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Individual-level differences in cumulative water stress drive threshold flowering responses in an endangered desert shrub

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In arid ecosystems, plant reproduction is strongly constrained by water availability, yet individuals within the same population can differ in reproductive output despite experiencing similar climatic conditions. Understanding how spatial variation in water availability translates into differences in growth and reproduction is essential for predicting population persistence under increasing aridity. We tested the hypothesis that spatial heterogeneity in soil water availability generates individual differences in cumulative water stress that influence physiological performance, growth, and flowering in *Myrcianthes coquimbensis*, an endangered shrub of the Atacama Desert. Over a 15-month period, we monitored soil water potential, predawn leaf water potential, photosynthesis, vegetative growth, and reproduction in a natural population, where individuals were classified based on recent reproductive history as annual-flowering or sporadic-flowering. Cumulative water stress during the growing season was quantified using the Water Stress Integral (WSI), which integrates the magnitude and duration of plant water deficit. Soil water availability was spatially heterogeneous, and this heterogeneity was reflected in consistent differences in plant water status among individuals. Although photosynthesis declined with decreasing plant water status in both reproductive groups, annual-flowering individuals maintained higher mean photosynthetic rates and experienced significantly lower WSI than sporadic-flowering plants. Higher WSI was associated with reduced relative growth rates and marginally lower annual growth. Flowering probability increased sharply as WSI became less negative and exceeded 50% at approximately -90 MPa, indicating a threshold-like relationship between cumulative stress and reproduction. These results show that spatial heterogeneity in soil water availability within a single population can generate individual differences in WSI that translate into nonlinear variation in growth and flowering. By integrating short-term physiological responses over time, WSI provides a mechanistic link between environmental variability and reproductive outcomes in dryland plants.

KEYWORDS

Atacama, Chile, conservation physiology, flowering probability, physiological thresholds, plant-water relations, within-population variability

1 Introduction

Water availability is the primary limiting factor for plant growth, survival, and reproduction in arid and semi-arid ecosystems, where precipitation is infrequent and highly unpredictable (Noy-Meir, 1973; Holmgren et al., 2006; Xu et al., 2019; DeSoto et al., 2020). In these environments, rainfall typically occurs as short pulses rather than sustained inputs, generating pronounced spatial and temporal variability in soil water availability at fine scales (Porporato et al., 2004; Reynolds et al., 2004; Zhu et al., 2025). As a consequence, individual plants within the same population may experience markedly different water availability (Tokumoto et al., 2014). Climate change is expected to further intensify this variability by increasing the frequency, duration, and severity of drought events across dryland regions (Chen et al., 2022; Salazar et al., 2024), thereby amplifying water stress and posing major challenges for the persistence of dryland species. Yet, individuals within the same population do not necessarily respond to increasing water stress with the same magnitude or sensitivity, even when exposed to broadly similar environmental conditions (Aranda et al., 2018). Although the impacts of water availability on plant physiology and performance are well documented (Osakabe et al., 2014; Sun et al., 2020), how differences in water availability experienced by individual plants translate into persistent variation in growth and reproduction, and how this variation may scale up to influence population dynamics, remains comparatively understudied. Accounting for individual-level variability is therefore critical for understanding plant performance and predicting population persistence under increasing aridity (da Silva et al., 2013).

Plants respond to reductions in water availability through a sequence of ecophysiological responses that operate across temporal scales (Chaves et al., 2002; Caser et al., 2018; Taiwo et al., 2020). Early in this sequence, stomatal closure acts as a primary tolerance mechanism that limits transpirational water loss but also restricts CO₂ uptake and photosynthetic activity (Flexas and Medrano, 2002; Bartlett et al., 2016; Buckley, 2019). This response is driven by declining leaf water potential through both passive hydraulic effects and active biochemical signaling (Buckley, 2019). As water stress intensifies, reduced hydraulic conductance and persistent stomatal limitation impose increasingly severe constraints on photosynthesis, diminishing carbon assimilation and slowing growth (Chaves et al., 2002; Medrano et al., 2002; Rodriguez-Dominguez and Brodribb, 2020). Growth reduction itself functions as both a consequence of limited carbon supply and an adaptive mechanism to conserve resources during prolonged water limitation (Seleiman et al., 2021). However, plants may vary in the sensitivity and timing of these responses, leading to pronounced individual differences in how drought impacts carbon balance and growth.

Under prolonged water limitation, plants shift from short-term physiological adjustments to long-term responses that prioritize survival and maintenance over reproduction (Chaves et al., 2002; Obeso, 2002; Osakabe et al., 2014; Sun et al., 2020). These responses include osmotic adjustment, antioxidant production, and increased investment in root growth to enhance water uptake, processes that

often involve the mobilization and reallocation of stored carbohydrates and nutrients that would otherwise support floral development (Chaves et al., 2003; Osakabe et al., 2014). Although the use of carbohydrate reserves helps sustain metabolic functioning when photosynthesis is limited by persistent stomatal closure and declining leaf water potential, it also reduces carbon availability for current-season growth and reproduction, particularly in species with indeterminate growth, where flowering depends on the production and elongation of new shoots (Obeso, 2002; Sun et al., 2020). In such species, drought-induced reductions in stem elongation directly constrain the formation of reproductive structures and limit flowering potential (Chaves et al., 2002; Bowers, 2006). Together, these physiological constraints and the indirect effects of carbon reallocation converge to suppress reproductive output under prolonged drought, with important consequences for individual fitness and population dynamics (Messina et al., 2019; Qian et al., 2025).

