

RESEARCH ARTICLE

Precipitation predictability drives evolution of drought strategies in the common poppy, *Papaver rhoeas*

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Abstract

1. Current climate change leads to an increase in the frequency and intensity of droughts and to a decreased precipitation predictability. The few studies investigating plant evolutionary responses to contrasting predictability regimes showed that intrinsic precipitation predictability shapes plant phenotypic variation, drives evolution of phenotypic plasticity and can vary in strength and direction of selection. This suggests that the selection pressure induced by decreased precipitation predictability may lead to plants coping better with severe drought events.
2. To investigate whether past precipitation predictability influences plant responses to different drought conditions, we performed a common-garden experiment applying control, short-term and long-term drought treatments on seedlings of *Papaver rhoeas* (Papaveraceae) whose progenitors experienced less versus more precipitation predictability treatments for three consecutive generations. In addition, to assess whether competition modulates plant responses, half of the plants were grown together with the widespread herbaceous plant *Galium album* (Rubiaceae).
3. In the presence of long drought episodes, plants whose progenitors experienced less predictable precipitation survived longer than those whose progenitors experienced more predictable precipitation. Furthermore, plants whose progenitors experienced less predictable precipitation had lower biomass, which is likely to reduce water loss via transpiration, and, across all drought treatments, they showed lower root investment. However, no trait differences were detected under competition, indicating that interspecific competition may limit the expression of evolutionary responses to changes induced by precipitation predictability.
4. Altogether our results indicate that lower precipitation predictability mainly promotes the evolution of drought-escape and drought-avoidance strategies. Overall, our experiment highlights that precipitation predictability is an important evolutionary driver of plant functional responses, potentially shifting evolutionary trajectories of plants under increasing intensity of drought events.

Katja Springer and Thibault Coquery contributed equally.

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KEYWORDS

climate change, common-garden experiment, competition, drought strategy, experimental evolution, natural selection, phenotypic plasticity, transgenerational responses

1 | INTRODUCTION

Current climate change leads to increased global temperatures, higher frequency and intensity of drought events, as well as to decreased precipitation predictability (Pörtner et al., 2022; Swain et al., 2018; Xu et al., 2020). Drought events are caused by changes in mean precipitation and lead to water scarcity (Dai, 2013), while changes in precipitation predictability are defined as the changes in the degree of temporal correlation between precipitation events (Ashander et al., 2016) and affect the temporal availability of water (Karl et al., 1995). Although both climatic factors are independent, drought and changes in precipitation predictability can occur simultaneously (Singh et al., 2018), with exacerbated effects for plant populations. Consequently, plants should continuously and rapidly evolve under these changing environmental conditions.

Drought hinders plant performance and usually increases mortality rates, reducing the persistence of plant populations (Maggio et al., 2018). Plants can successfully overcome unfavourable drought conditions by increased plasticity (Hoffmann & Sgrò, 2011; Lambrecht et al., 2020). They can also use a drought-escape, a drought-avoidance or a drought-tolerance strategy in order to deal with reduced precipitation (Bowles et al., 2021; Levitt, 1980; Rauschkolb et al., 2022). This would require rapid phenological, morphological or physiological adjustments. For instance, they can grow faster, reduce root allocation or flower earlier to escape from drought (Franks et al., 2007; Kooyers, 2015; Metz et al., 2020), and they may slow down their growth or generate longer roots to take up water from deeper soil layers and thus avoid water deficit (Anstett et al., 2021; Kooyers, 2015; Padilla & Pugnaire, 2007), or reduce water loss by changing leaf water potential in order to tolerate drought (Bartlett et al., 2014; Bowles et al., 2021; Májeková et al., 2019), respectively. However, how environmental conditions during previous generations shape plant strategies to current drought conditions has been little studied.

Environmental predictability can alter life-history traits and phenotypic variation and can affect the persistence of plant populations (Ashander et al., 2016; March-Salas et al., 2019; March-Salas & Fitze, 2019a; March-Salas & Perterra, 2020; Reed et al., 2010). Experimental studies showed advanced reproduction under less predictable conditions, which increased plant fitness (March-Salas et al., 2019; March-Salas, Fandos, et al., 2021). Decreased predictability may favour rapid transgenerational responses (March-Salas et al., 2019), increase selection pressure (March-Salas, van Kleunen, et al., 2021) and likely cause evolution of reduced phenotypic plasticity (Burgess & Marshall, 2014; Franch-Gras et al., 2017; Leung et al., 2020; March-Salas et al., 2022; Tufto, 2015; Yin et al., 2022). Transgenerational plasticity is normally selected in predictable environments and selected against under less predictable conditions,

the latter potentially favouring rapid evolution as well as trait adjustments to severe droughts, which may shield a population from selection (Burgess & Marshall, 2014; Merilä & Hendry, 2014; Metz et al., 2020). This is supported by previous studies which showed that less predictable precipitation can rapidly vary the root functional investment, favouring fitness changes in the next generation if these offspring were subjected to the parental conditions (March-Salas et al., 2022; March-Salas, van Kleunen, et al., 2021; Yamauchi et al., 2021; Zhou et al., 2019). Therefore, the degree of precipitation predictability in progenitors can evolve the functional strategy used by plants to deal with climatic stressors such as increasing frequency and intensity of drought conditions. It is then important to investigate whether plants are predisposed by progenitors (either through maternal effects or through selection) and whether they show evolutionary changes that allow them to cope with drought events. However, the presence of competitors can also strongly affect the expression of evolutionary responses to environmental cues, since interspecific competition can promote shifts in the soil properties and resource limitation that can mediate trait adjustments (Craine & Dyzinski, 2013; Palacio-López et al., 2020).

