Precipitation predictability shapes plant growth trajectories, climate sensitivity, and fitness pathways within and across generations

Running title: Predictability shapes population trajectories

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Abstract

Environmental predictability is increasingly altered under climate change, particularly through shifts in the temporal structure and autocorrelation of climatic variables. In plants, the interaction between precipitation predictability and temporal climatic variation can shape the magnitude, timing, and trajectory of growth, with cascading effects on phenological coordination, and ultimately on reproductive success, both within and across generations. Yet, the temporal dynamics and the evolutionary consequences arising from changes in predictability remain poorly understood. To address this, we experimentally manipulated precipitation predictability (*i.e.*, temporal autocorrelation among precipitation events) over four generations of the crop legume *Onobrychis viciifolia*, and assessed its effects on temporal growth dynamics, fitness pathways, and climate sensitivity to variation in mean temperature and precipitation. We observed that less predictable regimes promoted faster growth trajectories, with treatment differences emerging early in the season and intensifying over time, while more predictable regimes exhibited slower, more gradual growth. Growth responses were also strongly shaped by the interaction between natural climatic variation and predictability treatments, with stronger sensitivity to precipitation under lower predictability and comparatively weaker temperature sensitivity. Furthermore, climatic sensitivity sharply increased across generations, indicating dynamic transgenerational responses to environmental variation amplified under less predictable conditions. Contrary to the common assumption that transgenerational responses build up gradually, we found that climatic sensitivity, to both temperature and precipitation, remained approximately stable across the first three generations and then sharply emerged in the fourth. Finally, structural equation modelling revealed that precipitation predictability reshaped plant fitness indirectly by altering growth rates and phenological development. Together, our results establish that environmental predictability fundamentally shapes the magnitude and temporal dynamics of

plant growth response to short-term climatic fluctuations, with cascading effects on fitness pathways and the evolutionary trajectories of plant populations.

Keywords: Climate variability, Environmental predictability, Evolutionary experiments, Plant growth trajectories, Temporal dynamics, Transgenerational adjustments.

Introduction

Understanding how organisms respond to environmental variation through time is central to predicting the ecological and evolutionary consequences of global change. Changes in the temporal patterns of environmental conditions are occurring today at an unprecedented pace, as multiple climatic drivers are shifting simultaneously: temperatures are rising, precipitation regimes are being altered, and extreme events are becoming more frequent (IPCC, 2023; Swain et al., 2018; Xu et al., 2020). These changes are not only modifying mean conditions, but they also reshape the timing, variability, and predictability of environmental cues that organisms rely on (IPCC, 2023; Le et al., 2023). While much research attention has focused on shifts in mean conditions (Thomas et al., 2004), growing evidence shows that environmental predictability, defined as the temporal autocorrelation of environmental conditions, can strongly drive organisms' responses (March-Salas et al., 2019; March-Salas & Fitze, 2019a, 2019b; Reed et al., 2010; Springer et al., 2024). Yet, it is still unclear how temporal environmental variation shapes predictability and translates into phenotypic dynamics, and how they ultimately scale up to affect fitness within and across generations.

Despite widespread evidence of rapid phenological shifts (e.g., Anderson et al., 2012; Franks et al., 2007), the capacity of species to track such rapid changes, particularly when environmental cues become less predictable, remains unclear. While some species exhibit plastic or evolutionary adjustments that allow them to keep pace with changing conditions, others show limited responses or lag behind environmental change, potentially increasing their vulnerability (Schneider et al., 2026). For plants, whose growth and reproduction are tightly coupled to water availability, the timing and predictability of precipitation events can shape developmental trajectories, climate sensitivity (*i.e.*, slope of growth responses to temporal variation in temperature and precipitation), and ultimately life-history strategies

(Bykova et al., 2019; Liu et al., 2021; Zhou et al., 2025). However, this question remains scarcely tested.

In seasonal environments, the timing, or phenology, of life-stage transitions (e.g., germination, flowering, seed dispersal) may have important implications for fitness (Burghardt et al., 2015), ranging from a slight reduction in reproductive success to fatal consequences (McNamara et al., 2011). For instance, classical theories and recent experimental work predict that, under less predictable conditions, plants will shift their growing and flowering timing to ensure reproduction (March-Salas et al., 2019, 2021). However, earlier flowering may result in higher risk of failure and a reduction of the number of offspring produced (*i.e.*, lower number of seeds). In contrast, a delay in flowering can also endanger seed production, through exposure to higher temperatures and increased evapotranspiration, or by causing a phenological mismatch that decouples plant-pollinator interactions. Thus, under less predictable environmental conditions this cue-response framework might be less successful, as former reliable cues may no longer be associated with the beneficial timing of phenology or life history (Körner & Basler, 2010).

Environmental predictability may not only shape immediate responses but also responses across generations through transgenerational effects (Herman & Sultan, 2011). Such transgenerational effects can enhance offspring performance and may therefore be adaptive when parental environments provide reliable cues about the conditions their offspring will experience, including variation in within-generation environmental predictability (Yin et al., 2019). Transgenerational effects can influence the trajectories of trait responses, such as growth or phenology. Growth integrates plant responses to environmental conditions over time and across life stages, thereby influencing life-history traits, such as flowering onset and duration, which determine reproductive success and ultimately plant fitness (Violle et al., 2007). However, despite growing evidence for both transgenerational

responses and the importance of environmental predictability, it remains unclear how precipitation predictability shapes trait-mediated pathways to plant fitness within and across generations.

In spite of the importance of environmental predictability itself, climate factors interact in a complex way and may modify how environmental predictability shapes plant responses (Töpper et al., 2018). As a result, the effects of altered precipitation regimes can be amplified or mitigated by simultaneous variation in temperature or other climatic factors. Elevated temperatures, for example, may intensify water limitation or modify plant physiological responses, thereby altering precipitation variability-induced responses. The interaction among multiple climatic drivers can generate synergistic, additive, or antagonistic effects, which are increasingly recognized as central to ecological responses under climate change, yet they remain little investigated in the context of environmental predictability (Ramos-Muñoz et al., 2025). Moreover, these combined environmental effects are likely to be dynamic and transient, shifting as the season progresses. Predicting how plants respond to various, interacting climate-change components, and their evolutionary dynamics, therefore requires careful tracking of plant growth and phenology across different life-history stages, phenological developments, and even generations under multivariate environmental contexts.

We experimentally grew individuals of the widespread forage legume *Onobrychis viciifolia* under more and less predictable precipitation regimes over four consecutive years and generations, recording their growth, phenology, and reproduction weekly. We aimed to determine how precipitation predictability shapes plant growth dynamics, climate sensitivity, and trait-mediated pathways to reproductive performance across generations. Specifically, we hypothesized that: (1) precipitation predictability reshapes growth trajectories, with less predictable regimes promoting earlier and faster growth as a reproductive assurance strategy, while more predictable regimes sustain slower, cue-tracking growth within and across years;

(2) climate sensitivity is stronger under less predictable regimes, reflecting a tighter coupling between environmental conditions and growth responses; (3) precipitation predictability influences plant fitness indirectly, through its effects on growth and phenological timing, and trait-mediated pathways differing between predictability regimes; and (4) growth dynamics and climatic sensitivity shift across generations, reflecting transgenerational adjustments.

Methods

Study species and experimental setup

Onobrychis viciifolia Scop. (Fabaceae) was selected as a model species, as it is a perennial forb widely used in agriculture and characterized by a broad natural distribution and wide ecological amplitude, occurring across a range of climatic conditions, soil types, and soil moisture levels. Its native distribution spans the Mediterranean basin area, south-eastern Europe and Siberia, and it has been widely naturalized in other parts of Europe, Asia, North America, Australia and New Zealand. Moreover, in addition to its use as crop species, *O. viciifolia* provides multiple ecosystem services, including nitrogen fixation, forage production, and resources for pollinators (Kells, 2001; Carbonero et al., 2011; Nielsen, 2021; Craine et al., 2023). The plant reaches plant heights between 20 and 80 cm (rarely > 100 cm), and it produces dense inflorescences (Carbonero et al., 2011).

The seeds used to initiate the experiment (ancestors, G0) were collected in 2011 in Castillo de Lerés, approximately 23 km from the experimental field site, and were kept separated by maternal plants. This area experiences temperature and air humidity conditions similar to those naturally of the experimental site, but receives 200-270 mm less annual precipitation (data obtained from the Spanish Meteorological Agency (AEMET); www.aemet.es). The experiment was conducted in an outdoor common garden located at the experimental field station 'El Boalar' (42 33′N, 0 37′W, 705 m.a.s.l.; IPE-CSIC, Jaca, Huesca, Spain). This setup allowed plants to receive natural precipitation while being subjected to additional watering through irrigation events simulating different precipitation-predictability treatments (*see* below). Weather data 50 m away from the experimental plots were obtained from the Spanish Meteorological Agency (Fig. S1).

Seeds were sown in 16 open-air enclosures surrounded by metal walls and a mesh, which protected plants from local vertebrate herbivores, slugs, and birds, while allowed the

153 enclosure-level activity of local pollinators. Within each enclosure, a plot with 28 planting
154 positions spaced 40 cm apart was established (*see* March-Salas & Fitze, 2019a). In 2012,
155 randomly selected seeds from the field-origin generation (G0), known as ancestors, were
156 sown across all positions within each enclosure. In subsequent years (2013-2015), offspring
157 seeds produced by the previous experimental generation (*i.e.*, G0 grown in 2012, G1 in 2013
158 and G2 in 2014) were selected and sown, resulting in three descendant generations (*i.e.*, G1,
159 G2, and G3) grown in 2013, 2014 and 2015, respectively. Specifically, in 2013–2015
160 experimental seasons, the offspring seeds were sown in 21 positions per plot, resulting in
161 plants from three descendant generations (G1–3); in addition, seeds from the G0 field-origin
162 generation were sown in the remaining seven positions, resulting in ancestor plants grown in
163 the four experimental years: $G0_{2012}$, $G0_{2013}$, $G0_{2014}$, and $G0_{2015}$ (for further details on seed
164 selection, *see* March-Salas & Fitze (2019a)). Growing ancestors in all experimental years
165 allowed us to assess transgenerational responses controlling for potential year-to-year
166 environmental variations (Fig. S2).