Given the cumulative and time-dependent nature of plant responses to water stress, there is a clear need for approaches that quantify stress exposure over time and identify thresholds beyond which growth or reproduction is compromised. The Water Stress Integral (WSI) provides such a framework by integrating both the intensity and duration of water stress to generate a cumulative index of plant stress (Myers, 1988; Myers and Landsberg, 1989). Unlike single-point physiological measurements, WSI captures the temporal dynamics of drought and has been widely applied in forestry and agricultural systems (Gonzalez-Benecke and Dinger, 2018; Gauthier and Jacobs, 2019). Its potential value for ecological and conservation studies, however, remains largely unexplored.

Desert plants face extreme water limitation, and their ability to persist under prolonged drought makes them ideal systems for examining physiological variation among individuals. The Atacama Desert, one of the most arid regions on Earth, supports a suite of endemic plant species with specialized adaptations to water scarcity (Carvajal et al., 2019; Rios et al., 2025). These species are increasingly threatened by declining precipitation and rising evaporative demand driven by climate change (Salazar et al., 2024). *Myrcianthes coquimbensis*, an endangered shrub endemic to a narrow coastal strip of the Atacama Desert, offers an ideal system for exploring individual-level variation in responses to water stress and performance. Within populations, some plants flower in consecutive years, whereas others reproduce only intermittently (Loayza, unpublished data), despite similar size or habitat conditions. These contrasting recent flowering histories provide an opportunity to examine whether differences in plant water status and physiological performance are associated with variation in growth and reproductive outcomes, and whether differences in water availability experienced by individual plants in heterogeneous desert soils are reflected in their growth and reproduction.

Here, we build on this natural variation in reproductive strategies to test the hypothesis that differences in soil water availability contribute to variability in plant physiological performance, growth, and flowering outcomes. Specifically, we predict that (1) variation in soil water potential is reflected in plant water status and photosynthetic performance, and that plants experiencing consistently lower cumulative water stress during the

growing season, quantified using the Water Stress Integral (WSI), will (2) exhibit higher relative growth rates and greater vegetative growth, and (3) have a higher probability of flowering in the subsequent season.

2 Materials and methods

2.1 Study species

Myrcianthes coquimbensis (Myrtaceae) is an endangered, evergreen shrub endemic to a narrow coastal strip (<100 km²) and a few isolated populations along the southern margin of Chile's Atacama Desert, where it grows on ocean-facing slopes (Landrum and Grifo, 1988; García-Guzmán et al., 2012). It commonly occurs in association with large rocks, which provide microhabitats with higher soil moisture and cooler soil and air temperatures that favor seedling establishment (Loayza et al., 2017). The species is increasingly threatened by climate change, with regional models projecting a 30–40% decline in precipitation by 2100 (Salazar et al., 2024).

Vegetative growth begins in mid austral winter (around August) and continues until mid-spring (around November). Flower buds develop on the shoots produced during the same growing season; therefore, adult plants that fail to produce new growth in a given year will not flower. Nonetheless, not all individuals with new growth develop flowers. The flowering period extends from October to February, peaking in November, and ripe fruits appear the following year between August and December.

2.2 Study area

We conducted this study between August 2012 and November 2013 in a population located near the southern limit of *M. coquimbensis*'s distribution, approximately 26 km south of La Serena, Chile (30°04' S, 71°14' W; 0–33 m a.s.l.). This site lies within the transition zone between the coastal Atacama Desert and the Mediterranean-climate region of north-central Chile. Over the 15 years preceding the study, annual precipitation ranged from 21 to 122 mm (mean $\pm$ SD = 81 $\pm$ 28 mm; CEAZAMET), falling mostly between June and August. Mean annual temperature is approximately 14 °C and shows little interannual variation.

2.3 Heterogeneity in soil water availability

Soil water status was monitored throughout the study by measuring soil water potential (Ψ_{soil}) at 16 fixed sampling locations distributed across both rock and open habitats within the study site (Supplementary Figure 1, Supplementary Material). Sampling points were not assigned to specific individuals but were positioned to capture spatial at the population level. Locations were repeatedly sampled over time, with measurements taken monthly during most of the study period and every two weeks during the growing season to better resolve seasonal dynamics. Soil samples were collected at a depth of 30 cm, sealed immediately in plastic

bags, stored in a cooler, and analyzed in the laboratory within two hours using a WP4 Dewpoint PotentialMeter (Decagon Devices, Pullman, WA, USA).

2.4 Plant performance

We monitored 20 adult plants, of comparable size, selected from a larger demographic monitoring program in which individuals were classified by stage. Focal plants were chosen to minimize visible differences in stature and canopy development, and were monitored over a 15 month-period (August 2012 - November 2013), measuring predawn water potential (Ψ_{pd}) and photosynthetic rates monthly. Individuals were classified according to their recent reproductive history based on annual censuses conducted in 2010–2011 and 2011–2012 (Loayza, unpublished data). Ten individuals that flowered in both consecutive seasons preceding the 2012 growing season were categorized as annual-flowering, whereas 10 that flowered in only one or neither of those seasons year were categorized as sporadic-flowering plants (Supplementary Figure 1, Supplementary Material). Because classification was based on two consecutive years of observations, these categories reflect recent reproductive history rather than stable life-history types, and some interannual variability in flowering behavior is possible.