In our study, we selected maternal lines of the widespread annual herb *Papaver rhoeas* L. (Papaveraceae) that were experimentally exposed to more and to less predictable precipitation during three consecutive generations. To investigate whether plants show changes due to these past precipitation predictability treatments, we sowed seeds of the maternal lines in a common-garden experiment. To assess whether past precipitation predictability led to a specific plant strategy, and whether this strategy benefited them to withstand drought, the offspring of these selected maternal lines was exposed to control, short-term and long-term drought, and wilting time, plant size and root traits were measured. We expect: (i) that different past precipitation predictability treatments led to different phenotypes and to different plasticity, expressed under common-garden conditions; (ii) that evolutionary change was stronger under lower past precipitation predictability, given that progenitors under this treatment showed lower transgenerational trait plasticity in a previous study; and (iii) that lower past precipitation predictability favoured drought stress strategies that can help plants to avoid dehydration.

2 | MATERIALS AND METHODS

2.1 | Study species

The annual herb *P. rhoeas* L. (common poppy, Papaveraceae) is a cosmopolitan and fast-growing species. It is widespread throughout Europe, over central and northern Asia, North Africa and the Canary

Islands (McNaughton & Harper, 1964). This species is an erect herb, which is usually between 10 and 50 cm high. The leaves are hairy and particularly variable in their shape and size. The basal leaves form a rosette of pinnatifid and alternate leaves (Tutin et al., 1993). This species has a slender primary tap root with multiple lateral secondary roots (McNaughton & Harper, 1964). *Papaver rhoeas* can withstand dry conditions (Torra et al., 2011), being commonly associated with disturbed habitats, arable lands and cereal crops, where it occurs frequently with few or no competitors, and it also grows in communities with other herbaceous species (McNaughton & Harper, 1964).

2.2 | Past precipitation predictability treatments

In 2012, seeds of *P. rhoeas* were sown at the experimental field station 'El Boalar' (42°33' N, 0°37' W, 705 m a.s.l.; Jaca, Spain), where the natural intrinsic precipitation predictability was manipulated by means of an automated watering system (March-Salas et al., 2019; March-Salas & Fitze, 2019a). Plants were either exposed to more (M) or to less (L) predictable precipitation (March-Salas et al., 2019; March-Salas, van Kleunen, et al., 2021). To this end, supplemental watering events at regular time-intervals for the M treatment, and at random time-intervals for the L treatment, were added to the natural precipitation, resulting in a weighted permutation entropy (i.e. a measure that is inversely related to intrinsic predictability; Pennekamp et al., 2019) of 0.77 in M and 0.86 in L. Intrinsic precipitation predictability in M was equal to the one of natural precipitation, and the intrinsic precipitation predictability of L was 11.69% lower than that of M and of the natural precipitation (March-Salas et al., 2019). Each treatment was applied to four plots (i.e. in each predictability treatment, the time-interval between the watering events was the same for all four plots), and both treatments consisted of the same total amount of precipitation (natural + supplemental) and of 14 supplemental watering events per week (each of 1.3 mm). The same watering treatment was applied to each generation from April to the end of September.

To test whether precipitation predictability treatments cause transgenerational phenotypic changes, these treatments were applied over three consecutive generations in such a way that offspring seeds were always sown under the same precipitation predictability treatment, but never in the plot of the maternal plant. Seeds generated in 2012 (G1) were sown in 2013 and raised under the same treatment as their ancestor (G0). The seeds generated in 2013 (G2) were sown in 2014 and raised under the same treatment as their ancestors (G0 and G1). Finally, the seeds generated in 2014 (G3) were collected, separated by maternal plant and stored in dry and dark conditions. Seed collection and seed storage were standardized and conducted by the same person over all years. All seeds were collected at the same stage of capsule development (March-Salas et al., 2022), and directly after collection all seeds were stored at the same place. The collected seeds were from several outcrossed flowers of the same maternal plant, and the seedlings produced could be either half- or full-siblings. Each year, before the start of

the experiment, seed families were randomly selected for sowing, and we tested that the selected and not selected seed families were chosen randomly and that they did not differ in their maternal phenotypic characteristics (maternal size, maternal reproduction and maternal phenology). Thereafter, we randomly selected seeds to sow from each selected seed family, and we then tested that selected and not selected seeds of the same seed family did not differ in seed weight (March-Salas et al., 2019). Finally, to control for potential year effects, we have additionally sown each year seeds from the original natural population together with the descendant plants (for further details and results, see March-Salas et al., 2019).

2.3 | Experimental setup

In winter 2022–2023, a common-garden experiment with the G3 seeds was conducted in a greenhouse at Goethe University Frankfurt (50°10' N, 8°38' E, Frankfurt am Main, Germany). Six seed families were randomly selected from each predictability treatment for this experiment and sown in November 2022 in separate trays. This random selection included either one or two seed families from each plot. In December 2022, seedlings from each seed family and predictability treatment were randomly selected and transplanted into 0.75 L pots, testing that there were no differences in initial size among treatment groups. These seedlings were exposed to three levels of drought treatments and to two levels of competition (see details below). Four replicates per seed family were transplanted (each in a separate pot). Consequently, seedlings of each seed family were transplanted to $3 \times 2 \times 4 = 24$ pots. Moreover, to increase the chances of having one alive seedling per pot, we transplanted two seedlings from the same seed family in the middle of each pot and separated by approx. 3 cm. Thus, a total number of 576 seedlings (i.e. two predictability treatments $\times$ six seed families $\times$ three drought treatments $\times$ two competition treatments $\times$ four replicates $\times$ two seedlings per pot) were transplanted into 288 pots. Of each plant, the largest diameter (in cm) and the number of leaves were measured the day after the transplantation, and used in the analysis to account for potential effects of the initial size of the selected seedlings. The pots were positioned in 12 trays (each tray with 24 pots), and the position of the trays in the greenhouse as well as the position of the 24 pots within each tray was randomized once per week. Pots were watered with sufficient water for 2 weeks so that the plants could acclimate after the transplantation. After this establishment period, pots with two alive seedlings were randomly thinned to one seedling (hereafter referred to as Day 1).