167

168 ***Precipitation-predictability treatments***

169 We manipulated the degree of correlation among consecutive watering events, and together
170 with the natural precipitation, this led to the simulation of more *versus* less predictable
171 precipitation treatments. Particularly, these two precipitation predictability levels were
172 implemented by modifying the timing of watering events within and across weeks using an
173 automated watering system (March-Salas et al., 2019; March-Salas & Fitze, 2019a). Plants
174 assigned to the more predictable (M) treatment received supplemental watering events at
175 regular time intervals, whereas plants in the less predictable (L) treatment received the same
176 amount of supplemental water at random time intervals. Both treatments received the same
177 total amount of precipitation (natural plus supplemental) and the same number of watering

events, but L had 11.69% lower intrinsic precipitation predictability than M, and also lower predictability than the natural precipitation at the field site (March-Salas & Fitze, 2019a).

In addition, treatments were applied during two distinct seasons within each year. The spring season, corresponding to an early plant developmental stage, began in March–April and lasted until the end of June; this period is hereafter referred to as the "early treatment". The summer season followed immediately thereafter, extending from late June until October and corresponding to a later plant developmental stage; this period is hereafter referred to as the "late treatment". Inter-seasonal predictability (*i.e.*, the autocorrelation of precipitation predictability between spring and summer) was manipulated by exposing, during the summer season, half of the enclosures to the same predictability treatments as in spring, and the other half to the other predictability treatment. Thus, this design resulted in four treatment combinations: LL, LM, ML and MM, where the first letter denotes the spring (early) treatment and the second letter the summer (late) treatment.

Plant trait measurements

We weekly measured plant height and maximal diameter for all individuals to the nearest millimetre, and recorded the number of leaves and leaflets. As soon as the first flower opened, we measured the plant height including the flowering stem, as this provides an ontogenetic and phenological growth measure that is not confounded by subsequent developmental or senescence-related processes. Relative growth rate (RGR) was calculated from height measurements as the difference between the final and initial height divided by the number of weeks elapsed. From the second year of the experiment (2013) onwards, we also recorded the number of nodes per individual. These five traits (plant height, plant maximum diameter, number of leaves and leaflets, and number of nodes) measured weekly along the experiment are hereafter referred as growth traits.

In addition, we recorded flowering phenology on each flowering individual, including flowering onset (expressed as the number of weeks from seedling emergence to the opening of the first flower) and flowering duration (as the number of weeks from the opening of the first flower to the opening of last flower). Once seeds had ripened, they were harvested from each individual and the total number of seeds per plant was counted, here used as an estimate of plant fitness (hereafter referred as 'plant fitness').

Statistical analysis

All analysis were run in R version 4.5.1 (R Core Team, 2025). We first tested for treatment effects on growth traits (plant height, plant diameter, number of leaves, number of leaflets, number of nodes) across experimental years. For this purpose, we used weekly measurements on the growth traits until plants reached the maximum height, after fruit maturation and the onset of harvesting. We then fitted trait-specific linear mixed-effect models (LMM) using the *lme4* package and the *lmer* function (Bates et al., 2015). Early treatment (less predictable *versus* more predictable), late treatment (less predictable *versus* more predictable), generation (G0–G3), experimental week, and their two-, three-, and four-way interactions were included as fixed effects. Year (2012–2015), the individual identity, and the maternal line were included as random effects. For the number of nodes, we fitted a generalized linear mixed-effect model (GLMM) using the *glmmTMB* package (Brooks et al., 2017) with a negative binomial error distribution to account for overdispersion, while maintaining the same fixed and random effects as for the other growth traits. As responses are similar across the five growth traits (*see* Fig. S3), we only present the effects on plant height in the main text (results for the other traits can be found in Table S1 and Fig. S3).

Then, to test whether causal relationships among growth traits differed between precipitation treatments we first fitted a multigroup structural equation model (SEM) with the

lavaan package (Rosseel, 2012). As no significant differences were detected (*see* Fig. S4), we subsequently fitted a single SEM for individually ancestors (G0) and descendants (G1-G3) including early and late treatment as exogenous predictors using the same package. Early and late predictability treatments were included as binary variables (0 = less predictable (L), 1 = more predictable (M)), such that path coefficients represent the effect of more predictable conditions relative to less predictable ones. The model specified the pathway from precipitation predictability to plant fitness, mediated sequentially by plant growth and flowering phenology. We used RGR and plant height at flowering as proxies of plant growth, while flowering onset and flowering duration were used as proxies of phenology. This analysis allows us to quantify both direct and indirect effects of precipitation predictability on plant fitness.

As natural temperature and the precipitation across the four years where highly variable (Fig. S1), we investigated how these weather variables affected the predictability treatment effects on growth responses across time. To this end, we used the weekly height growth data until plants reached their maximum height and we calculated the mean temperature and the sum of precipitation for each week. To assess the growth differences for each week, we calculated the weekly growth rate based on the height of the individual plants (growth rate = Height(t)−Height(t−1); hereafter called "growth rate"). Previous work in vegetation ecology and demography has shown that climatic drivers often influence plant growth with a temporal lag rather than instantaneously (e.g., Cranko Page et al., 2021; Evers et al., 2021; Kuzyakov & Gavrichkova, 2010; Ren et al., 2023). To account for those delays, we calculated lagged variables for mean temperature and sum of precipitation for the previous week (t-1; equals to 8 to 14 days prior) and two weeks prior (t-2; equals to 15 to 21 prior) and z-transformed them to allow direct comparison of the effect sizes. These timeframes were selected as vegetative growth is expected to respond to environmental factors within two weeks (e.g., Kong et al., 2020). Lagged, or often also called accumulative variables allow

testing of delayed environmental effects on growth, consistent with prior studies (Pepe et al., 2022). To select the fitting lag variable for mean temperature and precipitation we fitted LOESS smoothing curves for each generation × treatment group, separately for temperature and precipitation and calculated the pseudo-R^2 (Fig. S5 and S6). Based on that for the following analysis a lag of one week (t-1) was selected for both mean temperature and sum of precipitation (afterwards called "lag temperature" and "lag precipitation" respectively). Finally, we fitted for the growth rate a LMM with the treatment combination (LL, LM, ML, MM), lag temperature, lag precipitation, the generation and the experimental week as well as all interaction as fixed factors and plot and individual as random factor to account for repeated measures and spatial clustering. To simplify the model, we performed a model selection using AIC.

For all LMMs and GLMMs, the significance of fixed effects was assessed using the R package *car* (Fox et al. 2012) with Type-III Wald χ^2. Post hoc tests were conducted using the *emtrends* and *emmeans* functions implemented in the *emmeans* package (Lenth & Piaskowski, 2017). Tukey-adjusted pairwise contrasts were used to compare growth slopes over time (estimated marginal trends) and treatment means at the final measurement time, whenever significant effects involved interactions or factors with more than two factor levels. We tested for all models the underlying assumptions with the *DHARMa* package (Hartig et al., 2024). For cases where the normality assumption was not met, we transformed the response variable (*see* Table 1).

Results

Temporal effects of precipitation predictability

Plant height increased steadily throughout the growing season in all treatments, but the magnitude and trajectory of this increase differed among precipitation predictability regimes (Fig. 1). The strength of precipitation predictability effects varied across the experimental weeks, as indicated by significant two-way interactions between early treatment and week ($\chi^2 = 87.08$, $p < 0.001$, Table 1) and late treatments and week ($\chi^2 = 25.36$, $p < 0.001$; Table 1), with treatment differences emerging and intensifying as the season progressed. The rate of plant height varied significantly among treatments, with individuals in the LL regime exhibiting the steepest increase in height over time (all: $z \geq 4.64$; $p < 0.001$; 0.10 cm ± 0.01 per week), whereas plants of the MM regime showed the slowest increase (all: $z \geq 3.21$; $p = 0.007$; 0.09 cm ± 0.01); the intermediate treatments (ML and LM) displayed similar trajectories, with significant differences between each other ($z = -3.43$; $p = 0.003$).

These patterns were not consistent across generations. Significant three- and four-way interactions involving early and late treatments, generation, and week (Table 1) indicate that the effects of precipitation predictability on growth trajectories changed both over time within seasons and across generations. Visual inspection of Fig. 1 further indicates that treatment differences were most pronounced in later experimental years, although in 2015 overall differences were more moderate , with divergence among treatments emerging earlier in the season and increasing in magnitude, particularly under less predictable (LL) *versus* more predictable (MM) conditions. However, these treatment differences were not consistent across years within the ancestral generation (G0; Fig. 1, top panel). In 2012, treatment effects were relatively weak, with all treatments following similar growth trajectories and only modest divergence late in the season. In contrast, in subsequent years (2013–2015), treatment differences became more pronounced, with divergence among treatments occurring earlier

and increasing in magnitude throughout the growing season. This pattern was particularly evident in 2013 and 2014, where LL plants showed markedly higher growth compared to the other treatments, while MM plants consistently exhibited reduced growth. By 2015, overall growth was higher across all treatments compared to other years. However, differences among predictability regimes were less pronounced in this year, although treatments kept the same ranking observed across the other three experimental years, indicating that responses to precipitation predictability were consistent through time.

Direct and indirect effects of precipitation predictability on plant fitness

Treatment effects on RGR were stronger in ancestors (G0) than in descendants (G1-G3; Fig. 2). In G0, plants exposed to more predictable regimes (M) during the late treatment were associated with reduced RGR compared to less predictable regimes (L), whereas effects of the early treatment were weaker and non-significant (Fig. 2). In contrast, descendants showed weaker direct effects of predictability on RGR overall, indicating a reduced sensitivity of growth to treatment conditions across generations.

RGR had a significant negative direct effect on flowering onset in both ancestors and descendants, with higher growth rates leading to earlier flowering (G0: $\beta = -0.23$, $p < 0.001$; G1–G3: $\beta = -0.11$, $p < 0.01$). However, the direct effects of precipitation predictability on flowering onset were stronger and they differed across generations. In the ancestral generation, the late treatment had a strong direct effect, with more predictable regimes delaying flowering ($\beta = 0.64$, $p < 0.001$; Fig. 2), whereas the early treatment had no significant effect. In contrast, in descendant generations, both early and late predictability treatments had significant and similarly sized direct effects on flowering onset (both: $\beta = 0.36$, $p < 0.001$). In both ancestors and descendants, flowering onset significantly influenced reproductive dynamics. Earlier flowering led to a significant longer flowering duration (G0: β

= −0.72, p < 0.001; G1-G3: β = −0.83, p < 0.001), which in turn had a strong positive effect on plant fitness (G0: β = 0.49, p < 0.001; G1-G3: β = 0.55, p < 0.001). Additionally, plant height at flowering had a direct positive effect on flowering duration (G0: β = 0.36, $p < 0.001$; G1–G3: β = 0.11, $p < 0.001$). Precipitation predictability had no significant direct effects on phenology (flowering duration) and plant fitness both in ancestors and descendants (all $p > 0.09$).

