no relationship between seed mass and light plasticity of germination (Fig. 3e). The main reason is that seed mass and light plasticity of germination showed opposite trends in the photostimulation and photoinhibition taxa (Fig. 3e). For photostimulation species, seed mass was significantly negatively associated with light plasticity of germination (Fig. 4h). In contrast, for photoinhibition species, seed mass was significantly positively associated with light plasticity of germination (Fig. 4i). Although a significantly negative relationship between seed shape and light plasticity of germination was found (Fig. 3f), the relationship was weak in SEM (Fig. 4h, i). Dispersal ability indirectly affected the light plasticity of germination by influencing the seed mass under photoinhibition taxa (Fig. 4i). Strongly dispersing species were more likely to have large seeds, thus increasing light plasticity of germination in photoinhibition species (Fig. 4i).

Elevation had no effect on the results of the phylogenetic SEM for light plasticity of germination (Fig. S2).

4. Discussion

4.1. Effects of seed mass, seed shape and photoblastic taxa on germination light plasticity

Our study illuminated the influence of seed shape on germination light plasticity, providing evidence that non-spherical (elongated or flat) seeds tended to exhibit reduced light germination plasticity. Notably, regardless of their photoblastic traits, non-spherical seeds, either elongated or flat, consistently displayed higher germination proportions. These results underscored the significant role of seed shape in influencing germination responses to light stimuli, suggesting advantages of non-spherical seeds in adapting to varying environmental light regimes. Elongated seeds were more likely to reach the soil surface by exploiting soil cracks, thereby enhancing their access to water and nutrients, which in turn enhanced the germination success (Harper et al., 1970; Chambers et al., 1991; Benvenuti, 2007). The non-spherical morphology may contribute to seeds germination in both exposed and shaded areas, reducing the risk of germination failure due to inadequate light signals in the environment (Long et al., 2015; Bu et al., 2017; Polli et al., 2020; Wang et al., 2021). In contrast, spherical seeds exhibited lower germination proportions, possibly due to heightened sensitivity to changes in light exposure. This heightened sensitivity to light-induced cues might result in reduced germination success, especially under conditions of variable or intense light. Our findings highlighted the importance of seed shape in influencing germination proportion and provided concrete evidence that non-spherical seeds typically exhibited low light plasticity of germination.

Furthermore, our research shows the significant impact of photoblastic taxa on the relationship between seed mass and light plasticity of germination. Specifically, distinct patterns were observed in this relationship in photostimulation and photoinhibition taxa. Among photostimulation species, small seeds demonstrated high light plasticity of germination (e.g., *Juncus thomsonii*, *Parnassia oreophila*), suggesting that greater flexibility of smaller seeds in adjusting their germination response to light cues. Conversely, in photoinhibition species, larger seeds exhibited high light plasticity of germination (e.g., *Vicia angustifolia*, *Astragalus floridus*), implying that higher sensitivity of larger seeds to light-induced germination cues. Our results of photoinhibited species were opposite to those of Carta et al. (2017). This could be attributed to seed mass and regional environment. The 301 photoinhibited species in Carta et al. (2017) from a global scale and had larger seed mass (1–27 mg, mean = 3.09 mg) than the 114 species collected the alpine meadow (0.04–21.4 mg, mean = 1.38 mg). Germination strategies across species levels at the local scale were different from those at the large scale in response to changes in the light environment. This also further implied that specific environmental selection of seed traits may affect the ability of germination to respond to light (Koutsovoulou et al., 2014; Flores et al., 2016; Zhang et al., 2022).

Our study emphasized the potential for combinations of species traits to enhance plant survival adaptability. Specifically, we found that photoinhibition species with small, elongated seeds exhibited insensitivity to germination-activating light signals but had higher germination rates. These small seeds can easily penetrate the soil due to their size, while their elongated shape prevents them from being buried deeply (Thompson et al., 1993). Therefore, species with this combination of seed traits (small and elongated) may remain closer to the soil surface and in a low-dormant state, being capable of initiating germination when conditions are suitable. In contrast, large, spherical seeds, while not suitable for deep burial in the soil, may be intercepted and covered by leaf litter in grasslands (Ruprecht and Szabó, 2012). Therefore, the high light plasticity of germination observed in photoinhibition species with large, spherical seeds could contribute to germination in low-light conditions and reduce the risk of surface mortality. Additionally, small, spherical seeds were more likely to form a persistent seed bank deep in the soil (Thompson et al., 1993; Rosbakh et al., 2022). This suggested that seed mass and shape may determine the spatial distribution of seeds in the soil and the germination strategies of species in response to long-term light stimulation signals, thus forming a relationship between seed morphology and light plasticity of germination. In summary, our observations shed light on the intricate relationship between seed mass and light plasticity of germination, highlighting how photoblastic taxa can influence these dynamics. This understanding contributed to our knowledge of the adaptive strategies of plant species in response to varying light environments.