From Day 1 and for almost 4 weeks, seedlings were exposed to long-term drought, short-term drought or to a control treatment (hereafter referred to as 'drought treatments'). Pots under the long-term drought treatment did not receive any water for the 4 weeks. Pots under the short-term drought treatment received sufficient water during the first week and were not watered during the next 3 weeks. The control pots received sufficient water during the 4 weeks. Each drought treatment was applied to one third of the

pots (i.e. 96 pots within four trays per drought treatment). The average soil humidity of each treatment was measured in three pots per tray (i.e. 12 pots per drought treatment) using soil moisture sensors (ML3 ThetaProbe; Delta-T Devices Ltd, Cambridge, UK), once in each of the last 3 weeks of the experiment. In the first of the last three experimental weeks (12 and 3 days after the long- and short-term drought treatments started, respectively), the driest pots were those of the long-term drought treatment, while the pots of the short-term drought treatment showed an intermediate soil humidity, and the pots of the control treatment showed the greatest humidity (Figure S1). The soil of the control treatment showed constant humidity during the last three experimental weeks, whereas the pots of both drought treatments showed significant and progressively decreasing humidity across measuring times (Figure S1).

In addition, since *P. rhoeas* grows in presence of no, few or many competitors (e.g. together with other forbs and grasses; McNaughton & Harper, 1964), we assessed whether the response of plants to the drought treatments differed when they grew or did not grow under competition. In half of the pots of each treatment, we used *Galium album* (Rubiaceae) as competitive species, since *Galium* species are commonly co-occurring with *P. rhoeas* (McNaughton & Harper, 1964). To do so, four seedlings of *G. album* were planted in each corner of the competition pots on the same day as the seedlings of *P. rhoeas* (Figure 1).

2.4 | Plant measurements

The wilting time, defined as the day when the leaves of *P. rhoeas* hung over the edge of the pots, was checked daily from the start of the drought treatment. When the plants started to wilt, we harvested them, and the nonwilted plants were harvested at the end of the

experiment. After harvesting, the total number of leaves (i.e. the wilted and nonwilted ones in the wilted plants) was counted, and the length of the longest leaf was measured to the nearest 0.5 cm. Additionally, roots were carefully dug out and washed to remove the substrate. The length of the longest root was measured to the nearest 1 mm as an estimate of maximum rooting depth. Plants were then dried in an oven for 72h at 60°C and both dry above-ground and belowground biomass (g) were determined. Lastly, the root:shoot ratio was calculated (dry above-ground biomass/dry belowground biomass).

2.5 | Replication statement

Scale of inference	Scale at which the factor of interest is applied	Number of replicates at the appropriate scale
Plant	Plot	4, 4 (for each past predictability treatment)
Seed family	Past predictability treatment	6 per past predictability treatment

2.6 | Statistical analysis

All statistical analyses were conducted with R version 4.1.1 (R Development Core Team, 2021). Linear mixed-effect models were applied for each of the seven response variables, using the 'lme4' package and the 'lmer' function (Bates et al., 2015). Past precipitation predictability treatment (more versus less), drought treatment (control, short-term and long-term drought) and competition treatment (without versus with competition) as well as their two- and

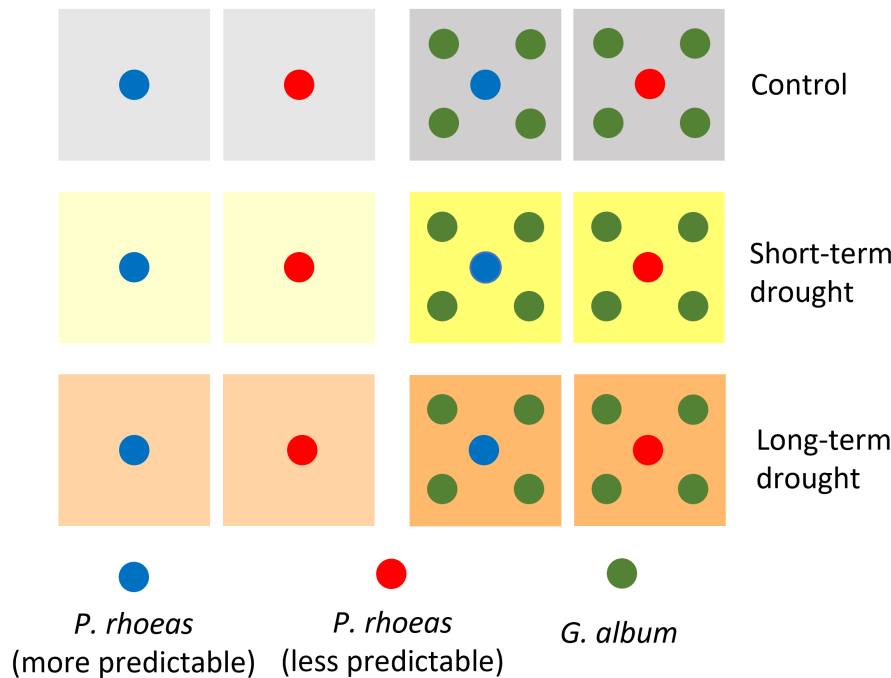


FIGURE 1 Design of the common-garden experiment. Each square represents one pot for each treatment level. Drought treatments are indicated by different background colours (grey: control treatment, yellow: short-term drought treatment, orange: long-term drought treatment). Blue and red dots represent *Papaver rhoeas* individuals whose progenitors experienced more (M) or less (L) predictable precipitation, respectively. In pots with competition, four individuals of *Galium album* (green dots) were planted in each corner. For each treatment level, we used six seed families with four replicates, resulting in 288 pots.