Climate-dependent effects of precipitation predictability within and across generations

Across generations, growth rates were strongly influenced by natural climatic conditions in the preceding week (Table 2). Both lagged temperature and lagged precipitation had significant effects on growth rates, with significant interactions between precipitation and precipitation predictability treatments showing that these effects depended on precipitation predictability treatments (Treat × Temp: $\chi^2 = 17.35$; $p = 0.001$; Treat × Precip: $\chi^2 = 11.74$; $p = 0.008$; Table 2). In particular, growth rate responses to natural precipitation varied markedly among predictability regimes: plants under the low predictability (LL) showed on average the strongest positive response to natural precipitation (slope = 0.11 ± 0.01, Fig. 3A), whereas those under high predictability (MM) exhibited a weaker response (0.06 ± 0.01, Fig. 3A). Intermediate treatments (LM and ML) displayed moderate sensitivities and did not differ significantly from each other, while LL responses were significantly greater than those of ML (z = 2.94, p = 0.017) and MM (z = 4.15, p < 0.001; Fig. 3).

In contrast, the growth rate responses to temperature were primarily driven by differences in final size among treatments, whereas differences in sensitivity (*i.e.*, slopes) to environmental variation were comparatively small and only weakly supported. However, the joint effects of temperature and precipitation were non-additive (Temp × Precip: $\chi^2 = 5.55$; p = 0.019; Table 2), indicating that growth rate responses to one climatic factor depended on

the levels of the other. Critically, this interaction also differed between ancestors and descendants (Generation × Temp × Precip: $\chi^2 = 104.95$; $p < 0.001$; Table 2): growth rates increased more strongly with temperature and precipitation in descendants than in ancestors, an effect most evident in the LL treatment, where the increase was particularly steep in descendants but comparatively modest in ancestors, while responses remained weaker overall under MM conditions in both generations (Fig. 4). Moreover, the higher the temperature, the more important became precipitation for growth; also precipitation was most important in LL of descendants, where the furthest right and uppermost gradient line was nearest to 45°). Together, these results indicate that precipitation predictability shapes how plants integrate short-term climatic variation into growth, primarily by modulating sensitivity to precipitation.

When considering the generations, the sensitivity of growth rates to climatic conditions changed significantly across generations and depended on precipitation predictability regimes (Treat × G × Temp: $\chi^2 = 29.39$; $p = 0.001$; Treat × G × Precip: $\chi^2 = 28.60$; $p = 0.001$ Table 2). Across all predictability regimes, temperature sensitivity increased over generations, with the strongest response observed in G3, as the last experimental generation (slope = 0.31 ± 0.01), which was significantly higher than in all preceding generations (all: $z < -6.53$; $p < 0.001$, Fig. 3B). In contrast, earlier generations (G0–G2) exhibited comparatively weak and similar responses to natural temperature, indicating limited climatic responsiveness at the onset of the experiment. A similar yet more pronounced pattern was observed for sensitivity to natural precipitation. Growth rate responses to natural precipitation were weak in early generations (G0–G2; slopes = 0.03 to 0.05) but increased sharply in G3 (0.21 ± 0.01 all: $z < -9.12$; $p < 0.001$), indicating a substantial shift in how plants track water availability over time.

These generational changes were significantly modulated by experimental precipitation predictability and climatic conditions (Treat × G × Temp × Precip: $\chi^2 = 30.51$;

$p = 0.001$; Table 2; Fig. 3), with stronger amplification of climate sensitivity under low predictability treatments (LL and LM), where growth rate responses to both temperature and precipitation became steeper and more nonlinear across environmental gradients. In contrast, plants under more predictable conditions (MM) showed more constrained and gradual responses. Overall, these results indicate that climate sensitivity is not static but increases gradually (Fig. 3A,B – LM) or sharply in the third generation (Fig. 3A,B – LL, ML, MM) across generations, with the magnitude and shape of this response strongly dependent on environmental predictability.

Finally, the effect of climatic conditions on growth rate varied across the experimental weeks and differed among treatments and generations. Significant four-way interactions (Treat × Week × G × Temp: $\chi^2 = 21.96$; $p = 0.009$; Treat × Week × G × Precip: $\chi^2 = 22.44$; $p = 0.008$; Table 2) indicate that the influence of temperature and precipitation on growth rate was not constant over time, but instead changed throughout the growing season, with both the magnitude and shape of these responses differing among treatments and generations. Across treatments and generations, favourable combinations of warmer temperatures and higher precipitation generally promoted higher growth rates, whereas cooler and drier conditions were associated with reduced growth rates (Fig. 3). However, the strength and configuration of these climate–growth rate relationships varied among treatments and generations and shifted over time. Notably, later generations exhibited greater climate sensitivity, with the strongest response observed under low predictability (LL) regimes (Fig. 3).

Discussion

How environmental predictability interacts with temporal fluctuations in mean climatic conditions to shape plant growth dynamics through time and the associated evolutionary consequences remains poorly understood, yet it is central to predicting species responses to climate change. By experimentally manipulating precipitation predictability across four consecutive generations of the crop legume *O. viciifolia* and tracking growth weekly, we show that precipitation predictability altered the temporal dynamics of plant growth, modulated climate sensitivity to fluctuations in mean climatic conditions, and shaped the trait-mediated pathways through which growth and phenology determine plant fitness. Notably, all these effects intensified across generations in a manner consistent with transgenerational adjustment. Together, these findings establish environmental predictability as a key but underappreciated dimension of climate change, with driven temporal dynamics and evolutionary consequences that extend beyond those attributable to shifts in mean conditions alone.

Does precipitation predictability reshape seasonal growth trajectories?

In our study, we observed that precipitation predictability reshaped plant growth trajectories both within and across growing seasons. Plants under less predictable regimes throughout the season grew faster, with treatment differences emerging early in the season and intensifying as the season progressed, whereas plants under more predictable regimes showed slower, more gradual increases in height (Fig. 1). These contrasting responses between less and more predictable regimes are in line with our 'first hypothesis'. Moreover, plants exposed to mixed, less and more predictable regimes across the season displayed intermediate responses, with this pattern being persistent across the four experimental years. The faster growth under less predictable conditions aligns with theoretical predictions that organisms facing unreliable

environmental cues should advance and accelerate developmental progression as a reproductive assurance strategy (McNamara et al., 2011; March-Salas et al., 2019). This finding is also consistent with the idea that rapid resource acquisition is a key adaptive response in temporally unpredictable environments (Angert et al., 2007; Lindh & Manzoni, 2021). Indeed, when the timing of favourable conditions is difficult to anticipate, delaying growth until predicted favourable conditions becomes risky, and initiating fast growth early may reduce the probability of missing the reproductive window and temporal matching with pollinators (ten Brink et al., 2020; Abley et al., 2024). In contrast, the slower growth trajectories under more predictable conditions resemble a cue-tracking strategy, in which plants integrate sequential environmental signals to time developmental transitions more precisely (Körner & Basler, 2010; Blackman, 2017). The consistent effects of both early and late seasonal predictability on growth trajectories further indicate that environmental predictability shapes plant development continuously throughout the growing season, rather than acting only in a single critical timespan.

Is climate sensitivity stronger under less predictable regimes?

Overall, plants under less predictable conditions showed stronger growth-rate responses to natural precipitation variation, consistent with our 'second hypothesis', while sensitivity to temperature differed comparatively less among treatments (Fig. 3). Specifically, precipitation sensitivity of growth rates was consistently higher under regimes with lower spring predictability (LL and LM) than under continuously more predictable conditions (MM), particularly in generations G0 and G2 (Fig. 3A). In contrast, temperature sensitivity showed smaller differences among predictability treatments within generations (Fig. 3B). This shows that less predictable regimes promote stronger growth responsiveness to short-term precipitation variation, potentially favouring rapid exploitation of transient water availability

(March-Salas et al. 2022). Conversely, more predictable regimes throughout the season may constrain rapid growth responses, at least during the first generations, potentially reflecting reduced reliance on instantaneous precipitation cues when water availability follows a more predictable pattern.

Crucially, these differences on the sensitivity to natural variation in precipitation and to temperature reflected how predictability strongly modulated the integration of natural climatic signals into growth responses, rather than simply affecting overall growth magnitude (Table 2). The observed asymmetry between precipitation and temperature sensitivity suggests that under unpredictable precipitation regimes, plants become more tightly coupled to instantaneous water availability signals, thus relying more heavily on real-time environmental information to regulate growth. This interpretation is congruent with previous studies showing that climate sensitivity of plant growth is strongly context-dependent (e.g., Kuijper & Hoyle, 2015; Heilman et al., 2021; Liu et al., 2021), and also aligns with theoretical expectations that organisms in less predictable environments rely more on instantaneous environmental signals rather than anticipatory cue-response mechanisms (Sultan, 2000; Donohue et al., 2010; Simons, 2011). Plants under more predictable regimes, however, had a weaker and less pronounced climate-induced response, likely reflecting a more conservative strategy characterized by reduced immediate sensitivity to climatic fluctuations (Didiano et al., 2018). Beyond the main effects, the joint influence of temperature and precipitation on growth rate was non-additive, with growth responses being strongest under combinations of high temperature and high precipitation, particularly under low predictability treatments. This synergistic interaction underscores that climate sensitivity cannot be adequately characterised by examining single climatic factors in isolation (Töpper et al., 2018; Ramos-Muñoz et al., 2025), with important implications for how plant populations will respond to the increasingly frequent co-occurrence of stressful climatic events projected under climate change scenarios. Strikingly, the importance of precipitation as

a growth driver increased progressively from the most predictable regime (MM) to the least predictable (LL), both in ancestors and, even more markedly, in descendants, suggesting that multigenerational exposure to unpredictable water availability renders populations increasingly precipitation-dependent, a dynamic that may become particularly consequential under global change scenarios where both precipitation unpredictability and intensity are projected to increase.

Does precipitation predictability shape plant fitness through its effect on growth rate and phenology?

