

# Neither advanced nor delayed germination is optimal for performance – dynamic morphological plasticity in response to germination timing in *Abutilon theophrasti* (Malvaceae)

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## Abstract

How plants respond to germination timing via morphological plasticity is not well documented, in spite of its importance for understanding plant strategies in dealing with natural environmental challenges of complicity, especially in the perspective of the entire life cycle of plants. To address this issue, we conducted a field experiment with *Abutilon theophrasti* by growing plants in four periods, as four germination treatments (GT1~GT4), before measuring a number of mass and morphological traits on them at three (or four) growth stages (EX, I~III). Results the optimal germination time for *A. theophrasti* was late spring, as plants that germinated in this period achieved the maximum total mass, with the highest stem and reproductive allocation and the lowest leaf allocation, among plants of all germination treatments. Plants that germinated earlier in spring used a longer time for vegetative growth and did not outperform late-spring germinants, probably due to exposure to spring drought and response to competition. Delaying germination into summer led to a faster growth, increased leaf allocation, decreased stem allocation, advanced reproduction and shorter life cycle, but further delay of germination into late summer led to insufficient reproduction and incomplete life cycle due to extremely short growth period. Results suggested plants that germinated within the optimal period can maximize their growth potential in relatively favorable conditions. In spite of conspicuous disadvantages, plants with advanced and delayed germinated were still able to use different strategies to better adapt to subsequent environments, via plasticity in a number of allocation and morphological traits. Root plasticity may play a predominant or fundamental role in plant response to environments, or it is crucial to maintain root allocation stable, while stem or leaf allocation can often be sacrificed depending on specific situations.

## Introduction

A fundamental goal in evolutionary ecology is understanding the timing of life history in variable environments (Gremer et al., 2020). As one of the crucial events in the life cycle of plants, the time of germination or seedling emergence often determines subsequent plant performance and success (Harper, 1977; Weiner, 1988). Short delays in germination can be magnified into large differences in final biomass and reproduction (Burghardt et al., 2015; Donohue, 2005; Galloway & Burgess, 2009; Wilczek et al., 2009), especially under competitive conditions (Dyer et al., 2000; Kelly & Levin, 1997).

Many annual herbaceous plants can germinate within a wide range of period, and subsequently face contrasting environmental circumstances, which may be of great complicity. Plants germinating in different periods can be exposed to different environmental cues or growing conditions, such as day length, temperature, water availability, and interactions with other individuals and species (Donohue et al., 2010; Lortie & Turkington, 2002; Verdu ´ & Traveset, 2005), which regulate plastic responses in life-history traits such as reproductive timing (Huang et al., 2016; Wilczek et al., 2009). The individuals that germinate early have more time to acquire resources to grow for reproduction, but may face an increased risk of mortality, since stresses often

occur earlier in the season such as drought, frost or predation (Donohue et al., 2010; Lortie & Turkington, 2002; Verdu´ & Traveset, 2005). Most of the previous studies believed early emergence benefits plant performance and survival (Abe et al., 2008; Afonso et al., 2014; Bianchi et al., 2019; Cogoni et al., 2013; Verdu´ & Traveset, 2005), the ecological significance of delayed emergence may have been underestimated (Verdu´ & Traveset, 2005; Wu & Owen, 2014). However, late germination can also confer higher fitness benefits (than neighbors) for plants (Castro, 2006; Leverett et al., 2018; Wu & Owen, 2014), by contributing more to seed production, in comparison to the more contribution to competition of the earlier germinants (Grundy, 2003). Therefore, selection may favour either early, intermediate, or late germination (Donohue et al., 2010; Kalisz, 1986; Verdu´ & Traveset, 2005), depending on specific circumstances, or there may be conflicting selections on germination timing (Akiyama & Ågren, 2014). An alternative perspective is that germination time can be influenced by a combination of different abiotic and biotic factors (Verdu´ & Traveset, 2005), and plants may evolve responses to these environmental cues to promote time emergence, growth and reproduction to coincide with favourable conditions (Andrés & Coupland, 2012; Blackman, 2017). Consequently, despite either advanced or delayed germination may have both advantages and disadvantages, there may be an optimal germination timing for plants in terms of overall performance in adaptation to unpredictable environments (Gremer et al., 2020; ten Brink et al., 2020). Unfortunately, we know little about the optimal germination time of wild plant species and its influences on plant subsequent performance.