TABLE 1 Results of the linear mixed-effects model including the effect of past precipitation predictability [P], competition [C], drought [D] and their two- and three-way interactions on trait responses of *Papaver rhoeas*.

Effect	df	Wilting time ¹	Above-ground biomass ²	Length of longest leaf ³	Number of leaves ⁴	Belowground biomass ⁵	Root length ⁵	Root:shoot ratio ⁶
Initial number of leaves	1	21.281***	25.730***	9.489**	44.120***	24.198***	0.807	0.712
Precipitation predictability [P]	1	0.012	1.881	4.276*	0.074	0.581	1.186	0.030
Competition [C]	1	186.271***	381.041***	79.409***	182.009***	339.743***	153.125***	0.465
Drought treatment [D]	2	672.698***	156.845***	153.852***	66.624***	69.765***	23.125***	31.891***
P×C	1	1.382	0.269	0.871	3.800•	0.007	7.872**	0.088
P×D	2	7.201*	6.162*	3.533	7.037*	4.729•	0.769	2.875
C×D	2	91.665***	17.215***	51.595***	13.261**	7.620*	1.981	11.293**
P×C×D	2	18.269***	3.500	8.176*	7.954*	12.683**	4.726•	24.701***

Note: Initial number of leaves was also included as covariate. Shown are chi-squared values followed by significance stars (bold): *0.05 > $p \geq 0.01$; **0.01 > $p \geq 0.001$; *** $p < 0.001$, and • reflects marginal effects ($0.1 > p \geq 0.05$). Sample size was 284. df, degrees of freedom. Response variables are wilting time (defined as number of days until wilting), above-ground biomass (g), belowground biomass (mg), root:shoot ratio, root length (cm), number of leaves and length of the longest leaf (cm). Transformations: ¹ $\wedge 3.5$; ² $\wedge 0.55$; ³ $\wedge 0.8$; ⁴ $\wedge 0.12$; ⁵ $\wedge 0.42$; ⁶ $\wedge 0.7$.

three-way interactions were included as fixed factors. Seed family nested in plot was included as random factor (1|plot/seed family) and initial number of leaves as covariate. In all models, we tested the assumptions of normality and homogeneity of variance of the residuals using the Shapiro–Wilk test and the Bartlett test, respectively. If the residuals were not normally distributed, we transformed the response variable (see transformations in Table 1). When we found significant interactions, we applied Tukey's post hoc contrasts using the 'lsmeans' package (Lenth, 2016) to understand which levels were significantly different.

3 | RESULTS

3.1 | Treatment effects on wilting time

Past precipitation predictability led to differences in wilting time in plants exposed to the long-term drought treatment without competition, but neither in the plants with competition, nor in the plants exposed to the short-term drought treatment. This result is shown by a significant past predictability × drought × competition three-way interaction (Table 1; Figure 2; Figure S2) and the post hoc contrasts shown in Figure S2. Plants whose progenitors experienced less (past L) predictable precipitation wilted significantly later than those whose progenitors experienced more (past M) predictable precipitation (post hoc contrast: $p = 0.005$) (Figure S2). This effect was evident from Day 20 to the end of the experiment, when the proportion of wilted plants was higher (i.e. the proportion of nonwilted plants was lower, Figure 2) if past predictability was M compared with L. Past predictability did not promote significant differences in wilting time under short-term drought or control treatments (Figure S2). Overall, in presences of droughts, plants without competition wilted significantly later than plants under competition (Figure 2; Figure S2). None of the plants of the control treatment wilted during the experiment (Figure 2; Figure S2).

3.2 | Treatment effects on above-ground traits

Past precipitation predictability led to differences in all three above-ground morphological traits, either in two-way interactions with the drought treatment for above-ground biomass and number of leaves, or in three-way interactions with the drought treatment and competition for maximum leaf length and number of leaves (Table 1). Under long-term drought and without competition, plants from past L showed significantly lower above-ground biomass ($p = 0.015$), shorter leaves ($p = 0.025$) and fewer leaves ($p = 0.047$) than plants from past M (Figure 3a–c). However, past predictability did not promote significant trait differences under long-term drought with competition. Nor did past predictability significantly affect above-ground trait responses in the control or short-term drought treatments, irrespective of the competition treatment. In addition, plants from past L showed overall significantly shorter leaves compared with the plants from past M, as indicated by the past predictability main effect (Table 1). Furthermore, under long-term drought, significant differences between competition treatments existed for all above-ground traits in plants from past M but in plants from past L only for above-ground biomass (Figure 3a–c), indicating that the past predictability treatments led to differences in plasticity to competition.