According to our findings, precipitation predictability also influenced plant fitness through trait-mediated indirect pathways, with growth rate shaping phenological timing, which in turn affected plant fitness (Fig. 2). Specifically, less predictable regimes promoted faster growth rates and earlier flowering onset, which extended flowering duration and ultimately increased fitness, in accordance with our 'third hypothesis'. This indicates a more opportunistic strategy, consistent with coordinated shifts toward faster development and earlier flowering reported under altered environmental conditions (Franks & Weis, 2008; Wolfe & Tonsor, 2014; Zhou et al., 2025). This fitness pathway, in which predictability acts upstream of a growth-phenology-fitness cascade, was broadly consistent across ancestors and descendants, confirming that growth-phenology coordination is a robust mechanism linking environmental conditions to reproductive outcomes (Violle et al., 2007; Burghardt et al., 2015). However, the relative contributions of early and late seasonal predictability to this cascade shifted between generations. In ancestors, the late-season treatment imposed direct effects on both, growth and flowering onset, and also indirect, likely additive, effects on flowering onset through the late predictability effect on growth. These results reflect the importance of summer water availability for timing reproductive transitions in this species. In descendants,

by contrast, both early and late treatments contributed with similar magnitude to effects on flowering onset, suggesting that repeated multigenerational exposure to the experimental treatments broadened the developmental window over which precipitation predictability shapes phenological trajectories. This shift may reflect an increasing integration of predictability cues across the full growing season as generations progressed, consistent with a progressive retuning of developmental sensitivity to the experimental environments (e.g., Auge et al., 2017; Leung et al., 2020; March-Salas et al., 2022). Additionally, we observed that in both ancestors and descendants, earlier flowering onset and higher plant height at flowering led to longer flowering duration, which in turn strongly increased plant fitness, reinforcing the central role of phenological timing as a mediator of climate effects on reproduction (Bykova et al., 2019; Iler et al., 2019).

Do growth dynamics and climate sensitivity shift across generations?

Climate sensitivity to natural precipitation increased sharply across generations, with the most pronounced shift occurring in G3, and this increase was amplified under less predictable regimes (Fig. 3). Growth trajectories were generally faster under less predictable conditions in both ancestors and descendant generations (Fig. 3–4). But they also became progressively more divergent across generations under contrasting predictability treatments, with plants experiencing less predictable regimes showing increasingly faster growth relative to those growing under more predictable conditions in later generations (Fig. 3–4). Together, these patterns point to dynamic transgenerational adjustments as a key mechanism shaping plant responses to precipitation predictability over time, as indicated in our 'fourth hypothesis'. Although within four generations, lacking a common garden experiment we cannot conclusively distinguish between epigenetic inheritance, maternal provisioning, and selection-driven evolutionary change. But the directional and treatment-dependent nature of these shifts

is consistent with transgenerational plasticity theory, which predicts that parental environments providing reliable information about future offspring conditions should favour the inheritance of matching phenotypic adjustments (Galloway & Etterson, 2007; Herman & Sultan, 2011; Auge et al., 2017; Yin et al., 2019). The increased sensitivity under less predictable regimes suggests that these transgenerational effects are not merely passive carry-over responses, but reflect an active retuning of plant sensitivity to environmental fluctuations, consistent with the idea that cross-generational plasticity can complement within-generation plasticity in tracking variable environments (McIntyre & Strauss, 2014; Auge et al., 2017; March-Salas et al., 2022). The sharp increase in sensitivity specifically in G3, with G0-G2 remaining comparatively similar (Fig. 3), raises the possibility that transgenerational effects may accumulate non-linearly across generations, as documented in other plant systems where repeated multigenerational exposure to stress produces progressively stronger offspring responses (e.g., Herman et al., 2012; Ramos-Muñoz et al., 2024).

Conclusions

Our study highlights that precipitation predictability has the potential to shape plant growth temporal dynamics and the extent of climate sensitivity to other climatic factors, with crucial cascading effects on plant fitness. Further, our findings demonstrate that these plant responses are not static but intensify and are partly dynamic across generations, consistent with transgenerational adjustments that amplify plant responsiveness to environmental fluctuations under less predictable conditions. Critically, the dependence on precipitation as a growth driver increased progressively with decreasing predictability and became even stronger in descendants, pointing to a self-reinforcing feedback dynamic across generations that may render populations increasingly vulnerable to the compound effects of rising temperatures and

545 altered precipitation regimes. Overall, our results suggest that investigating environmental
546 predictability, alongside mean environmental conditions, is essential for accurate predictions
547 of species evolutionary trajectories and persistence, including the responses of crop cultivars
548 under climate change.

Author Contributions

MMS and PSF designed the field experiment, and MMS and GM conducted the experiment and took the plant measurements. KS together with MMS and LL analysed the data and wrote the first draft of the manuscript, and all authors contributed to revisions.

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Conflicts of Interest

All authors declare no conflicts of interest.

Data Availability Statement

Data will be made available upon publication.

Figures and Tables:

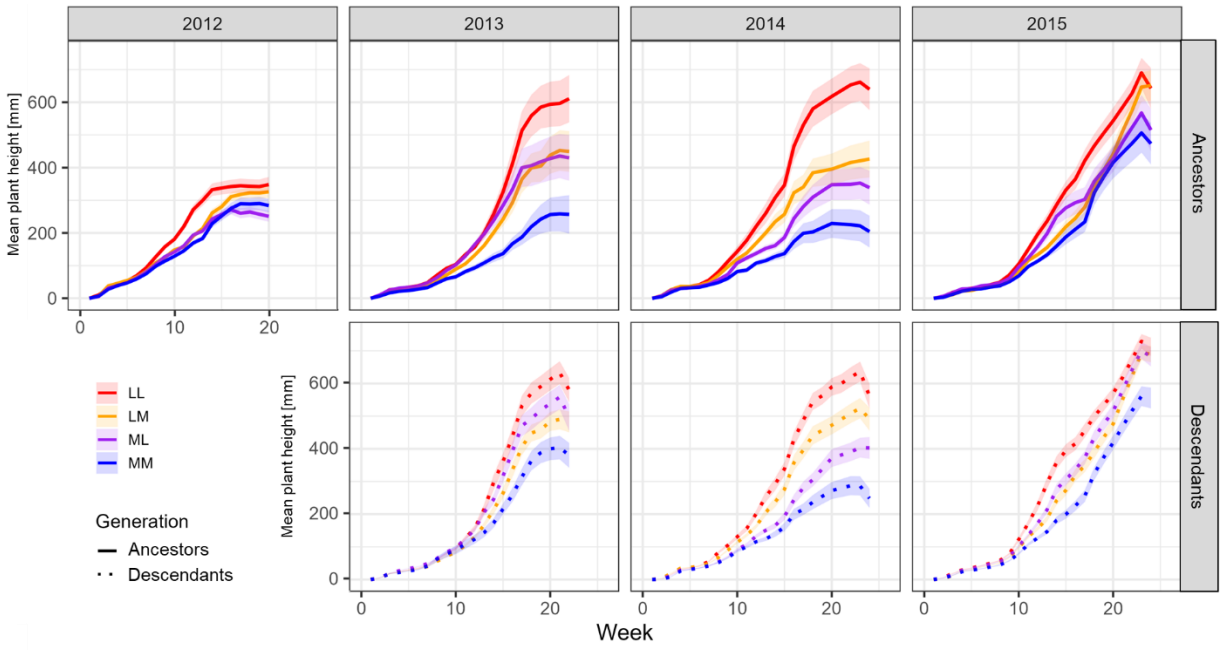


Figure 1: Temporal trajectories of mean plant height [mm] across weeks for all experimental years, shown separately for generation (Ancestors –G0–: above with solid lines; descendants –G1 to G3–: below with dotted lines) and treatment combination (LL, LM, ML, MM; coloured lines). The M treatments represent a more predictable precipitation while the L treatments indicate a less predictable precipitation. The first letter stands for the early treatment, while the later letter represents the late treatment. Ribbons represent ± standard error.