Phenotypic plasticity, defined as the ability of a genotype to produce different phenotypes under different environmental conditions, allows a plant to make morphological and physical adjustments during the entire life cycle (Bradshaw, 1965). Plants germinating at different times may be able to cope with environments of different biotic and abiotic complexity later in their lives, by modifying life-history traits. For instance, spring-germinating plants may have prolonged vegetative growth and life cycle with delayed reproduction, as a strategy of competitors (C), whereas summer-germinating plants tended towards the strategy of ruderals (R): having a compressed vegetative growth and initiating reproduction at a smaller size, due to shortened life cycles, than early germinants (Zhou et al., 2005). However, the phenotypic response at the whole-plant level constitutes integrated responses of plant modules and characters (de Kroon et al., 2005), the local responses may be different and even contrary (Wang & Zhou, 2021). Shifts in germination timing can cause cascading effects on different modules or traits and thus fitness (Gremer et al., 2020), and different local responses may interact to determine the final phenotype of plants. It is unclear how plants regulate a number of traits in contribution to their strategies of coping with variations in germination timing (Verdu´ & Traveset, 2005), and the strategy of plants that germinate with in the optimal time.

Another important aspect should be the effects of plant ontogeny. Most studies on effects of germination timing have examined plant performance in morphological traits at the final growth stage (Afonso et al., 2014; Wang et al., 2006; Zhou et al., 2005), lacking the information on their dynamic changes or comparison on their performances in the same growth period. For example, by comparing final performances, it is easy to find early germinants can perform better than late germinants since they use more time for growth; whereas late germinants may accumulate greater biomass and reproduction within the same growth period as early germinants. And the pattern of biomass allocation varies with different stages due to allometric growth (Weiner, 2004), the responses of plants to germination timing may largely depend on specific growth stages, which may contribute to the discrepancy in relevant results. To address the effects of germination timing, requires the information on dynamic pattern of plasticity in traits (ten Brink et al., 2020).

To better understand how plants respond to germination timing via morphological plasticity at different stages of plant growth, we conducted a field experiment, with an annual weed species of *Abutilon theophrasti*, by growing plants in four times of growth season including spring, late spring, summer and late summer, as four germination treatments, and measured a number of mass and morphological traits on plants at three (or four) stages. We ask the following questions: 1) is there an optimal germination time for plants? If yes, which time of germination can lead to the best performance of plants? 2) How plants respond to germination timing via plasticity in different mass and morphological traits? And 3) do these responses vary with different stages of plant growth?

## Materials and Methods

### Study species

*Abutilon theophrasti* Medicus (Malvaceae) is an annual weedy species native to China and India, but now spreads worldwide. Generally, its germination period ranges from April to July, and it grows rapidly to a height of 1-1.5 m with stout stems, reaching reproductive maturity within 90 days, and completes its life cycle in about five months (McConnaughay & Coleman, 1999). It colonizes relatively nutrient-rich habitats, and has substantial plasticity in allocation, morphology and architecture in response to varying environmental factors (McConnaughay & Bazzaz, 1992).