3.3 | Treatment effects on belowground traits

Past precipitation predictability led to differences in all three belowground traits either in two-way interactions with the drought treatment for belowground biomass (marginally significant, Table 1) and with competition for root length as well as in three-way interactions with drought and competition for belowground biomass and root:shoot ratio (Table 1). Under long-term drought and without competition, plants from past L showed a significantly lower belowground biomass ($p = 0.028$) and a lower root:shoot ratio ($p = 0.036$)

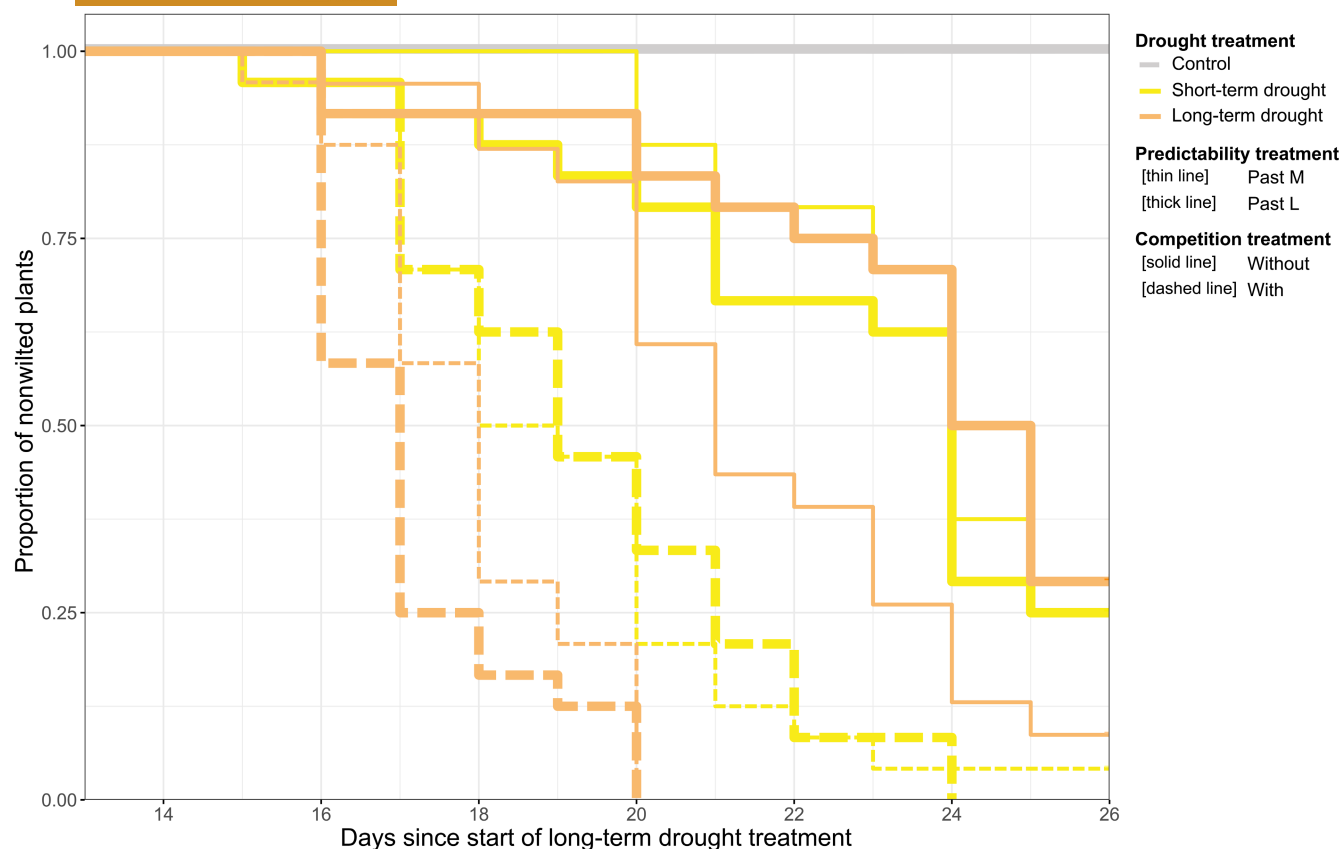


FIGURE 2 Proportion of nonwilted *Papaver rhoeas* plants during the experiment per treatment level. The grey lines represent the control treatment, yellow the short-term drought treatment, and orange the long-term drought treatment. Within each drought treatment level, thin lines represent plants whose progenitors experienced more (M) predictable precipitation while thick lines represent those that experienced less (L) predictable precipitation. Solid lines show *P. rhoeas* plants without competition while the dashed lines show plants growing with competition. The x-axis shows the number of days since the start of the long-term drought treatment.

than plants from past M (Figure 3d,f). This effect was also found under control conditions with competition in the root:shoot ratio ($p=0.043$), but no significant differences were found in the short-term drought treatment (Figure 3f). Under long-term drought, significant differences between competition treatments existed for root:shoot ratio in plants from past L but not in plants from past M, and the opposite was true in the control treatment (Figure 3f). The effect of past predictability on the root length varied with the competition treatment (Table 1). Across the three drought treatments, plants from past L growing under competition showed significantly shorter roots compared with the plants from past M growing under competition ($p=0.008$), but no significant differences between the past predictability treatments were found within drought-treatments, independent of whether plants grew with or without competition (Figure 3E).