To measure Ψ_{pd} , we collected an apical branch from each plant before sunrise (04:00 - 05:30 h). Samples were sealed immediately in Whirl-Pak[®] bags, stored in a cooler with ice, and transported to the laboratory for measurement using a Scholander pressure chamber (PMS Instruments, OR, USA).

During the 2012 growing season (mid-October to late November), Ψ_{pd} measurements were used to calculate the Water Stress Integral (WSI; MPa-day) for each plant (Myers, 1988). The WSI was originally developed as a plant-based cumulative water stress index calculated from plant water status (Myers, 1988) and has been widely used to explain variation in plant growth and reproduction (Nepstad et al., 2007; Gonzalez-Benecke and Dinger, 2018). The integration window corresponded to the period of active shoot elongation, determined from repeated phenological observations. Ψ_{pd} was measured approximately every 14 days during this interval. WSI was calculated as:

$$WSI = \left| \sum_{i=0}^t [(\Psi_{\text{pd}})_i, i+1 - (\Psi_{\text{pd}})_{\text{max}}] n \right|$$

where $(\Psi_{\text{pd}})_i, i+1$ is the mean predawn water potential for a given interval, $(\Psi_{\text{pd}})_{\text{max}}$ is the least negative value recorded during the season (-0.08 MPa in this study), and n is the number of days in the interval (calculated from actual sampling dates; approximately 14 days). By integrating both the magnitude and duration of deviation from the seasonal maximum, WSI quantifies cumulative plant water stress over the defined growing-season window. More negative WSI values indicate higher cumulative water stress.

Gas-exchange measurements were conducted on fully expanded leaves between 10:30 and 12:00 h, coinciding with Ψ_{pd} sampling. We used an open gas-exchange system (LI-6400, LI-COR Inc., Lincoln, NE, USA) with a light level of 1500 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ (10% blue), chamber temperature of 25 °C, and an ambient CO₂ concentration of 380 $\mu\text{mol mol}^{-1}$. Measurements were conducted

monthly throughout the 15-month monitoring period and every two weeks during the 2012 growing season in parallel with shoot-growth assessments.

To quantify growth and flowering during the 2012 growing season, we marked five apical branches on each of the 20 focal plants at the onset of the season. Branches were monitored every two weeks for up to six weeks. During each evaluation, we measured shoot length and recorded flower development. Relative growth rate (RGR; day⁻¹) was calculated as:

$$RGR = \frac{\ln(\text{final shoot length}) - \ln(\text{initial shoot length})}{t}$$

where t is the number of days between measurements.

2.5 Statistical analyses

To characterize temporal dynamics in soil water heterogeneity, we quantified variability in soil water potential for each sampling date using the coefficient of variation (CV, %). CV was calculated from the absolute value of Ψ_{soil} ($|\Psi_{\text{soil}}|$) to avoid inflation when mean Ψ_{soil} approached zero during wet periods. We examined how soil water potential influenced Ψ_{pd} by fitting separate linear regression models for annual- and sporadic-flowering plants. Soil and leaf water potential measurements collected on the same sampling dates were paired, and predawn values were averaged within each reproductive strategy. Models were fitted independently with mean Ψ_{pd} as the response and mean Ψ_{soil} as the predictor, and parameter estimates and model fit statistics were obtained using the broom package.

To assess how photosynthesis varied with plant water status and whether this relationship differed between flowering strategies, we fitted a linear model relating mean photosynthesis to mean predawn water potential (Ψ_{pd}), flowering strategy, and their interaction. The interaction term was used to test for differences in the photosynthesis– Ψ_{pd} relationship between strategies.

To test whether flowering strategies differed in overall photosynthetic performance during the 2012 growing season while accounting for repeated measurements, we fitted a linear mixed-effects model fitted with the *lme4* package, with flowering strategy as a fixed effect, and plant identity as a random intercept. Statistical significance of fixed effects was evaluated using Type III ANOVA with Satterthwaite's approximation for degrees of freedom.

We used Welch's t-tests (unequal variances) to test whether mean annual growth and WSI differed between reproductive strategies. Standardized effect sizes (Cohen's d) and their 95% confidence intervals were computed with the *effectsize* package (Ben-Shachar et al., 2020). Following Cohen (2013), values of $|d| \approx 0.2$ were interpreted as small, ≈ 0.5 as moderate, and ≥ 0.8 as large effects.

To evaluate how cumulative water stress influenced flowering probability across all plants, we fitted logistic regression models using a binomial error distribution with a logit link function. The effect of WSI was assessed via likelihood ratio tests comparing the full model to an intercept-only model. Coefficients were exponentiated to obtain odds ratios with 95% confidence intervals. Model fit was evaluated using Hosmer–Lemeshow tests and by examining the ratio of residual

deviance to degrees of freedom to assess overdispersion, implemented with the *ResourceSelection* package.

To evaluate the robustness of WSI to parameterization choices, we recalculated WSI using alternative reference values for Ψ_{pdmax} (a fixed -0.10 MPa threshold and the mean of the upper 5% of observed Ψ_{pd} values) and under both exact day counts and fixed 14-day intervals, and compared statistical inferences across all parameterizations (See [Supplementary Material](#)). Finally, we fitted a simple linear regression to examine how relative growth rate (RGR) varied with cumulative water stress during the growing season (WSI).