### Experimental design

We conducted the field experiment in 2007 at the Pasture Ecological Research Station of Northeast Normal University, Changling, Jilin province, China (44°45' N, 123°45' E). The original soil of experimental field (aeolian sandy soil, pH = 8.3) at the station had been used annually for many years, thereby low in nutrients availability (organic C 3.1 mg kg<sup>-1</sup>, available N 21.0 mg kg<sup>-1</sup>, and available P 1.1 mg kg<sup>-1</sup>) during the growth season of 2007 (Zhao et al., 2010). Seeds of *A. theophrasti* were collected from local wild populations near the research station in late August 2006 and dry stored at -4°C. We applied a randomized block design, with germination timing (GT) as the main factor, and block as the sub-factor. The whole plot was divided into twelve 2 × 3 m sub-plots, which were randomly assigned with four GT treatments and three blocks. Seeds of *A. theophrasti* were sown at an inter-planting distance of 10 cm on June 7, June 27, July 17 and August 7, as four GT treatments of spring (GT1), late spring (GT2), summer (GT3) and late summer (GT4). The treatments of germination timing accorded with the time range of germination of *A. theophrasti* in its nature habitats in northeast of China. Most seeds emerged four days after sowing. Seedlings were thinned at four-leaf stage and plots were hand-weeded when necessary and watered regularly.

### Data collection

For each treatment, we arranged three to four times of sampling, according to their growth stages and the lengths of life cycle, and generally harvested them at the stages of vegetative growth, late vegetative or early reproductive growth, and middle to late reproductive growth respectively (Table 1). For individuals that germinated in spring (GT1), we took an additional sample at their early vegetative growth stage as an extra harvest (EX), as a second reference (the first one is the vegetative growth stage) for comparison with the first samplings of other treatments, since the plants germinated early had a prolonged vegetative growth. At each harvest, five to six individual plants were randomly chosen from each plot, making a maximum total of 6 replicates × 3 blocks × 4 treatments × 3 harvests + 6 replicates × 3 blocks × 1 treatments (SP) × 1 harvest = 234 samplings. For each individual plant, the following traits were measured (if applicable): main root length, diameter at the basal of the main root, length and number of lateral roots (above or equal to 1 mm in diameter along the main root), the length of stem, diameter at the base of stem, petiole length and angle, leaf number, lamina width (leaf size, abbreviations for all traits are in Table 2). For individuals from GT1 and GT4 treatments, some traits were unavailable for measurement at early growth stages due to small plant sizes. Each plant individual was then separated into roots, stems, petioles, laminas, reproductive modules and branches (if there were any), oven-dried at 75°C for two days and weighed. Reproductive modules consisted of flowers and fruits produced along the main stem and branches, and branches included the stems and leaves on branches. Total mass and mass allocation traits were calculated.

### Statistical analysis

Statistical analyses were conducted using SAS statistical software (SAS Institute 9.0 Inc., 2002). All measured and calculated traits were used for analysis (Table 2). To minimize variance heterogeneity, all data were log-transformed, except for petiole angles and branch angles (square root-transformed), before statistical analysis. For plant total mass, we applied two-way ANOVA to analyze effects of germination timing, sampling time and their interactions, and one-way ANOVA to analyze the effects of germination timing or sampling time within each or across all of the other treatments. Plant size (e. g. total mass) can have very significant

effects on other traits, which may bias the effects of germination time. Therefore, for all the other traits, we applied two-way ANCOVA to evaluate overall effects of germination timing, sampling time and their interactions, and one-way ANCOVAs for effects of germination timing or sampling time within each or across all of the other treatments, with total mass as a covariate. For a given trait, significant contribution of total biomass (plant size) to its variation in response to germination timing indicates an occurrence of apparent plasticity (McConnaughay & Coleman, 1999). When effects of total mass were removed, the variation due to germination timing in trait expression was an indication of true plasticity (Weiner, 2004). Multiple comparisons used the Least Significant Difference (LSD) method in the General Linear Model (GLM) program, which produced adjusted mean values and standard errors in one-way ANCOVA.