4 | DISCUSSION

Our study shows that lower precipitation predictability experimentally applied over multiple generations caused drought escape and

avoidance strategies in *P. rhoeas*. Lower past precipitation predictability caused trait differences of the offspring plants growing in common-garden conditions, suggesting that precipitation predictability triggered evolutionary differences. The results on plant wilting show that, under severe drought, plants whose progenitors experienced less predictable precipitation survived longer than those whose progenitors experienced more predictable precipitation, which may also be in line with a drought-tolerance strategy. However, plants from the less predictable treatment had lower biomass and less leaves, suggesting that lower predictability can cause evolution towards a drought-escape strategy, helping to reduce water loss. In addition, in line with findings in the previous generations exposed to differences in precipitation predictability (e.g. March-Salas, van Kleunen, et al., 2021; March-Salas et al., 2022), under long-term drought and the control treatment the investment into roots was lower in plants from the less predictable treatment compared with the more predictable treatment when they were growing without or with competition, respectively. This also indicates that the root trait expression was shaped by differences in precipitation predictability, and altogether this suggests that lower precipitation predictability led to combined drought stress strategies that enhanced plant survival.

Past precipitation predictability ● More ● Less

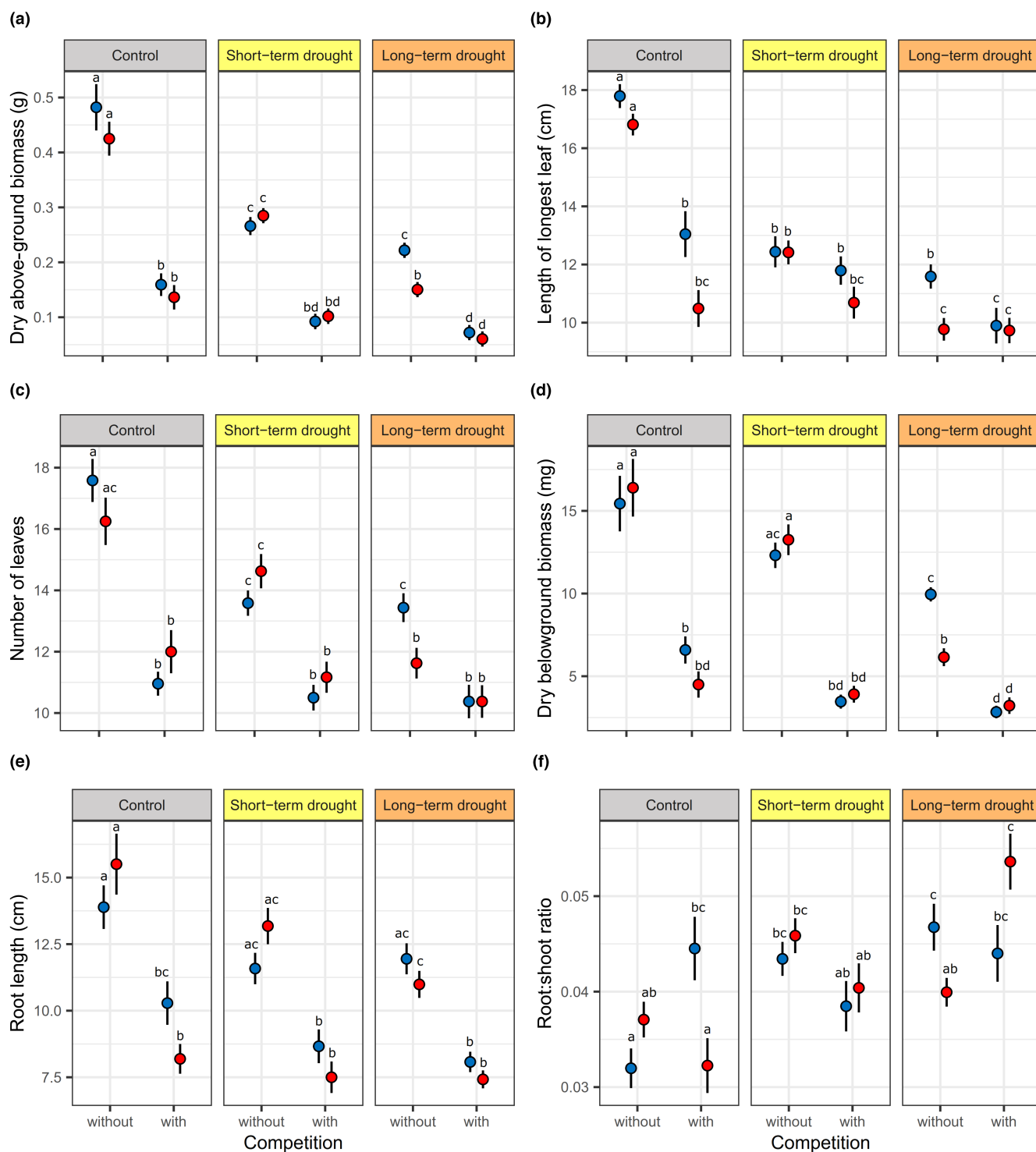


FIGURE 3 Treatment effects on morphological traits of *Papaver rhoeas*: (a) Dry above-ground biomass; (b) Length of the longest leaf; (c) Number of leaves; (d) Dry belowground biomass; (e) Root length; and (f) Root:shoot ratio. The panels show the different drought treatments, while the past predictability and competition treatments are represented on the x-axis. Blue and red colours indicate the plants whose progenitors were exposed to more or to less predictable precipitation, respectively. Mean $\pm$ standard error (SE) are shown. Post hoc contrasts among all treatment combinations are indicated with letters.

4.1 | Is past precipitation predictability promoting different plant phenotypes under common-garden conditions?