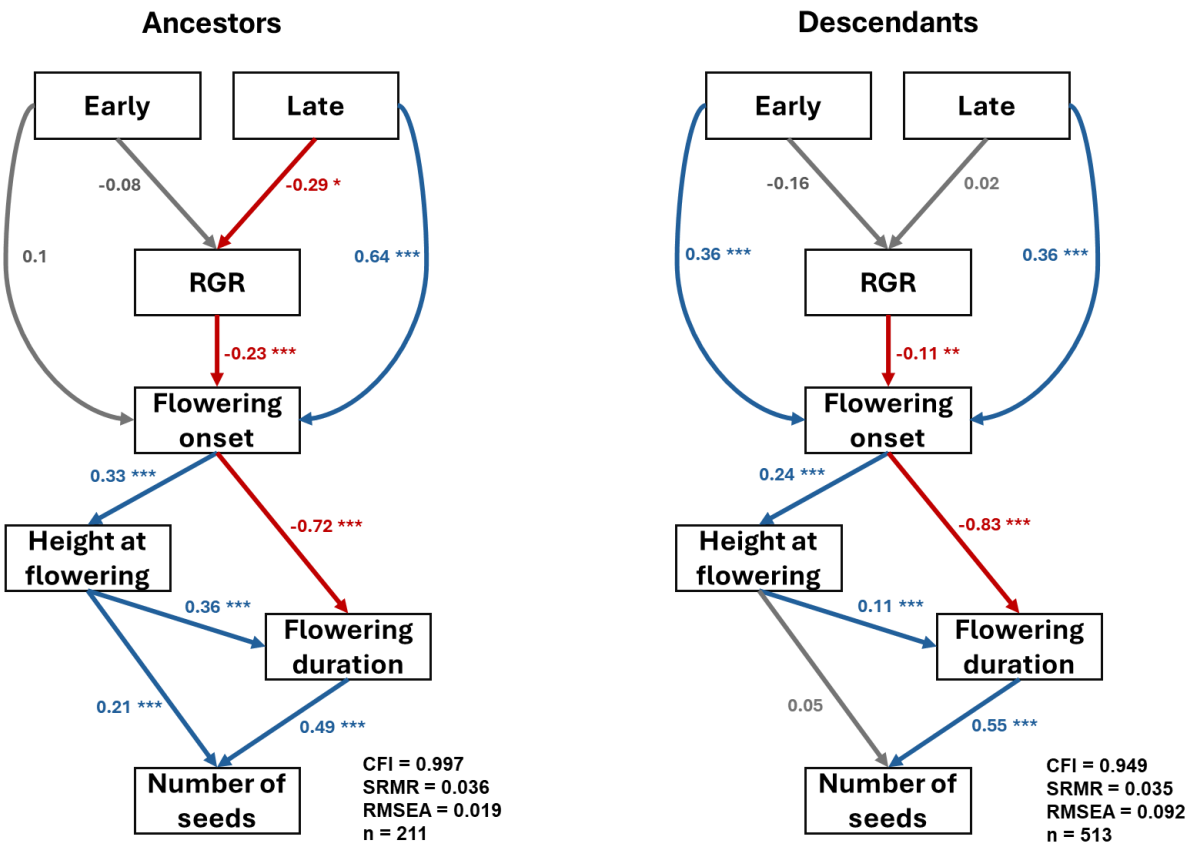


Figure 2: Structural equation models (SEMs) illustrating the direct and indirect effects of precipitation predictability on plant growth, phenology, and plant fitness for (left) the ancestral generation (G0) and (right) descendant generations (G1–G3). Early and late precipitation predictability treatments were included as exogenous variables (coded as 0 = less predictable, 1 = more predictable), such that path coefficients represent the effect of more predictable relative to less predictable conditions. The model describes a cascade from growth, *i.e.*, relative growth rate (RGR) and plant height at flowering, to phenology, *i.e.*, flowering onset and flowering duration, and ultimately to plant fitness (number of seeds). Arrows indicate standardized path coefficients; significant positive effects are shown in blue, significant negative effects in red, and non-significant paths in grey. Significant results are further indicated with asterisks (* 0.05 > p; ** 0.01 > p; *** p < 0.001).

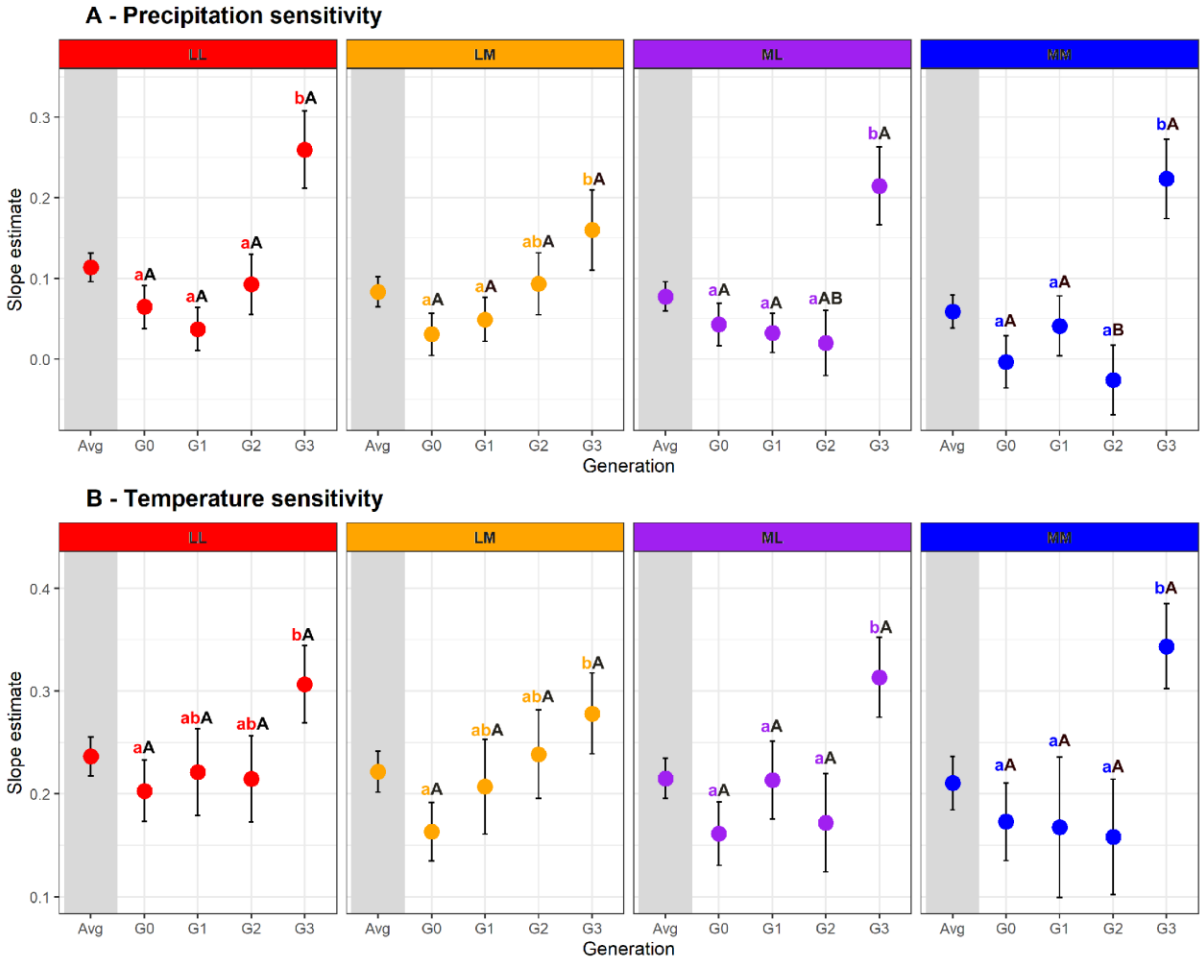
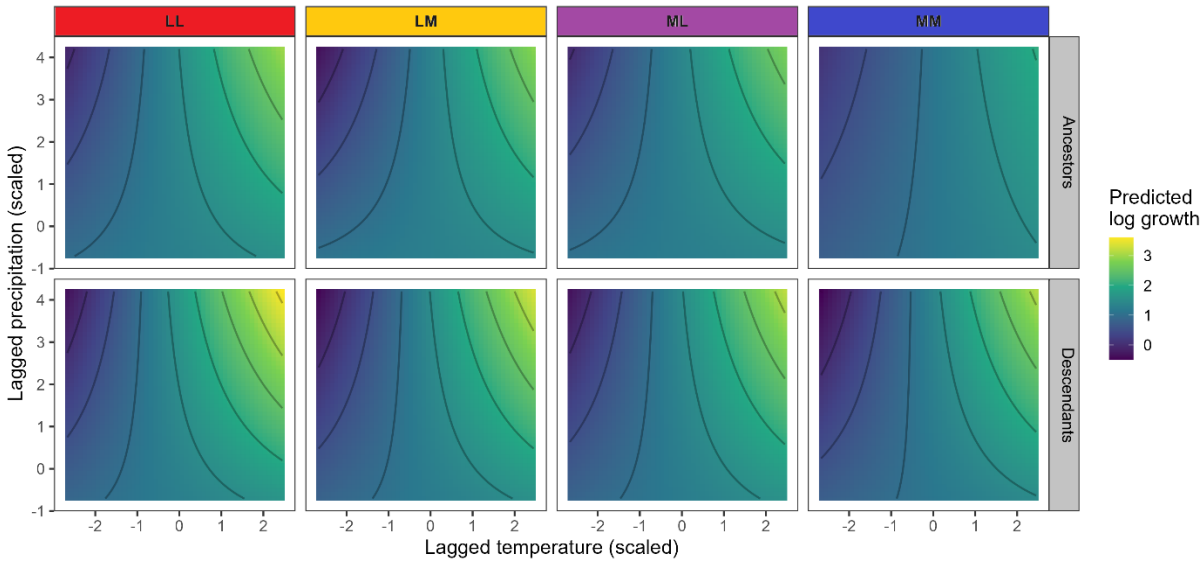


Figure 3: Climate sensitivity of growth rates across precipitation predictability regimes and generations. Panels show standardized slope estimates (± SE) of weekly growth rate responses to (A) lagged precipitation and (B) lagged temperature derived from the linear mixed-effects model. Estimates are presented for each treatment combination (LL, LM, ML, MM) and generation (G0–G3), as well as the overall mean across generations (Avg, grey-shaded area) The M treatments represent a more predictable precipitation while the L treatments indicate a less predictable precipitation, and in combination, the first letter stands for the early treatment, while the later letter represents the late treatment. Significant posthoc differences ($p < 0.05$) are denoted by different letters. Lowercase and coloured letters indicate pairwise comparisons among generations within the same treatment; uppercase black letters indicate pairwise comparisons among treatments within the same generation.



603

604 **Figure 4:** Model-predicted log growth across gradients of lagged temperature and lagged
605 precipitation, shown separately for generation (Ancestors (G0) vs. Descendants (G1-G3)) and
606 treatment combination (LL, LM, ML, MM). The M treatments represent a more predictable
607 precipitation while the L treatments indicate a less predictable precipitation. The first letter
608 stands for the early treatment, while the later letter represents the late treatment. Colours
609 represent predicted log growth values from the fitted model, with darker colours indicating
610 lower values and yellow indicating higher values. Contours illustrate gradients in predicted
611 response across the environmental space. Axes show standardized lagged temperature (x-axis)
612 and standardized lagged precipitation (y-axis). Black lines represent isolines.

Table 1: Results of the linear mixed-effects model testing the effects of precipitation predictability, generation and experimental week on the weekly measured plant height of each individual. The model included the early treatment (less predictable *versus* more predictable), the late treatment (less predictable *versus* more predictable), Generation (G0–G3), experimental week, and their two-, three-, and four-way interactions as fixed effects, and year (2012–2015), the individual nested in plot, and maternal line as random effects. The weekly plant height was transformed using a power transformation (y^0.2) to meet model assumptions. Reported are likelihood ratio test statistics (χ^2), degrees of freedom (df), and associated p-values. Significant effects are indicated in bold (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$).