All analyses were conducted in R (R Core Team, 2025). Model assumptions were evaluated using residual diagnostics appropriate to each model type. For linear models, assumptions were assessed using the performance package (Lüdtke et al., 2021). For mixed-effects and binomial models, simulation-based residual diagnostics were implemented using *DHARMa*, and overdispersion was assessed where relevant. Results of the diagnostic tests are provided in the [Supplementary Material](#).

Due to intermittent malfunctions in field equipment, complete and reliable measurements were not available for three sampling months (December 2012, August 2013, and September 2013). To maintain consistency across datasets, observations from these months were excluded from all analyses.

3 Results

Soil water potential exhibited pronounced temporal variation, with broad within-date distributions indicating persistent spatial heterogeneity across sampling dates (Figure 1). In 2012, relative spatial heterogeneity peaked during the growing season (mid-October to late November), when the mean coefficient of variation was higher (mean CV = 81%) than during the preceding months (mean CV = 40%). By contrast, the subsequent summer drought period (January to March 2013) showed broader absolute ranges of soil water potential but comparatively lower relative variability than the growing season (mean CV = 64%). During the remainder of 2013 (April to November), spatial heterogeneity remained high, with elevated relative variability persisting across non-growing and early growing-season periods.

Predawn leaf water potential closely reflected Ψ_{soil} in both flowering strategies (Figure 2). When averaged by sampling date within each strategy ($n = 8$ dates), mean Ψ_{pd} declined linearly with decreasing Ψ_{soil} . Across the observed range of soil water potential, Ψ_{soil} accounted for 78% of the variation in predawn values in sporadic-flowering individuals ($\beta = 0.127 \pm 0.025$; adjusted $R^2 = 0.78$; $F_{1,6} = 25.3$, $p = 0.002$) and 84% in annual-flowering individuals ($\beta = 0.128 \pm 0.021$; adjusted $R^2 = 0.84$; $F_{1,6} = 38.9$, $p < 0.001$).

Photosynthesis significantly increased with Ψ_{pd} in both flowering strategies (Figure 3A). The interaction between Ψ_{pd} and flowering strategy was not significant, indicating similar sensitivity of photosynthesis to Ψ_{pd} in annual- and sporadic-flowering plants. Despite this shared response to plant water status, overall photosynthetic performance differed between strategies. Annual-

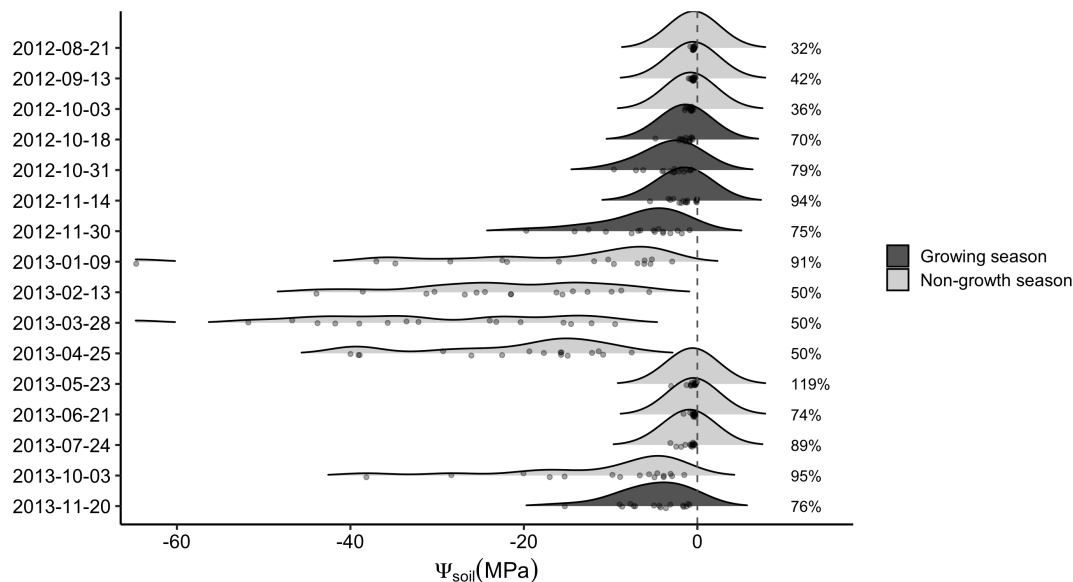


FIGURE 1

Temporal dynamics of spatial variability in soil water potential. Each horizontal ridge represents the kernel density distribution of soil water potential (Ψ_{soil}) measured across 16 spatially distributed sampling sites on a given date. Individual points show Ψ_{soil} values at each sampling site, representing spatial variation within each sampling date. Darker ridges indicate measurements taken during the growing season of each season. The vertical dashed line denotes $\Psi_{\text{soil}} = 0$ MPa. Percent values shown to the right of each ridge indicate the coefficient of variation (%) of $|\Psi_{\text{soil}}|$ for that sampling date.

flowering plants exhibited significantly higher photosynthetic rates than sporadic-flowering individuals (Type III ANOVA; $F_{1, 78} = 36.5$, $p < 0.001$), with mean rates of 9.86 and $6.07 \mu\text{mol m}^{-2} \text{s}^{-1}$, respectively (Figure 3B). In the mixed-effects model, the variance of the random intercept was close to zero, indicating minimal between-plant variation relative to within-plant temporal variability.