4.2. Effects of life history and dispersal ability on light plasticity of germination

Our findings suggest that life history characteristics, particularly whether a plant is perennial or an annual, indirectly affect germination in photoblastic taxa by influencing seed shape. We noticed that perennials tended to produce a higher proportion of non-spherical seeds compared to annuals. More specifically, non-spherical seeds in perennial plants display reduced sensitivity to light-induced germination stimuli compared with those in annual plants. Perennial plants typically have longer life and reproductive cycles (Jurado et al., 1991), resulting in non-spherical seeds that are more inclined towards a low-dormant state, facilitating rapid seed germination and establishment (Tunjai and Elliott, 2012). Seeds produced by short-lived annual plants tend to remain buried and dormant in the soil rather than dispersing due to dormancy-dispersal trade-offs (Chen et al., 2020; Wang et al., 2024). These indirect relationships between life history traits, seed shape, and light plasticity of germination highlight the complex ways in which plant traits interact to shape their reproductive strategies and adaptations to their environment.

Furthermore, our results indicate that seed dispersal ability indirectly influences light plasticity of germination through effect on seed shape. Specifically, we found that strongly dispersing species tend to produce a higher proportion of non-spherical (elongated or flat) seeds, while weakly dispersing species are more likely to produce spherical seeds. Non-spherical seeds, in turn, exhibit lower light plasticity of germination. Strongly dispersing species may benefit from the production of non-spherical seeds, as these shapes are better suited for long-distance dispersal, particularly by wind (Zhu et al., 2016; Augspurger et al., 2017). However, given the species' spatiotemporal dispersal trade-off strategies, the advantage of strong dispersal abilities may come at the cost of reduced dormancy strategies (Chen et al., 2020). Therefore, the limitation of species on spatio-temporal dispersal of resource inputs may lead to a lack of

strong light plasticity germination strategies to cope with uncertain environments. For example, if the seeds from a strongly dispersing species diffuse into a shaded environment, and germination is likely to fail due to hindered photosynthesis during plant growth, thus reducing the effectiveness of species dispersal. In contrast, weakly dispersed species may rely on gravity or short-range dispersal mechanisms, possibly favoring spherical seeds adapted to low-light environments and persistent seed banks in the soil. This complex interplay between seed dispersal, seed shape, and light plasticity of germination highlights the intricate ecological strategies that plants employ to adapt to their environments and effectively disperse their seeds (Galloway et al., 2007; Kimball et al., 2013; Saatkamp et al., 2019; Zhang et al., 2022).

5. Conclusion

In summary, our study revealed that non-spherical seeds, characterized by elongated or flat shapes, exhibit low light plasticity of germination. This trait allows species with strong dispersal capabilities to overcome the limitations of light-stimulated germination and establish themselves rapidly, improving their survival and dispersal effectiveness. We also found that the relationship between seed mass and light plasticity of germination varies among different photoblastic taxa. Seed mass and shape determine the spatial distribution of seeds after dispersal, enabling adaptation to different light conditions. This differentiation in seed traits allows species to occupy germination niches and adapt to changing environments, influencing population spatial distributions and regeneration niches.

Furthermore, life history traits and dispersal ability indirectly affect germination light plasticity through their impact on seed traits, highlighting the complexity of species' responses to environmental changes. Plant species employ intricate trait networks and multifaceted life strategies to adapt to environment change. In essence, our study enhances our understanding of how seed traits, light plasticity of germination, and ecological strategies interact, shaping the spatial distribution and roles of plant species under environment change.

CRedit authorship contribution statement

Wei Qi: Writing – review & editing. **Kun Liu:** Writing – review & editing. **Li Ma:** Writing – review & editing, Writing – original draft, Funding acquisition. **Huakun Zhou:** Writing – review & editing, Writing – original draft, Funding acquisition. **Gengchen Yang:** Writing – review & editing. **Wenjing Ge:** Writing – review & editing, Data curation. **Mingting Zhang:** Writing – review & editing, Writing – original draft, Formal analysis, Data curation. **Xianhui Zhou:** Writing – review & editing, Writing – original draft, Visualization, Formal analysis, Data curation. **Xuejing Wang:** Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Haiyan Bu:** Writing – review & editing, Writing – original draft, Visualization, Supervision, Funding acquisition, Formal analysis, Data curation, Conceptualization.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.gecco.2024.e02896](https://doi.org/10.1016/j.gecco.2024.e02896).

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Further reading

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