Effect	**df**	**χ^2**	**p-value**	
Early	1	0.35	0.555	
Late	1	0.13	0.721	
Generation [G]	3	**94.02**	**<0.001**	***
Week	1	**11,757.63**	**<0.001**	***
Early × Late	1	0.77	0.380	
Early × G	3	**15.62**	**0.001**	**
Late × G	3	**23.34**	**<0.001**	***
Early × Week	1	**87.08**	**<0.001**	***
Late × Week	1	**25.36**	**<0.001**	***
G × Week	3	**81.66**	**<0.001**	***
Early × Late × G	3	**8.27**	**0.041**	*
Early × Late × Week	1	**2.16**	**0.141**	
Early × G × Week	3	**50.08**	**<0.001**	***
Late × G × Week	3	**24.91**	**<0.001**	***
Early × Late × G × Week	3	**15.55**	**0.001**	**

Table 2: Results of the linear mixed-effects model testing the effects of precipitation predictability treatments, climatic conditions, and their interactions on weekly plant growth rate. The model included treatment combination (Treat: LL, LM, ML, MM), experimental week (Week), generation (G: G0–G3), lagged mean temperature (Temp; one-week lag), and lagged precipitation (Precip; one-week lag) as fixed effects, as well as all AIC selected interaction terms. Plot and individual identity were included as random effects to account for spatial structure and repeated measurements. Reported are likelihood ratio test statistics (χ^2), degrees of freedom (df), and associated p-values. Significant effects are indicated in bold (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$).

Effect	df	χ^2	p-value	
Treatment [Treat]	3	**43.67**	**<0.001**	***
Week	1	**38.20**	**<0.001**	***
Generation [G]	3	**37.59**	**<0.001**	***
Lag temperature [Temp]	1	**92.31**	**<0.001**	***
Lag precipitation [Precip]	1	**21.68**	**<0.001**	***
Treat × Week	3	**28.42**	**<0.001**	***
Treat × G	9	**42.07**	**<0.001**	***
Week × G	3	**36.16**	**<0.001**	***
Treat × Temp	3	**17.35**	**0.001**	***
Week × Temp	1	**13.22**	**<0.001**	***
Gen × Temp	3	**15.56**	**0.001**	**
Treat × Precip	3	**11.74**	**0.008**	**
Week × Precip	1	**12.67**	**<0.001**	***
Gen × Precip	3	**54.46**	**<0.001**	***
Temp × Precip	1	**5.55**	**0.019**	*
Treat × Week × G	9	**42.15**	**<0.001**	***
Treat × Week × Temp	3	**12.81**	**0.005**	**
Treat × G × Temp	9	**29.39**	**0.001**	***
Week × G × Temp	3	**9.44**	**0.024**	*
Treat × Week × Precip	3	**8.32**	**0.034**	*
Treat × G × Precip	9	**28.60**	**0.001**	***
Week × G × Precip	3	**36.49**	**<0.001**	***
Treat × Temp × Precip	3	6.13	0.105	
Week × Temp × Precip	1	**3.04**	**0.081**	.
Gen × Temp × Precip	3	**104.95**	**<0.001**	***
Treat × Week × G × Temp	9	**21.96**	**0.009**	**
Treat × Week × G × Precip	9	**22.44**	**0.008**	**
Treat × G × Temp × Precip	9	**30.51**	**<0.001**	***
Week × G × Temp × Precip	3	**105.17**	**<0.001**	***

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Supplementary Material

Table S1: Results of the linear mixed-effects model testing the effects of precipitation predictability, generation and experimental week on the weekly measured growth variables (diameter, number of leaves, number of leaflets and number of nodes) of each individual. The model included the early treatment (less predictable *versus* more predictable), the late treatment (less predictable *versus* more predictable), Generation (G0–G3), experimental week, and their two-, three-, and four-way interactions as fixed effects, and year (2012–2015), the individual nested in plot (1–16), and the maternal line as random effects. The weekly plant height was transformed using a power transformation (y^0.2) to meet model assumptions. Reported are likelihood ratio test statistics (χ^2), degrees of freedom (df), and associated p-values. Significant effects are indicated in bold (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$).

		Diameter[1]			**Number of leaves[2]**			**Number of leaflets[2]**			**Number of nodes**		
Effect	**df**	**χ^2**	**p**		**χ^2**	**p**		**χ^2**	**p**		**χ^2**	**p**	
Early	1	0.33	0.566		0.26	0.607		0.02	0.884		**4.89**	**0.027**	*
Late	1	2.79	0.095		0.11	0.739		0.01	0.917		**4.47**	**0.034**	*
Generation [G]	3	**212.67**	**<0.001**	***	**170.42**	**<0.001**	***	**137.14**	**<0.001**	***	**98.96**	**<0.001**	***
Week	1	**9850.26**	**<0.001**	***	**14726.23**	**<0.001**	***	**21291.64**	**<0.001**	***	**4299.51**	**<0.001**	***
Early × Late	1	1.15	0.283		0.64	0.424		1.24	0.265		0.05	0.831	
Early × G	3	**52.78**	**<0.001**	***	**23.96**	**<0.001**	***	**40.85**	**<0.001**	***	**9.60**	**0.022**	*
Late × G	3	1.57	0.666		7.81	0.050		**9.69**	**<0.001**	***	0.50	0.920	
Early × Week	1	3.60	0.058		**48.15**	**<0.001**	***	**45.30**	**<0.001**	***	**3.51**	**0.061**	.
Late × Week	1	2.53	0.112		**27.85**	**<0.001**	***	**20.35**	**<0.001**	***	0.04	0.837	
G × Week	3	**216.43**	**<0.001**	***	**234.32**	**<0.001**	***	**238.40**	**<0.001**	***	**137.21**	**<0.001**	***
Early × Late × G	3	**18.67**	**<0.001**	***	**20.88**	**<0.001**	***	**16.68**	**0.001**	**	1.49	0.684	
Early × Late × Week	1	0.02	0.897		0.05	0.816		0.72	0.397		0.73	0.394	
Early × G × Week	3	**29.00**	**<0.001**	***	**32.73**	**<0.001**	***	**40.98**	**<0.001**	***	**17.14**	**0.001**	**
Late × G × Week	3	**17.47**	**0.001**	**	**37.21**	**<0.001**	***	**31.10**	**<0.001**	***	2.73	0.435	
Early × Late × G × Week	3	3.74	0.291		**21.80**	**<0.001**	***	**9.07**	**0.028**	*	1.26	0.740	

Transformations: [1] *log10;* [2] *log*

Figure S1: Weekly temperature (mean, min, max) and sum of weekly precipitation across the experimental weeks in the four different years.

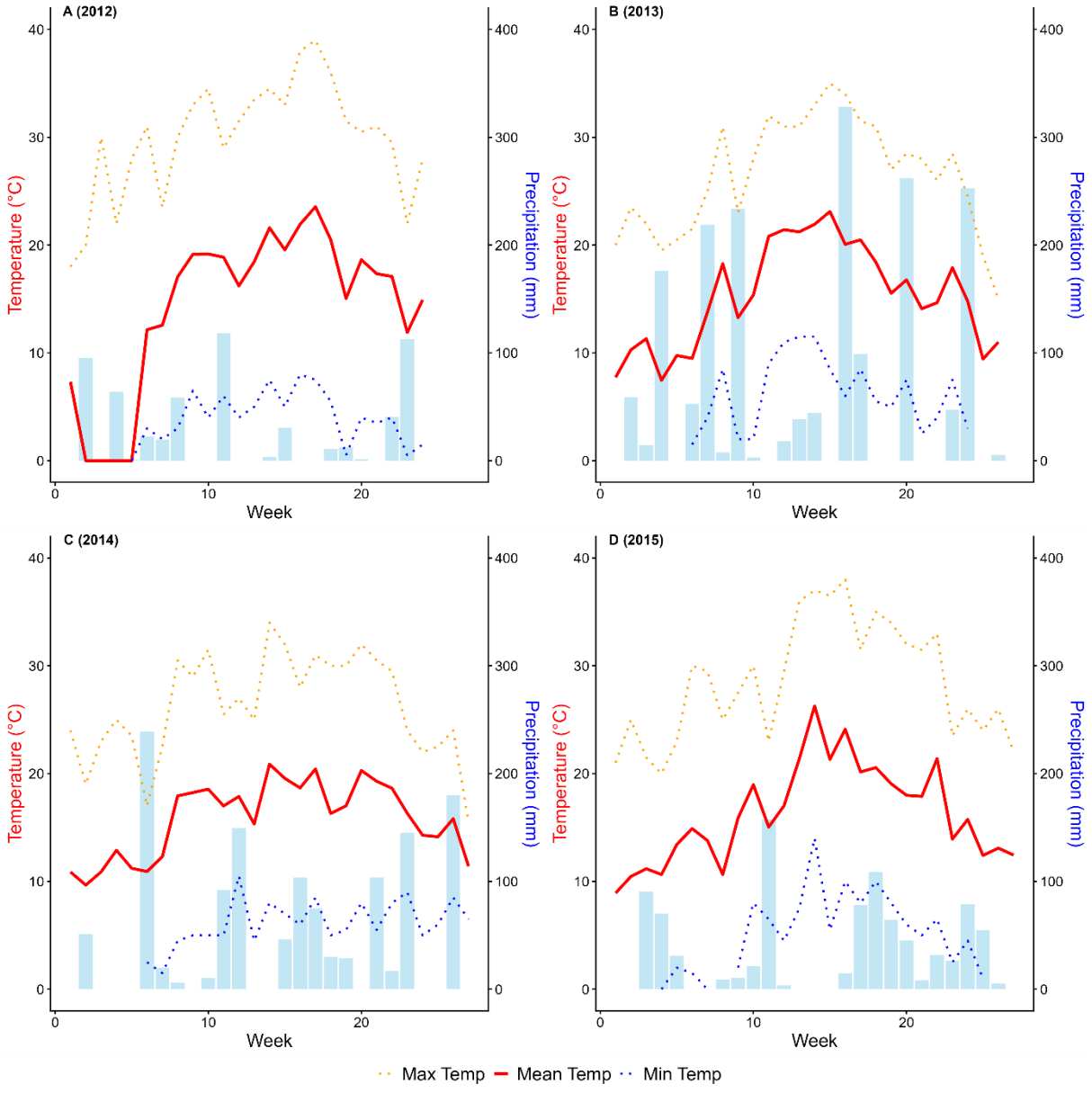
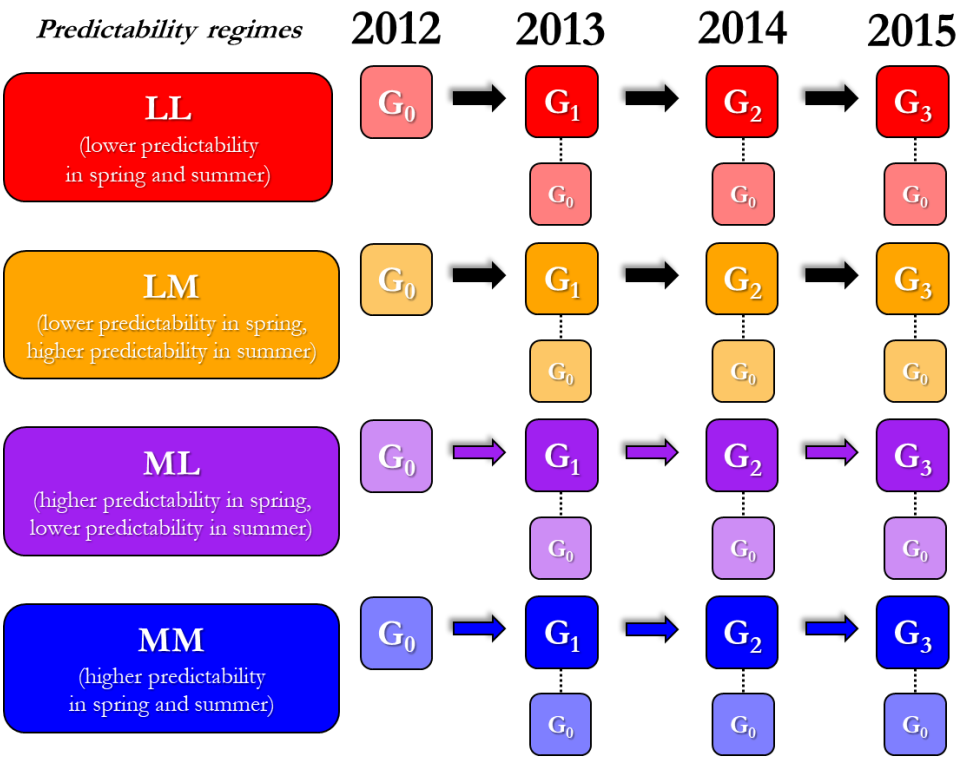