Mean annual growth tended to differ between flowering strategies, though the difference was not statistically significant ($t = -1.8$, $df = 18$, $p = 0.09$; Figure 4A). Sporadic-flowering plants grew an average of $13.8 \text{ mm year}^{-1}$, compared with $21.9 \text{ mm year}^{-1}$ in annual-flowering individuals. The effect size was moderate (Cohen's $d = 0.80$), indicating a biologically meaningful but non-significant trend toward lower growth of sporadic-flowering plants (Figure 4B).

The WSI differed markedly between flowering strategies ($t = -3.3$, $df = 18$, $p = 0.004$; Figure 4C). Sporadic-flowering individuals experienced more negative WSI (-118.6 MPa) than annual-flowering plants (-74.5 MPa). The effect size was large (Cohen's $d = 1.48$; Figure 4C), indicating that sporadic plants were exposed to greater water deficit during the growing season. RGR (day^{-1}) showed a positive relationship with WSI ($\beta = 0.00013 \pm 0.00004$; $t = 3.19$, $p = 0.005$; Figure 4D), with WSI explaining 37.5% of the variation in growth (adjusted $R^2 = 0.34$).

The probability of flowering increased as the WSI became less negative during the growing season ($\beta = 0.050$, $p = 0.027$; Figure 5). Specifically, the odds of flowering increased by approximately 5% for each unit increase in the WSI (OR = 1.05; 95% CI: 1.02–1.12),

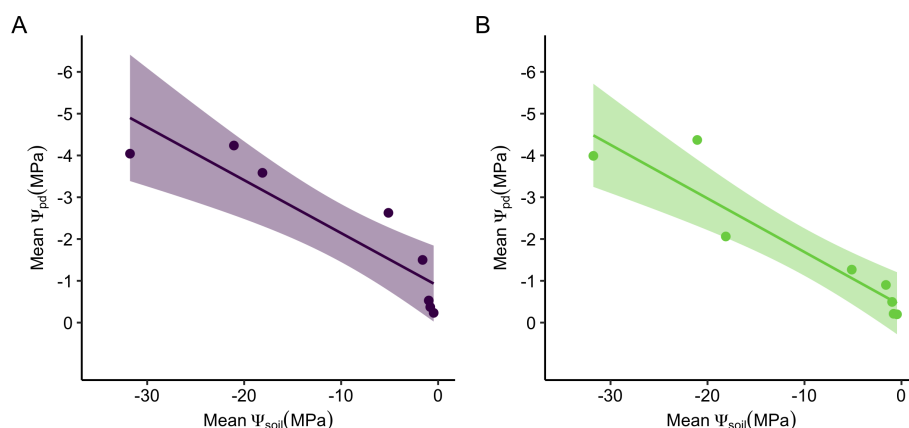


FIGURE 2

Relationship between mean soil water potential (Ψ_{soil}) at 30 cm depth and mean predawn leaf water potential (Ψ_{pd}) in *M. coquimbensis* individuals with (A) sporadic flowering and (B) annual flowering. Points represent sampling-date means for each flowering strategy ($n = 8$ dates). Shaded ribbons denote 95% confidence intervals.

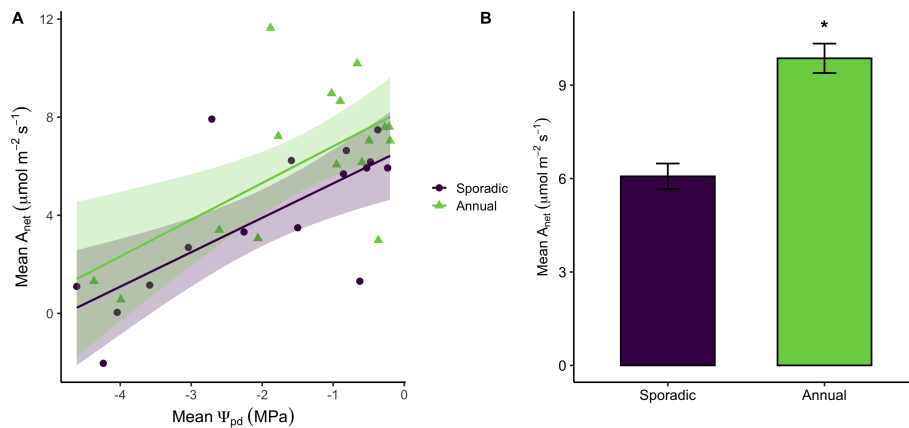


FIGURE 3

Photosynthetic responses to plant water status and flowering strategy in *Myrcianthes coquimbensis*. (A) Relationship between mean net photosynthetic rate (A_{net}) and mean predawn leaf water potential (Ψ_{pd}). Points represent Date $\times$ flowering strategy means for sporadic- and annual-flowering individuals. Lines show fitted values from a linear model including Ψ_{pd} , flowering strategy, and their interaction, with shaded ribbons indicating 95% confidence intervals. (B) Mean net photosynthetic rate ($A_{net} \pm \text{SE}$) of sporadic- and annual-flowering plants during the 2012 growing season (mid-October to late November). The asterisk indicates a significant difference between flowering strategies ($p < 0.05$).

indicating that individuals experiencing lower cumulative water stress were more likely to initiate flowering. Moreover, the probability of flowering exceeded 50% when WSI values were greater than -90 .