## Results

After size effects were removed, germination time, sampling time and their interaction had significant effects on most traits (Table 2). Total mass increased over time (LSD,  $p < 0.05$ ) for all germination treatments (GT) except for those germinated in late spring (GT2), which had no difference in total mass between the second and third samplings (Fig. 1). Individuals that germinated in spring (GT1) experienced a long growth period (110 days) to reach 6.10 g of final total mass, whereas those germinated in late spring (GT2) and summer (GT3) grew rapidly, reaching 8.08g and 4.93g of total mass within 70 days, which was higher ( $p < 0.001$ ) or did not differ from that of spring germinants. GT2 germinants had the greatest total mass of all at the second stage ( $p < 0.001$ ), even greater than the final total mass of GT1 germinants ( $p = 0.001$ ). The individuals germinated in late summer (GT4) had the lowest total mass (2.41 g) of all at the final harvest ( $p < 0.001$ ), only reaching 29.8% of the final total mass of GT2 ones.

Across all harvests, earlier germinants (GT1 and GT2) had higher stem mass and allocation, root mass and allocation, with greater stem length, stem diameter and main root diameter, while germinants of GT2 and GT3 had higher reproductive mass and allocation, with more-parallel and larger leaves, and GT4 germinants had the higher leaf (petiole and lamina) mass and allocation, compared to other germinants ( $p < 0.05$ ); meanwhile, main root length and lateral root length were less affected by germination timing, especially at the last two stages (Fig. 2, 3). Individuals of GT2 had the highest petiole length and lamina size of all ( $p < 0.05$ ), GT3 germinants had the greatest petiole angle of all ( $p < 0.01$ ), and GT4 germinants had the most leaves of all ( $p < 0.05$ ; Fig. 3).

For all GT treatments, as plants grew, stem mass, reproductive mass and all morphological traits except for leaf number and lateral root number tended to increase in most cases ( $p < 0.05$ ), petiole mass allocation and lamina mass allocation tended to decrease ( $p < 0.05$ ) and lamina mass decreased from the second to the third harvest ( $p < 0.001$ ; Fig. 2, 3), and stem mass allocation decreased over time for individuals of GT3 only ( $p < 0.05$ ; Fig. 2). Because of the changes in these traits over time, their responses to germination timing also varied with different stages (Fig. 2, 3). For example, differences between different GT treatments became less significant in root allocation, petiole length, main root length and lateral root length as plant grew larger. GT2 germinants had the highest reproductive mass and allocation at the second stage, but the highest ones became GT3 germinants at the third stage. GT1 germinants had more leaves than others at the first stage, while GT3 and/or GT4 had more leaves than others at the second and third stages. GT1 and GT2 germinants had higher lateral root length at the first stage, but such advantages of them disappeared over time, they instead had a greater number of lateral roots, compared to other germinants.

## Discussion

Plants of *Abutilon theophrasti* can germinate over a wide range of period in growth seasons. Germination timing can influence the strength and direction of selection on plant performance and response in growth and reproductive traits later in the life cycle (Donohue et al., 2005; Mercer et al., 2011; Weinig, 2000). Germinating earlier generally results in higher fecundity, but selection on survival may favour early, intermediate, or late germination (Donohue et al., 2010; Kalisz, 1986; Verdu & Traveset, 2005), and thereby selection on germination timing may be conflicting (Akiyama & Ågren, 2014). It suggested there is an optimal germination time for plants (Gremer et al., 2020; ten Brink et al., 2020). This was supported by our results that the

optimal germination time for *A. theophrasti* was late spring, earlier or later germination had adverse effects on plant performance to different extents. In spite of this, individuals with advanced or delayed germination can still adopt different strategies in coping with subsequent environmental conditions via plasticity in biomass allocation and morphological traits.