Figure S2: Schematic representation of the transgenerational experimental design. In 2012, randomly selected seeds from the field-origin generation (G0; ancestors) were sown. In subsequent years (2013–2015), offspring seeds produced by the previous experimental generation (i.e. G0 grown in 2012, G1 in 2013, and G2 in 2014) were selected and sown, resulting in three descendant generations (G1, G2, and G3) grown in 2013, 2014, and 2015, respectively. In addition, from 2013 to 2015, ancestor seeds were also sown, together with those of the descendant generations, allowing to assess transgenerational differences while controlling for potential year-to-year environmental variation. This transgenerational design was applied to each of the four combinations of predictability treatments, consisting of less (L) or more (M) predictable regimes during spring and summer, resulting in LL (red), LM (orange), ML (purple), and MM (blue).



Parental generation (G_0): seeds from the field-origin generation sown in each experimental year.

Descendant generations ($G_{n = 1–3}$): offspring seeds produced by the previous experimental generation.

Figure S3: Temporal trajectories of: (a) mean plant diameter [mm], (b) number of leaves, (c) number of leaflets and (d) number of nodes across weeks for all experimental years, shown separately for generation (Ancestors: solid lines; descendants: dotted lines) and treatment combination (LL, LM, ML, MM; coloured lines). Ribbons represent ± standard error.

Figure S3a: Plant diameter

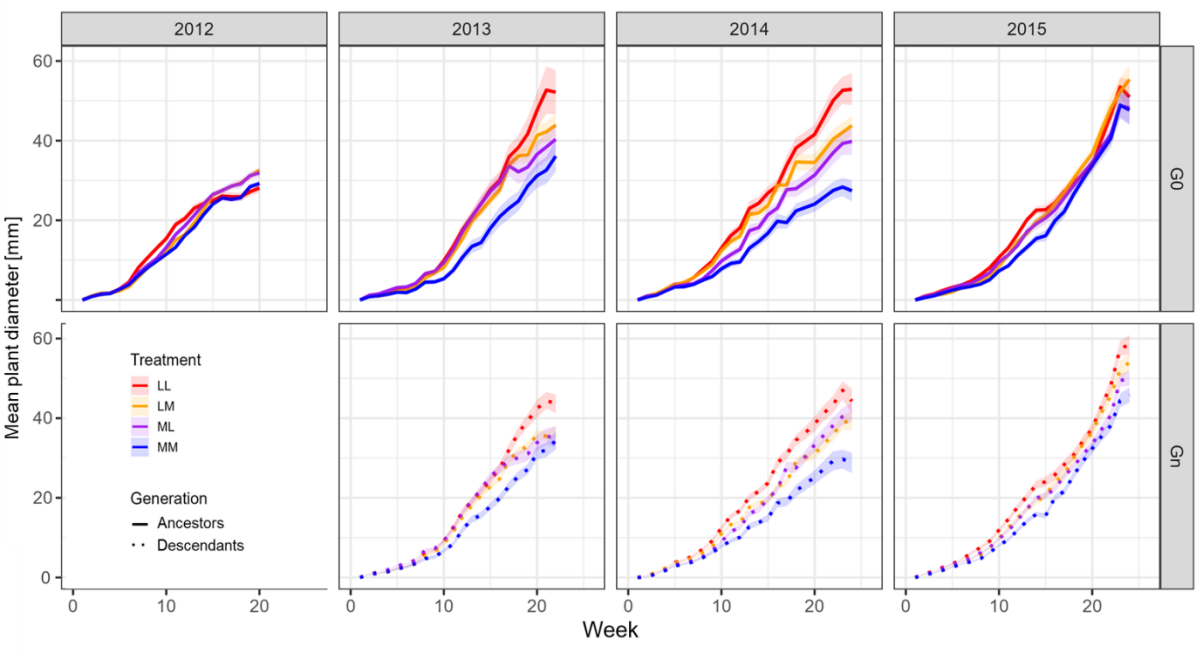


Figure S3b: Number of leaves

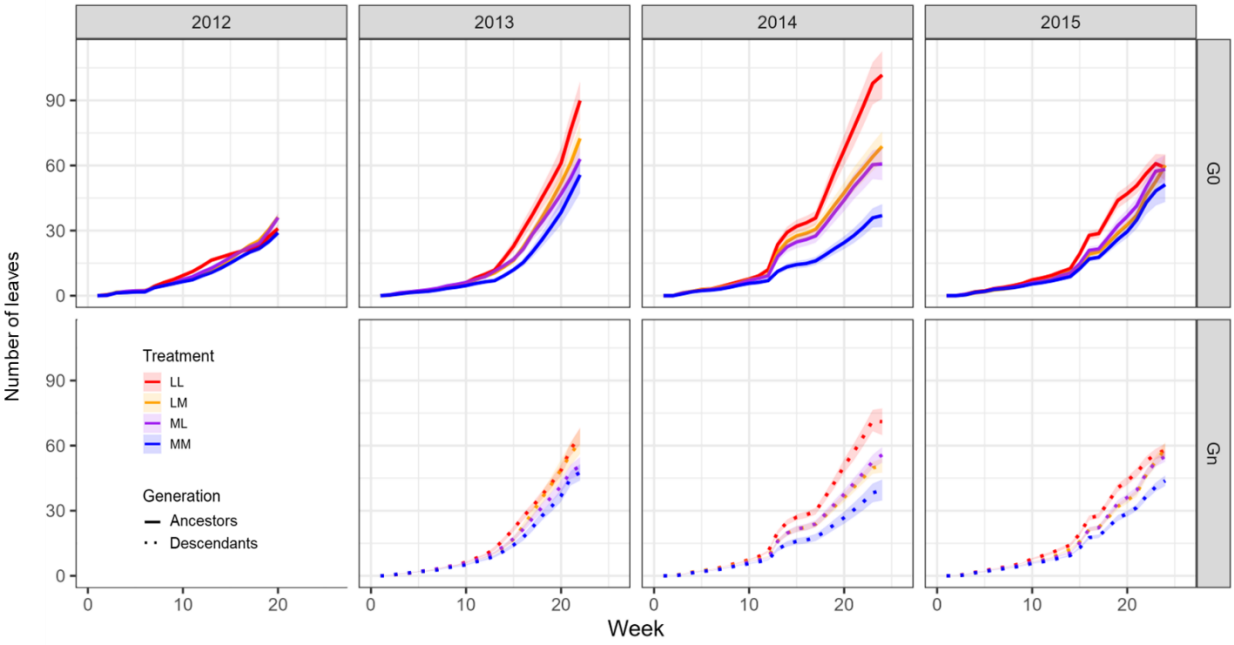


Figure S3c: Number of leaflets

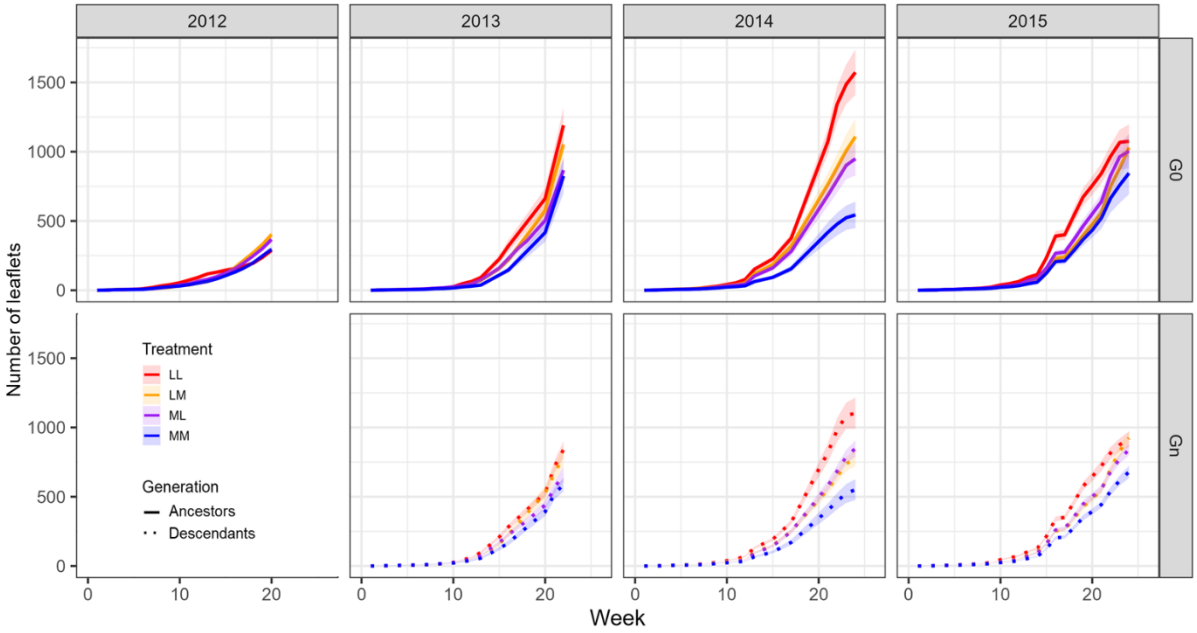


Figure S3d: Number of nodes (only measured from 2013 onwards)