4 Discussion

In drylands worldwide, climate change is projected to intensify aridity and increase the frequency of drought (Trenberth et al., 2014; Schlaepfer et al., 2017). At local scales, these broader climatic

trends are often expressed as spatial and temporal heterogeneity in soil water availability, with important consequences for plant physiological performance, growth, and reproduction. Here, we tested the hypothesis that fine-scale variation in soil water availability generates persistent differences in cumulative water stress among individuals, which in turn shape physiological performance, growth, and flowering outcomes within a single population. As predicted, individuals differed in the cumulative water stress they experienced during the growing season. Plants that experienced lower cumulative water stress maintained higher plant

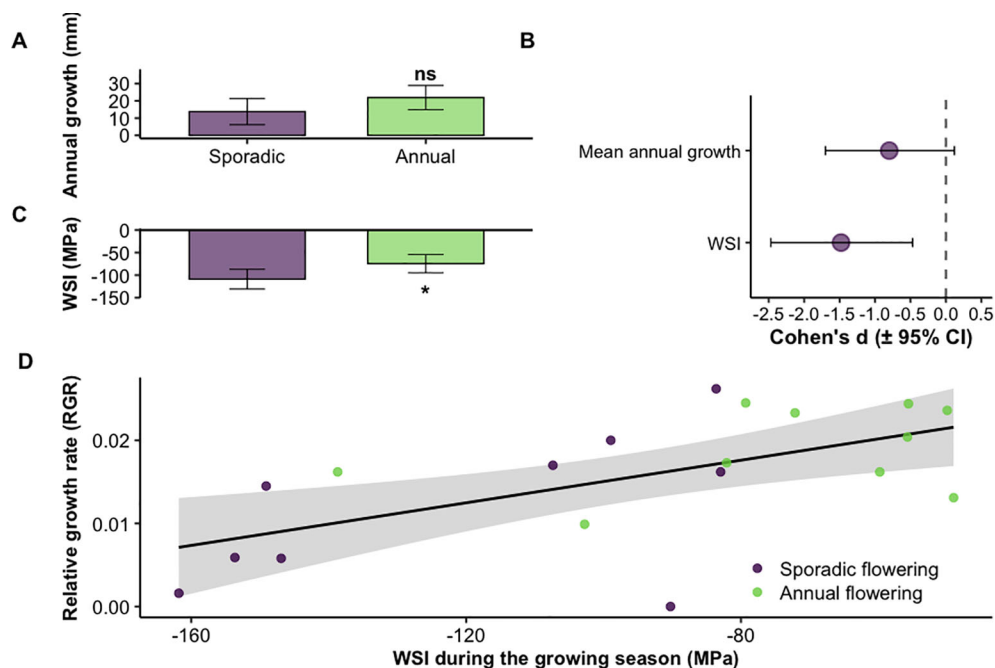
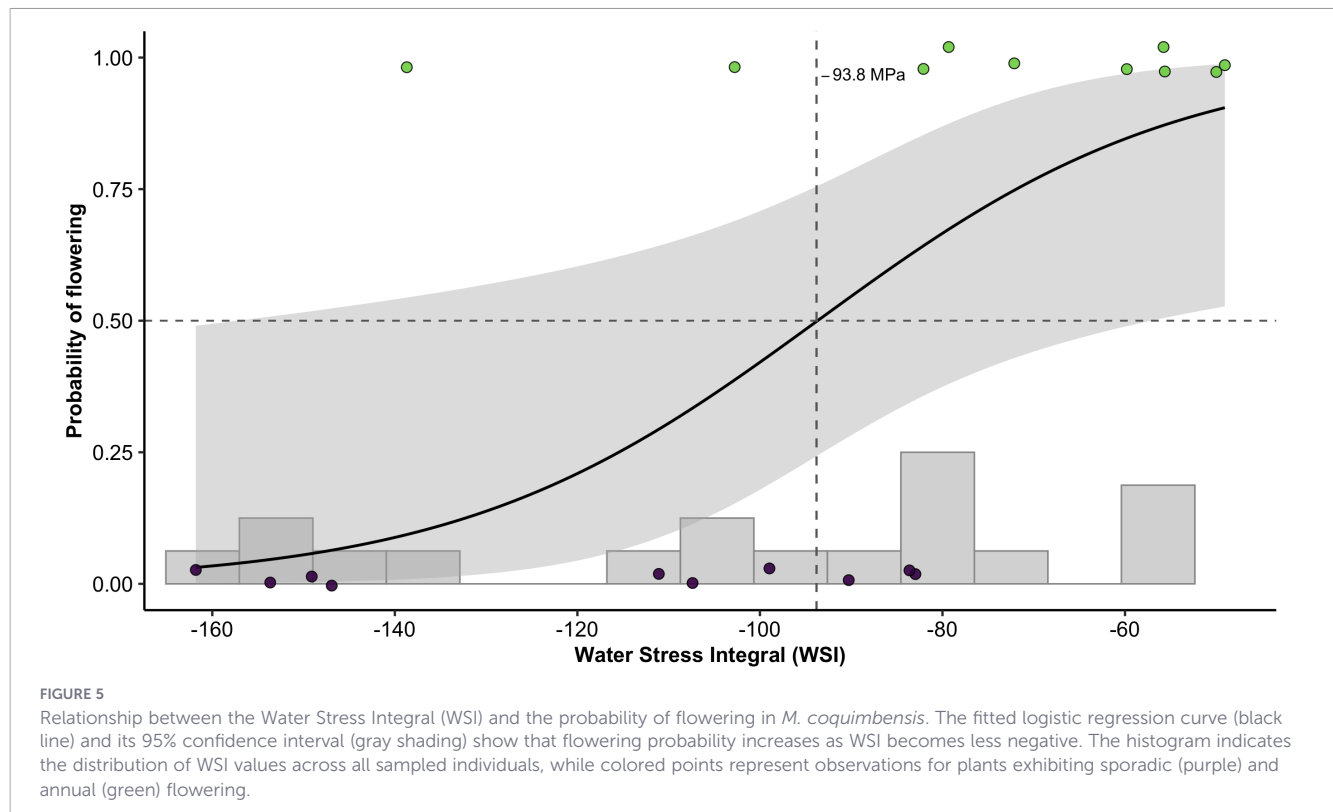