In line with our first hypothesis, simulated precipitation predictability during three consecutive generations caused different plant phenotypes under common-garden conditions. All above- and belowground traits were significantly affected either by past precipitation predictability as main effect or by interactions of past predictability with drought and/or competition (Table 1). This suggests that differences in past precipitation predictability induced differences in the transgenerational effects but it could also indicate differences in selection within the same generation (i.e. from sowing to the end of the reproductive cycle), which would be in line with previous results in other species showing that different precipitation predictability treatments induced differences in the selective regime (March-Salas, Fandos, et al., 2021; Yin et al., 2022). However, in *P. rhoeas*, our previous results suggest that trait selection did not differ between precipitation predictability treatments (March-Salas, van Kleunen, et al., 2021). It is thus unlikely that the observed differences are the result of differential survival selection. Phenotypic differences shown in our common-garden could also be mediated by maternal effects. However, potential maternal effects were controlled in the models by including early size as a covariate, as maternal effects are mainly expressed in plant early stages (Donohue, 2009). Early size was not significantly different between past predictability treatments (initial number of leaves: Chi-sq. = 1.223; $p = 0.269$; initial largest diameter: Chi-sq. = 0.858; $p = 0.354$). Thus, it is unlikely that phenotypic differences found in our common-garden are the result of maternal seed provisioning. The observed responses may therefore be the result of transgenerational plasticity, including epigenetic modifications, as indicated in previous generations exposed to different degrees of precipitation predictability (March-Salas et al., 2019, 2022).

Past precipitation predictability then played a role in the plasticity expressed by the offspring grown under different treatments in the common-garden experiment. Reduced plasticity to competition was found in plants from the less predictable compared with the more predictable treatment in above- and belowground biomass, leaf length and number of leaves if they were exposed to the long-term drought treatment (Figure 3). This result is consistent with other studies suggesting that the precipitation predictability in the environment of origin can shape the evolution of phenotypic plasticity (Yin et al., 2022) or that the precipitation predictability of the maternal environment determines the variation in the descendants' responses (Leung et al., 2020; March-Salas et al., 2022). Since environments that fluctuate less predictably induce mismatches between plastic responses and selective pressures, organisms may evolve lower plasticity under decreased predictability (Leung et al., 2020). However, the degree and direction of plasticity to competition differed between past predictability treatments and drought treatments in root:shoot ratio (Figure 3F). These findings thus indicate that the effect of precipitation predictability on the

direction of plastic responses depended on the measured trait, and that differences in plasticity to competition were mainly expressed under the long-drought treatment.

Strong trait plasticity can hinder rapid evolution (Metz et al., 2020). In our previous experiments on *P. rhoeas*, progenitor plants exhibited reduced transgenerational plasticity in root functional traits and investment strategies under less predictable conditions compared with those under more predictable conditions (March-Salas et al., 2022). In our common-garden experiment, plants from the less predictable treatment showed smaller plant size in terms of above-ground biomass and leaf length and lower root investment in the presence of long-term drought. Our results thus suggest that reduced plasticity caused by lower predictability goes hand-in-hand with rapid evolution of traits while evolutionary shifts are less likely if progenitors showed high trait plasticity, in line with our second hypothesis and other studies (Merilä & Hendry, 2014; Metz et al., 2020).

4.2 | Is past precipitation predictability affecting the strategy expressed by offspring plants under drought stress?

In line with our third hypothesis, our results indicate that the degree of precipitation predictability experienced during three consecutive generations caused differences in the plants' responses to severe drought events. Overall, in the long-term drought treatment, plants from the less predictable treatment started wilting significantly later than those from the more predictable treatment, which shows longer plant survival if progenitor plants were exposed to less predictable precipitation. Higher survival rates under less predictable conditions were also found in the experiments with the progenitors (March-Salas & Fitze, 2019a), showing the relevant role of precipitation predictability in natural selection processes. Lower predictability entails less-regular water availability, which may prime plants to certain drought events and to environmental variation. In other words, offspring plants can evolve mechanisms to 'remember' water stress experienced by progenitors (i.e. progenitors exposed to past less predictable precipitation), anticipating this stressors in order to enhance its performance and survival (Hilker & Schmölling, 2019). Nevertheless, short-term drought did not promote significant trait differences, suggesting that the severity of the drought conditions is relevant to understand the role of past environmental predictability on plant functional responses.

The presumed longer survival of plants from the less predictable treatment may be explained by their reduced size. Plants from the less predictable treatment showed lower biomass, smaller leaves and a lower number of leaves. These phenotypic responses may help to better withstand water-deficit conditions (Lei et al., 2006), since smaller size prevents plants from water loss through transpiration (Aroca, 2012; Chaves, 2002). This can be understood as a physiological adjustment induced by the progenitor's precipitation predictability (March-Salas & Fitze, 2019b) and allows plants to avoid or even

tolerate drought stress (Májeková et al., 2019) and increase their leaf water content (Bartlett et al., 2014; Blum, 2005). This indicates a drought-avoidance strategy promoted by reduced growth and likely driven by rapid evolution of plants in response to less predictable precipitation, preparing them as well against drought events (Kozioł et al., 2012; Rauschkolb et al., 2022). Past precipitation predictability thus resulted in changes in the morphological and physiological trait expression that may help plants to avoid future extinction of populations under climate change (Maggio et al., 2018).