### *The strategies of plants germinating in the optimal time*

Our results showed plants that germinated in late spring performed the best in total mass and reproduction among all treatments, and they had the highest stem mass and allocation, and the lowest leaf allocation. It is reported that early emergence can improve the performance and survival of plants (Abe et al., 2008; Afonso et al., 2014; Bianchi et al., 2019; Cogoni et al., 2013; Verdu´ & Traveset, 2005), due to the profits from a long growing season for growth and reproduction (Donohue et al., 2010; Stratton, 1992). Meanwhile, the climate and soil conditions in late spring should also be more favorable for rapid biomass accumulation, making them less likely to expose to environmental hazards than those germinated in earlier time of spring. Consequently, they can optimize performance in relatively more favorable environmental conditions, leading to an extensive vegetative growth and improved reproduction. In this term, plants that germinate early can have a strong competitive advantage over those germinate late, especially at high population densities (Miller et al., 1994; Orrock & Christopher, 2010). The planting density applied in this study was a little high (plants were sown with an inter-plant distance of 10 cm), which may cause some extent of competition, inducing additional stem elongation, especially for those germinated earlier in spring and late spring and when they grew to larger plant sizes.

The timing of germination determines the environmental cues plants expose to, such as day length, temperature and water availability, which influence the responses of life history traits (Huang et al., 2016; Wilczek et al., 2009). Plants can perceive and transmit the signals of changing photoperiod and temperature (Zhou et al., 2005), to promote time emergence, growth and reproduction to coincide with favourable conditions (Andrés & Coupland, 2012; Blackman, 2017). It suggests they are able to judge the environmental changes by these signals, and determine which strategy to use in dealing with the circumstances indicated by the environmental cues. Consequently, when they did not germinate within the optimal period, plants may still be able to adjust their growth strategy in exposure to unfavorable conditions due to advanced or delayed germination.

### *The strategies of plants with advanced vs. delayed germination*

Plants that germinated earlier in spring also had prolonged vegetative growth and life cycle, even longer than those germinating in late spring, but they had similar or lower performance in total mass and reproduction as late-spring germinants. This was probably due to the unfavorable environments in early and middle spring. Early germinants may experience a higher risk of mortality, due to seasonal hazards such as pathogens, predation, desiccation (Donohue, 2014; Jones & Sharitz, 1989; Mercer et al., 2011; Rice, 1990), in spite of the importance of early emergence and establishment (Miller et al., 1994). Especially in this study, although the season between April and May is in spring in northeast of China, the climate then is usually chilling, with unpredictable precipitation and frequent drought mortality, similar to the situation of other studies (Weekley et al., 2007), when early germination becomes a ‘high-risk high-gain’ strategy (ten Brink et al., 2020). Spring-germinants had smaller leaves and more-vertical petioles, which is a “shade avoidance” response (Wang et al., 2017; Wang & Zhou, 2021), indicating they experienced stronger intraspecific competition than those germinated in late spring and summer. Limited resources may decelerate the growth of early seedlings, reducing the differences between them and late seedlings (Verdu´ & Traveset, 2005). Therefore, spring-germinants did not outperform late-spring germinants, although their longer growing period allows a longer vegetative and reproductive growth than the latter. The disadvantage of advanced germination may partially explain why seed germination can spread over several years via dormancy, to reduce the risk of failure within growth seasons of fluctuating abiotic conditions (ten Brink et al., 2020). But it is worth noting that in spite of the possible damage of early drought stress and reduction in growth rate, plants with advanced germination were still able to survive and perform better than those germinated too late, by virtue of the benefits from longer growing period and greater plant size, substantial seedling height and greater number

of leaves (Bianchi et al., 2019).