FIGURE 4

Differences in growth and water stress for annual- and sporadic-flowering *M. coquimbensis* plants. (A) Mean annual growth. (B) Standardized effect sizes (Cohen's d) indicating lower growth and higher cumulative stress in sporadic-flowering individuals. (C) Water Stress Integral (WSI). (D) Relationship between accumulated water stress (WSI) and relative growth rate (RGR). The asterisk indicates significant differences between flowering strategies ($p < 0.05$). Error bars and shaded ribbons represent 95% confidence intervals.



water status and photosynthetic rates, exhibited higher relative growth rates and greater vegetative growth, and had a higher probability of flowering in the subsequent season. In contrast, sporadic-flowering individuals accumulated higher water stress and showed reduced physiological performance and growth. Together, these findings suggest that water limitation within this population is not experienced uniformly, but is instead filtered through fine-scale soil heterogeneity.

Our findings indicate that soil water availability in this arid ecosystem is characterized by pronounced spatial heterogeneity. Such heterogeneity is a well-established driver of ecosystem dynamics in arid environments (Maestre et al., 2003; Wu et al., 2014), and was a prominent feature of our system. Relative spatial variability in Ψ_{soil} remained consistently high across sampling dates, including the growing season. By contrast, periods of extreme drought exhibited broader absolute ranges of Ψ_{soil} but comparatively lower relative variability. High spatial variability in soil moisture is typical of arid and semi-arid systems, where episodic rainfall, microsite effects, and soil physical heterogeneity generate strongly patchy water distributions (Reynolds et al., 2004). When integrated over time, repeated exposure to such spatially heterogeneous soil moisture conditions is likely to contribute to divergent WSI values among individuals.

Spatial heterogeneity in soil-based resources can strongly influence individual plant growth and biomass allocation, particularly in resource-limited environments (Hutchings et al., 2003; Liu et al., 2021). Plant responses to heterogeneous resource distributions depend on the spatial correspondence between resource patchiness and the foraging scale of individual root systems (Hutchings et al., 2003). Qualitative field observations

from two excavated individuals of *M. coquimbensis* suggest that this species possesses a dimorphic root system, with well-developed lateral roots concentrated in the upper 50 cm of soil and finer roots extending to deeper horizons. Because the species is endangered, destructive sampling is highly restricted, and root traits were not systematically quantified nor measured in the focal individuals analyzed here. If representative, such architecture could enable individuals to exploit shallow, temporally variable water resources, while also accessing more stable moisture at depth. When soil moisture patches are finer, more transient, or vertically stratified relative to root architecture, however, spatial heterogeneity is unlikely to translate into uniform plant responses. Instead, individuals may differ in their capacity to access available water, resulting in divergence in plant water status and accumulated water stress over time. Under these conditions, soil moisture is likely to generate persistent individual differences in cumulative water stress, effectively acting as an ecological filter. Consistent with this interpretation, Tokumoto et al. (2014) showed that small-scale variability in soil water storage and recharge generated persistent differences in Ψ_{pd} among neighboring trees, reflecting unequal access to plant-available water despite shared climatic forcing.

Variation in Ψ_{soil} explained a substantial proportion of the variation in Ψ_{pd} in both sporadic- (78%) and annual-flowering (84%) individuals, indicating tight temporal coupling between soil and plant water status within each strategy. Predawn water status, in turn, constrained photosynthetic performance in both strategies, although the magnitude of this constraint differed between flowering strategies. photosynthesis declined more steeply with decreasing Ψ_{pd} (adj. $R^2 = 0.49$), indicating stronger sensitivity of carbon assimilation to short-term water limitation, likely mediated by stomatal regulation (Flexas and Medrano, 2002).

In contrast, annual-flowering individuals showed a weaker dependence of photosynthesis on Ψ_{pd} (adj. $R^2 = 0.34$), maintaining higher assimilation across the observed water-potential range, as reflected in both a higher mean photosynthetic rate and a higher intercept of the A_{net} – Ψ_{pd} relationship. This pattern suggests that individuals differ not only in the sensitivity of carbon gain to increasing water stress, but also in their baseline capacity for gas exchange, such that some plants maintain higher photosynthetic rates than others even under comparable plant water status. These differences may reflect individual-level variation in stomatal regulation, hydraulic functioning, or photosynthetic capacity, rather than differences in water availability per se (Gilbert et al., 2011). Such variability is consistent with evidence that stomatal responses to declining water potential vary along a continuum and are closely linked to hydraulic traits that govern water transport within plants (Klein, 2014). At the within-population level, differences in photosynthesis and stomatal conductance under drought have been reported despite shared declines in plant water status, highlighting substantial individual-level variation in physiological responses to water limitation (Aranda et al., 2018). Moreover, Sánchez-Gómez and Aranda (2024) showed that variation in stomatal sensitivity within populations can be largely decoupled from drought resistance or post-drought recovery, emphasizing that drought performance emerges from the integration of multiple physiological traits rather than from stomatal regulation alone. Together, these findings suggest that although photosynthesis in both flowering strategies is water-limited, sporadic-flowering individuals exhibit a steeper decline in photosynthesis with decreasing Ψ_{pd} , whereas annual-flowering plants sustain higher carbon gain across the observed range of plant water status.