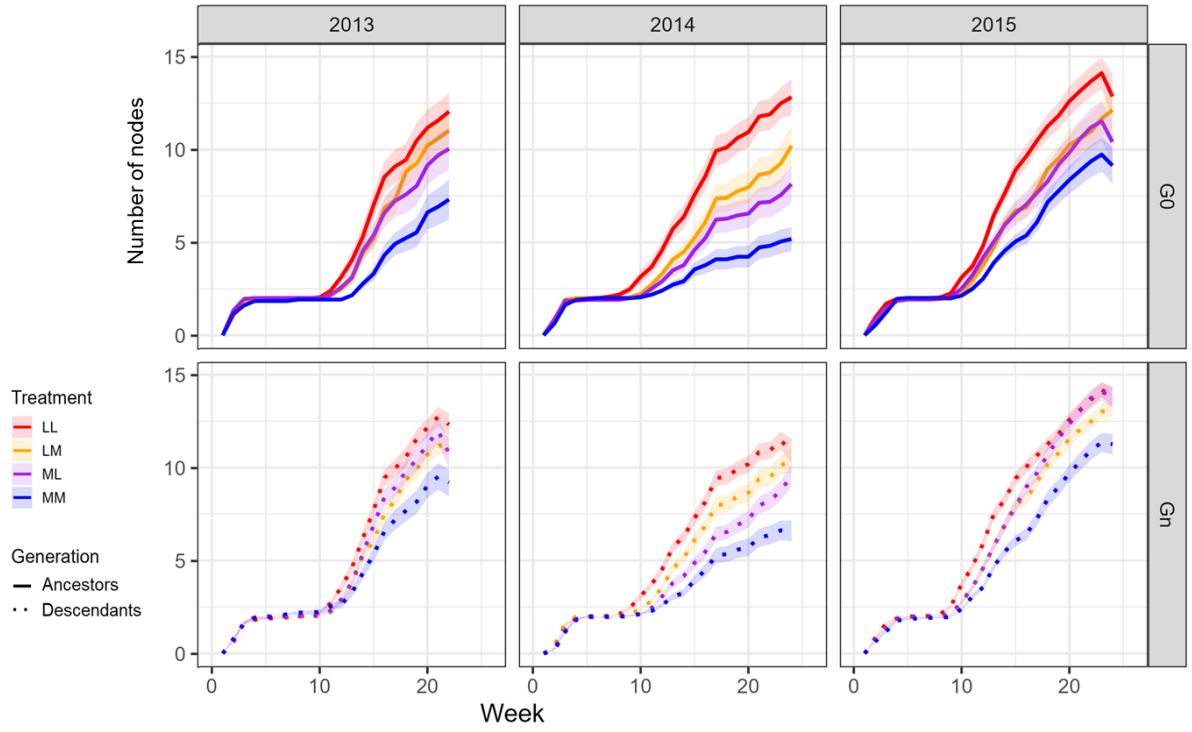


Figure S4: Multigroup SEM with paths of Number of leaves, Height and diameter to number of seeds. Colours indicate the treatment (shown estimate + significance level (* 0.05 > p; ** 0.01 > p; *** p < 0.001)). We used G0 of 2015 with 211 observations (211 plants reproduced = seed number available) across all treatment combinations: LL = 76, LM= 61, ML = 45, MM = 29). We calculated the maximum value for number of leaves, plant height and diameter per plant and fitted a multigroup SEM to check if there are differences between the treatments. The constrained model fitted with a χ^2 of 24.04 (p = 0.083), a CFI of 0.971 and an SRMR of 0.084. The model allowing all regression paths to vary among treatments did not fit the data better than a model constraining paths to be equal across treatments ($\Delta\chi^2$ = 12.7, Δdf = 15, p = 0.63). This indicates that treatments did not significantly alter the relationships among leaf number, plant size, and seed production. Instead, treatment effects were expressed through differences in intercepts and residual variances, reflecting shifts in trait magnitudes rather than changes in underlying growth–reproduction relationships. The model was able to explain between 33% and 52% of the variance in seed number across treatments (LL = 33.4%, LM = 36.9%, ML = 51.7%, MM = 38.7%).

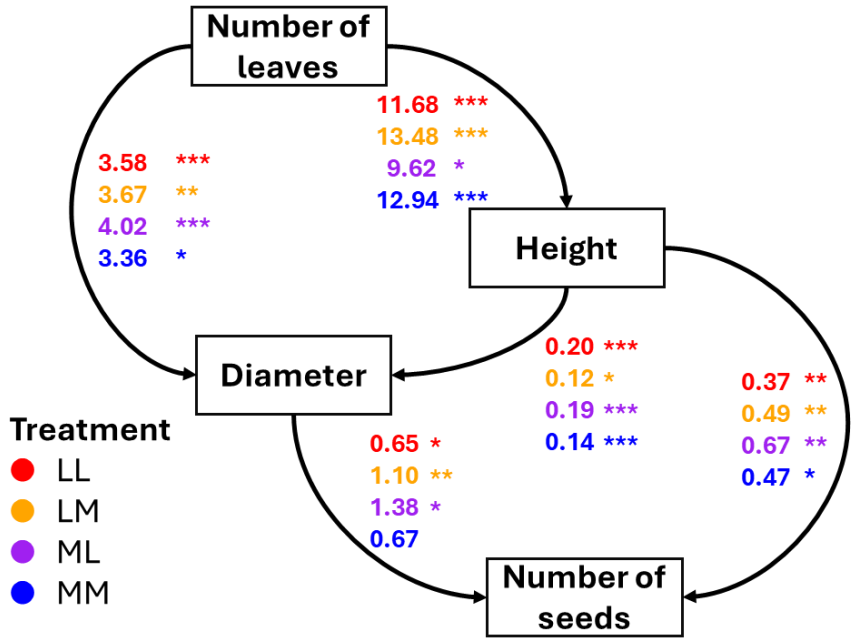


Figure S5: LOESS curves for growth rate (based on weekly height increase per plant) and temperature (same week (t), t-1 and t-2).

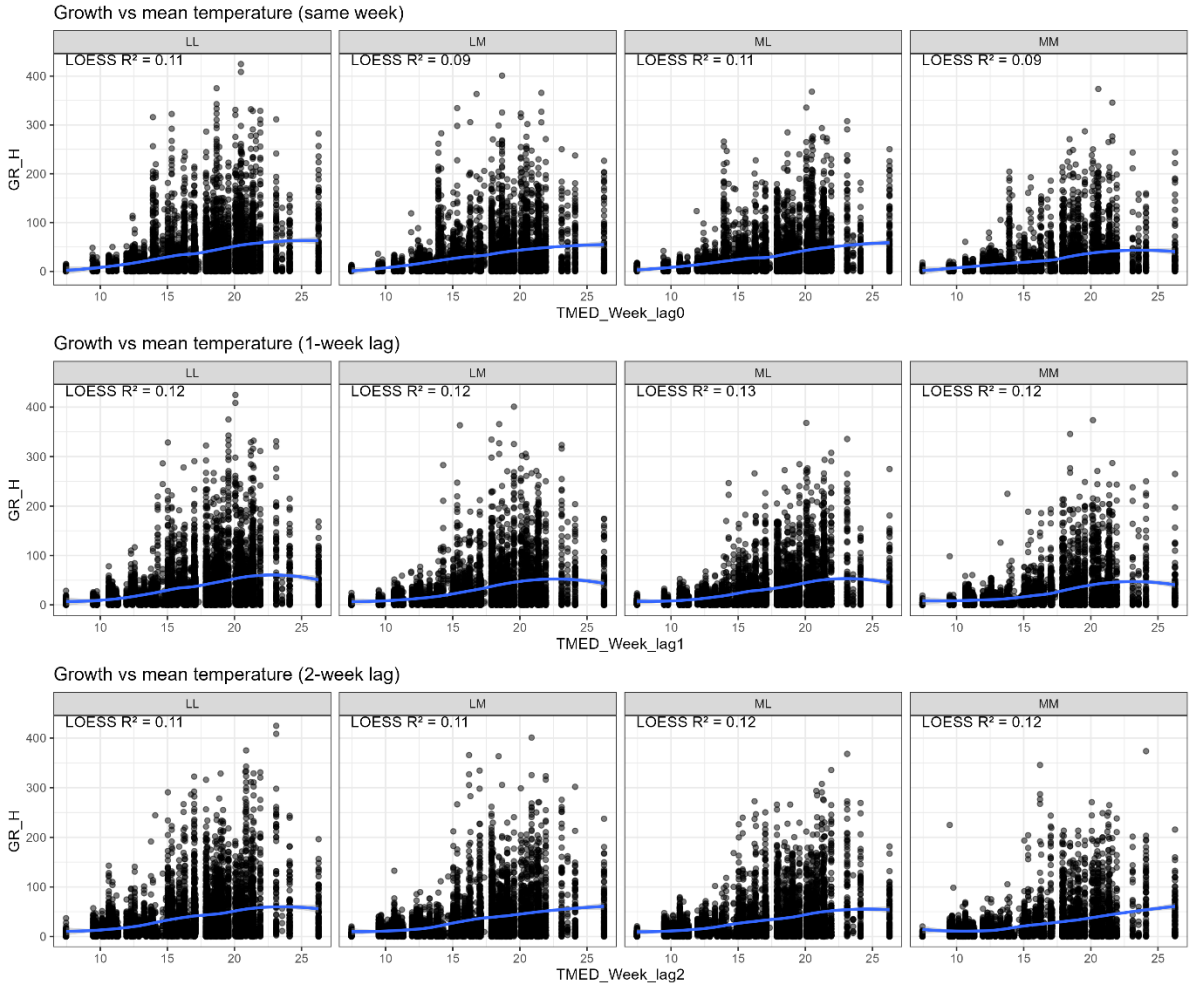


Figure S6: LOESS Curves for growth rate (based on weekly height increase per plant) and precipitation (same week (t), t-1 and t-2).