Developing a deeper root system or greater root biomass can help plants to avoid drought, since obtaining water from deeper soil layers prevents water deficit and increases survival rates (Aroca, 2012; Gowda et al., 2011; Kavar et al., 2008; Padilla & Pugnaire, 2007). Across all past predictability and competition treatments, our experiment shows a lower root biomass and shorter roots but a greater relative investment into roots (i.e., the root:shoot ratio) in plants under longer drought (compared to the control and short-term drought treatment). However, the root trait response to drought was affected by the past predictability precipitation. Under long drought conditions and no competition, plants from the less predictable treatment produced lower root biomass and lower root:shoot ratio than plants from the more predictable treatment. This shows that the progenitor's precipitation predictability regime leads to a different root response under severe drought of its offspring, indicating an evolutionary response to lower predictability in water availability (March-Salas et al., 2022; Yamauchi et al., 2021; Zhou et al., 2019). Plants of the control and competition treatment also showed a greater root response in plants from the more predictable compared to those from the less predictable treatment, which could be related to a water deficit mediated by the competitor plants. In the progenitor generations, plants under less predictable conditions exhibited reduced root investment, which increased their fitness (March-Salas et al., 2022). Lower predictability more likely reduces the length of the primary root while it can promote lateral root branching in order to help plants to withstand stressful conditions such as water deficits (Gallego-Tévar et al., 2022; March-Salas et al., 2022). This strategy is expected in annual species, which aim to absorb available resources close to the soil surface, but not necessarily in perennial plants, which generally root deeper (March-Salas, van Kleunen, et al., 2021). Overall, the root trait responses show that lower precipitation predictability is more likely to induce a drought-escape strategy but other responses are also in line with a functional stress-avoidance and -tolerance mechanisms (Kooyers, 2015).

In addition, for all traits except root:shoot ratio, no effects of past precipitation predictability existed under competition. In the short and long drought treatments, competition for limiting resources led to no morphological changes between plants with different past precipitation predictability, as would be expected (Craine & Dybzinski, 2013; Johansson, 2008). Given that no significant differences in seedling size existed between past precipitation predictability treatments, the observed differences without competition occurred thereafter through differential growth and strategy, that

is when the drought treatments already started to show effects. Competition thus accelerated death and reduced plant size, but it also hindered the development of phenotypic differences between plants with different past precipitation predictability. This result is most likely because water availability was even lower in pots with competition, as more plants competed for the limiting resources in the drought treatments, preventing differential functional strategies. Yet, differences in plasticity to competition seems to appear in leaf length and root length under short-term drought and in all measured traits except for root length under long-term drought. Our results are in line with previous theoretical studies indicating that interspecific competition may influence the evolutionary trajectories of plant populations (Craine & Dybzinski, 2013; Johansson, 2008). This then indicates that potential evolutionary changes driven by precipitation predictability may not manifest if plants are exposed to competition.

5 | CONCLUSIONS

An organism's evolutionary response to differences in environmental predictability is of great interest given the current and projected reduction in climatic predictability. Here, we assessed whether past precipitation predictability promoted a specific functional strategy to their offspring to deal with longer drought episodes. The results of this study show that ancestors exposed to less predictable precipitation produced offspring with enhanced functional trait strategies that help escape and avoid drought, as offspring had reduced root allocation, reduced plant size and took longer to wilt when exposed to long drought episodes. This supports earlier results on the progenitor generations (i.e. March-Salas et al., 2019; March-Salas et al., 2022; March-Salas & Fitze, 2019a), which showed that less predictable precipitation may not be detrimental for plants and may rather favour rapid evolutionary responses. Lower predictability may cause more prolonged droughts, which is likely to be a key factor driving the observed evolutionary changes. However, phenotypic differences disappeared if plants were grown under competition, indicating that interspecific competition may slow down evolutionary trajectories driven by precipitation predictability. In conclusion, our study provides new insights into the evolution of plants in a changing climate, highlighting that precipitation predictability is an important evolutionary driver of plant drought strategies.

AUTHOR CONTRIBUTIONS

Martí March-Salas with Patrick S. Fitze conducted the evolutionary experiments that gave rise to the original seed material. Katja Springer, Thibault Coquery, J. F. Scheepens and Martí March-Salas designed the common-garden experiment. Katja Springer and Thibault Coquery conducted the experiment, measured the plants and analysed the data with inputs from J. F. Scheepens, Vera Holland and Martí March-Salas. Martí March-Salas with Katja Springer and Thibault Coquery wrote the first draft of the manuscript, and all authors contributed to revisions.

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CONFLICT OF INTEREST STATEMENT

All authors declare there are no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data deposited in the Dryad Digital Repository <https://doi.org/10.5061/dryad.p2ngf1vxn> (March-Salas et al., 2023).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure S1: Relative soil humidity (%) measured in the pots per drought treatment and time. Relative soil humidity was measured in each of the last 3 weeks of the experiment (i.e. 12, 19 and 26 days after the long drought treatment started). The relative soil humidity in the control treatment is coloured in grey, the short-term drought treatment in yellow and the long-term drought treatment in orange. Significant post hoc contrasts among time-measures within each drought treatment level are indicated with letters. The mean temperature in the greenhouse was 20.1°C, and the mean light intensity was 2300 lux.

Figure S2: Wilting time of *Papaver rhoeas* plants per treatment combination. The panels represent the different drought treatments, and the past precipitation predictability and competition treatments are represented on the x-axis. Blue and red colours indicate that progenitors were exposed to more or to less predictable

precipitation, respectively, and the coloured bars indicate until which day plants were alive. Note that no signs of wilting were observed on control plants at Day 26, when the drought treatment and the experiment ended. Mean $\pm$ standard error (SE) are shown in the bar plots. Post hoc contrasts among all treatment combinations are indicated with letters. Sample size per treatment combination is indicated at the bottom of each bar. The horizontal, thick and dashed grey line indicates the end of the experiment.

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