By contrast, plants germinated later in summer had accelerated growth, and accumulated total biomass to the same level as spring germinants within much shorter time. They shortened vegetative growth, to initiate reproductive growth earlier, in order to complete their life cycles before the climate became stressful or lethal. This may be achieved by perceiving signals of shorter daylight, indicative of inadequate time for completing life cycles. Finally, they also had increased reproductive mass and allocation, compared to earlier germinants, consistent with other results (Hartzler et al., 2004; Wu & Owen, 2014). This to a large extent be due to the benefits of their increased investment to leaf mass and allocation, and their responses of many morphological traits, such as a greater number of leaves and less-vertical petioles, lower stem mass and allocation, shorter and thinner stems and roots, compared to spring germinants. If relative plant size is associated with resource overlap, later germination could promote resource partitioning (Leverett et al., 2018) or higher efficiencies of resource allocation (Wu & Owen, 2014). Plants that emerged in spring had increasing stem mass and allocation and decreasing leaf mass and allocation as they grew larger, while those emerged in summer had decreasing stem mass allocation over time, suggesting the plants with delayed germination may give the priority to the growth of leaves and reproduction, avoiding extensive stem growth, to ensure the completion of an entire life cycle.

Plants emerged in late summer adopted the same strategy of reducing stem growth and enhancing leaf mass and allocation. Delaying germination further into late summer also led to a faster growth, but reduced total mass and reproduction due to insufficient time for completing a life cycle at the end of growth season. The delay of germination is costly to fitness (Metcalf et al., 2003; Tuljapurkar, 1990), especially when it led to incomplete life cycle. Plants germinated in late summer produced flowers, but did not have time for fruit shaping and ripening. In addition, delaying germination into late summer also led to decreased mass allocated to roots and stems, but the highest leaf mass and allocation of all, suggesting that trade-off not only occurs between vegetative growth and reproductive growth, but also between different vegetative organs. In response to the seasonal changes, late-summer germinants also produced more and smaller leaves with shorter petioles than other germinants. This may because the growth rate of individual leaves or analogous repetitively generated organs is relatively fixed, and it cannot be easily altered by environmental conditions, so that plants can only increase the investment to leaf population by producing a greater number of leaves.

Moreover, the increased allocation to leaves was at the cost of reduced stem allocation, rather than root allocation. It suggested that the canalization of root mass allocation is more important than stem allocation for maintaining plant growth and functions. This was supported by the attenuated effects of germination timing on the length of main root and lateral roots over time, and plants with delayed germination (GT3 and GT4) even had more lateral roots at the first or second stage. And evidence also came from the more-stabilized root mass allocation over different densities, compared to the responses of shoot or above-ground modular mass allocation to density, as plants grew (Wang et al., 2017, 2021). It demonstrated that *A. theophrasti* can respond to germination timing though the plasticity in a number of traits, and there were some differences in responses of allocation and morphological traits. Firstly, plastic responses of morphological traits may precede responses of biomass allocation (Wang et al., 2017). Secondly, in response to delayed germination, they may first increase root morphological traits such as lateral root numbers, then increase the lengths of main root and lateral roots, in order to keep root mass allocation stable, before enhancing leaf morphological traits such as leaf size, leaf number, petiole angle and length, to increase the leaf mass allocation, ultimately for canalizing reproductive efforts. In other words, plasticity of root traits may occur before those of leaf traits, in response to germination timing. It suggested root plasticity plays a predominant role in plant response to environments, probably orientating, regulating and determining the responses of above-ground organs; or alternatively, root plasticity provides a basic premise for growth and adjustments of other organs due to their important supporting functions. Consequently, in face of any environmental changes, it is more crucial for plants to maintain root mass allocation, whereas investments put into stem or leaves can always be deliberated and balanced depending on specific situations. When competition for light is more emergent, the additional stem elongation can be at the cost of leaf growth (Wang et al., 2017); if growth time becomes more limited, leaf growth prevails over stem elongation, which can be sacrificed. Of course, plants will always

adjust or canalize vegetative organs in order to achieve stable reproductive efforts.