Cumulative water stress experienced during the growing season differed between flowering strategies and was closely associated with variation in growth performance. Sporadic-flowering individuals accumulated higher (i.e., more negative) WSI than annual-flowering plants and exhibited lower relative growth rates and marginally reduced annual growth, indicating that sustained water limitation imposes a constraint on carbon accumulation and biomass production (Reynolds et al., 2004; McDowell et al., 2008; Sun et al., 2020). Comparable patterns have been reported for other woody species. For example, in young Douglas-fir stands, higher WSIs were closely associated with reduced stem growth and productivity, reflecting the cumulative impact of repeated moderate water deficits rather than isolated drought events (Gonzalez-Benecke and Dinger, 2018). Similarly, in *Eucalyptus* plantations in central Chile, individuals or genotypes experiencing higher cumulative water stress exhibited lower growth rates despite maintaining photosynthetic activity during parts of the growing season (de Oliveira et al., 2022). Notably, these growth reductions were associated with cumulative water stress despite relatively modest differences in predawn water potential, consistent with the idea that growth responses integrate water stress over time rather than responding solely to instantaneous plant water status.

Cumulative water stress during the growing season was a strong predictor of flowering probability in *M. coquimbensis*, with annual-flowering individuals experiencing lower WSI during the growing season than sporadic-flowering plants. The sigmoidal relationship

between WSI and flowering probability suggests a relatively sharp shift from low to high flowering probability across a narrow range of cumulative water stress (approximately -110 to -90 MPa), consistent with a threshold-type response to drought exposure during the growing season. In this population, flowering probability exceeded 50% at WSI values greater than approximately -94 MPa; this inflection point may represent a population-level threshold beyond which cumulative stress likely constrains the physiological and developmental processes required for floral initiation. Non-linear responses of this kind suggest that reproduction in perennial shrubs may depend on meeting minimum resource thresholds during the growing season rather than responding proportionally to incremental changes in water availability.

Prolonged water limitation is known to reduce stomatal conductance and net carbon assimilation, thereby limiting the assimilate available for growth (Chaves et al., 2002). When such constraints persist over the growing season, cumulative reductions in carbon gain are expected to restrict current-season shoot extension (Muller et al., 2011). In indeterminately growing species such as *M. coquimbensis*, flowering depends on the production and elongation of current-season shoots, meaning that vegetative growth plays a central role in linking water stress to reproductive output. Under high cumulative water stress, reduced shoot extension is therefore expected to limit the number of flowering nodes and, in turn, lower flowering probability (Guédon et al., 2001; Bowers, 2006). Similar patterns have been reported in other perennial species, where insufficient shoot development can prevent flowering regardless of otherwise favorable conditions (Sola and Ehrlén, 2007; Capelli et al., 2016).

Reduced flowering at the individual level may scale up to demographic consequences in small and spatially restricted populations. Across the distribution range of *M. coquimbensis*, approximately 35% of adult individuals during and after the study period did not flower for at least four consecutive years (unpublished data), effectively reducing the number of reproductive plants. A high proportion of non-flowering individuals could increase spatial and temporal isolation among reproductive plants, potentially intensifying genetic and demographic risks, particularly in a species characterized by small population sizes, a restricted geographic range, and endangered status (Hoban et al., 2020).

Understanding dryland ecosystems increasingly requires linking plant physiological processes to population-level dynamics as aridity intensifies under climate change (Salazar et al., 2024). Our study shows that water limitation is not experienced uniformly across plants within populations but is filtered through fine-scale soil heterogeneity and plant physiological responses, generating persistent individual differences in cumulative water stress. By integrating short-term physiological responses across the growing season, cumulative water stress provides a useful framework for examining how small-scale environmental variability translates into contrasting growth trajectories and flowering probabilities among individuals. The divergent responses of growth and reproduction to accumulated water stress suggest a pathway through which physiological performance may influence demographic processes in dryland plant populations. Together, these findings indicate that

accounting for individual-level physiological variation may be important for understanding population structure and persistence in dryland plant species under increasing aridity.

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Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Author contributions

AL: Conceptualization, Formal analysis, Validation, Data curation, Project administration, Methodology, Writing – review & editing, Investigation, Writing – original draft, Visualization, Funding acquisition. DC: Investigation, Writing – review & editing, Methodology. PG-G: Methodology, Investigation, Writing – review & editing. RR: Writing – review & editing. FS: Supervision, Resources, Writing – review & editing.

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Conflict of interest

The author(s) declared that this work was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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The author(s) declared that generative AI was used in the creation of this manuscript. Generative AI was used exclusively for language proofreading and editing to improve grammar, and readability. The authors reviewed and approved all revisions and take full responsibility for the content of the manuscript.

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Supplementary material

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fevo.2026.1789799/full#supplementary-material>

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