In spite of the conspicuous disadvantages in comparison with late-spring germinants, plants with advanced and delayed germination still can use different strategies to reduce the adverse effects of germination timing. Natural selection may favour germination at different times or a mixed, bet-hedging strategy (Silvertown, 1988; Zhou et al., 2005). Natural selection for competitive traits include large plant size (e. g. height, total biomass) and long life span; conversely, small size, high relative growth rate and reproductive allocation indicate ruderal selection (Grime, 1979; Hodgson, 1999). Plants germinated earlier have prolonged vegetative growth and life cycle, and delayed reproduction; plants with delayed germination have compressed vegetative growth, advanced reproduction, and shortened life cycles. Therefore, plants that germinated in spring and late spring tended to adopt the strategies of competitors (C), while those with delayed germination tended towards ruderal strategies (R) (Zhou et al., 2005). The coexistence of multiple germination strategies may result from the density dependence of plant growth (Metcalf et al., 2015; Poethke et al., 2016), since plants were growing in relatively dense population in this study. The phenotypic plasticity in growth strategy may compete with bet hedging as a way to deal with environmental variation (Donaldson-Matasci et al., 2013; Xue & Leibler, 2018), if cues allow some aspects of the environment to be measured or predicted (ten Brink et al., 2020). For future work, it is worthwhile to study how variable conditions in growth season, such as water, nutrients and light resources, affects germination strategies (ten Brink et al., 2020).

## Conclusions

Our results showed that there is an optimal germination time, and it was late spring in this study, when plants can maximize their growth potential in relatively favorable conditions. Plants that germinated earlier in spring used a longer time for vegetative growth and did not outperform late-spring germinants, probably due to exposure to spring drought and response to competition. Delaying germination into summer led to a faster growth, increased leaf allocation, decreased stem allocation, advanced reproduction and shorter life cycle, but further delay of germination into late summer led to insufficient reproduction and incomplete life cycle due to extremely short growth period. In response to delayed germination, plants may first increase root morphological traits before enhancing leaf morphological traits, in order to achieve stable reproductive efforts. They may increase the leaf allocation by producing more leaves than increasing individual leaf mass, at the cost of reduced stem allocation, rather than root allocation. These suggested root plasticity plays a predominant or fundamental role in plant response to environments, probably orientating, regulating and determining the responses of above-ground organs. Therefore, it is more crucial for plants to maintain root allocation stable, whereas mass allocated to stem or leaves can always be deliberated and balanced depending on specific situations. In spite of conspicuous disadvantages, plants with advanced and delayed germinated were still able to use different strategies to better adapt to subsequent environments, via modifying a number of allocation and morphological traits. Plasticity in these traits may play an important role in determining plant survival and success in face of the environmental challenges due to inopportune germination timing.

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## Conflict of interests

The authors have no conflict of interest to declare.

## Author contributions

**Shu Wang** : Conceptualization (lead); Project administration (lead); Data curation (lead); Formal analysis (lead); Funding acquisition (lead); Investigation (lead); Methodology (lead); Visualization (lead); Writing-original draft (lead); Writing-review & editing (lead). **Dao-Wei Zhou** : Conceptualization (supporting);

Funding acquisition (supporting); Methodology (supporting).

## Data availability

Data are available via the Dryad Digital Repository:

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**Table 1** The information on germination treatments, planting and sampling in this study.

Germination time	Abbreviation	Planting date	Sampling time	Growth period (d)
Spring	GT1	Jun. 7	EX	30
			I	50
			II	80
			III	110
Late spring	GT2	Jun. 27	I	50
			II	70
			III	90
Summer	GT3	Jul. 17	I	30
			II	50
			III	80
Late summer	GT4	Aug. 7	I	30
			II	40
			III	50

**Table 2** *F*-values from two-way ANCOVA on all traits (with abbreviations), for effects of germination timing (GT), sampling time (ST) and their interactions, with total mass (TM) as a covariate. N indicates the total number of individual plants measured for a given trait. \*  $p < 0.05$ , \*\*  $p < 0.01$ , \*\*\* $p < 0.001$ .

Trait	N	TM (df = 1)	GT (df = 3)	ST (df = 3)	GT × ST (df = 6)
Total mass	216		82.71***	98.11***	13.39***
Root mass	216	196.30***	4.57***	6.76***	5.22**
Stem mass	216	481.15***	54.02***	71.99***	19.374***
Petiole mass	202	54.45***	1.89	9.58***	4.28**
Lamina mass	216	152.08***	15.84***	27.45***	16.42***
Branch mass	64	6.51*	0.25	2.98	—
Reproductive mass	165	360.83***	1.486	7.74***	0.44
Root mass ratio	216	13.10***	4.50***	5.68**	3.46**
Stem mass ratio	216	38.45***	116.93***	81.84***	29.74***
Petiole mass ratio	202	0.58	47.64***	28.02***	0.79
Lamina mass ratio	216	8.69**	133.54***	200.96***	20.10***

Reproductive mass ratio	165	51.31***	9.72***	9.59***	26.26***
Branch mass ratio	64	0.94	0.35	2.82	—
Main root length	188	2.12	9.83***	15.41***	30.70***
Main root diameter	188	48.23***	32.89***	16.46***	4.83***
Lateral root length	170	5.97*	9.66***	3.85***	2.84*
Lateral root number	170	7.45*	0.84	3.90*	2.74*
Stem length	202	19.09***	88.96***	111.15***	20.77***
Stem diameter	202	35.98***	112.47***	35.02***	144.83***
Petiole length	170	6.14*	0.38	0.63	0.10
Petiole angle	170	0.74	55.35***	50.42***	15.18***
Lamina size	205	47.96***	18.66***	5.19**	19.64***
Leaf number	170	1.45	17.53***	54.25***	19.23***

## Figure legends

**Fig. 1** Mean values ( $\pm$ SE) of total biomass of plants that germinated in spring (GT1), late spring (GT2), summer (GT3) and late summer (GT4) and harvested at different growth stages (growth period).

**Fig. 2** Mean values ( $\pm$ SE) of the mass of various organs for plants that germinated in spring (GT1), late spring (GT2), summer (GT3) and late summer (GT4) and harvested at different growth stages (I~III and EX for GT1). Different lowercase letters indicate significant difference between growth stages within germination treatment (GT), different uppercase letters indicate significant difference between GT treatments for each stage ( $p < 0.05$ ). The extra sampling (EX) for spring germinants (GT1) was taken before the first time of GT1 sampling as a reference for comparisons.

**Fig. 3** Mean values ( $\pm$ SE) of morphological traits for plants that germinated in spring (GT1), late spring (GT2), summer (GT3) and late summer (GT4) and harvested at different growth stages (I~III). Different lowercase letters indicate significant difference between growth stages within each germination treatment (GT), different uppercase letters indicate significant difference between GT treatments within each stage ( $p < 0.05$ ).

**Fig. 1** Mean total biomass ( $\pm$ SE) of plants that germinated in spring (GT1), late spring (GT2), summer (GT3) and late summer (GT4) and harvested at different growth stages (growth period).

**Fig. 2** Mean values ( $\pm$ SE) of the mass of various organs for plants that germinated in spring (GT1), late spring (GT2), summer (GT3) and late summer (GT4) and harvested at different growth stages (I~III and EX for GT1). Different lowercase letters indicate significant difference between growth stages within germination treatment (GT), different uppercase letters indicate significant difference between GT treatments for each stage ( $p < 0.05$ ). The extra sampling (EX) for spring germinants (GT1) was taken before the first time of GT1 sampling as a reference for comparisons.

**Fig. 3** Mean values ( $\pm$ SE) of morphological traits for individual plants that germinated in spring (GT1), late spring (GT2), summer (GT3) and late summer (GT4) and harvested at different growth stages (I~III). Different lowercase letters indicate significant difference between growth stages within each germination treatment (GT), different uppercase letters indicate significant difference between GT treatments within each stage ( $p < 0.05$ ).