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Interactions among intrinsic water-use efficiency and climate influence growth and flowering in a common desert shrub

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Abstract

Plants make leaf-level trade-offs between photosynthetic carbon assimilation and water loss, and the optimal balance between the two is dependent, in part, on water availability. "Conservative" water-use strategies, in which minimizing water loss is prioritized over assimilating carbon, tend to be favored in arid environments, while "aggressive" water-use strategies, in which carbon assimilation is prioritized over water conservation, are often favored in mesic environments. When derived from foliar carbon isotope ratios, intrinsic water-use efficiency (iWUE) serves as a seasonally integrated indicator of the balance of carbon assimilation to water loss at the leaf level. Here, we used a multi-decadal record of annual iWUE, growth, and flowering from a single population of *Encelia farinosa* in the Mojave Desert to evaluate the effect of iWUE on plant performance across interannual fluctuations in water availability. We identified substantial variability in iWUE among individuals and found that iWUE interacted with water availability to significantly influence growth and flowering. However, the relationships between iWUE, water availability, and plant performance did not universally suggest that "conservative" water-use strategies were advantageous in dry years or that "aggressive" strategies were advantageous in wet years. iWUE was positively related to the odds of growth regardless of water availability and to the odds of flowering in dry years, but negatively related to growth rates in dry years. In addition, we found that leaf nitrogen content affected interannual plant performance and that an individual's iWUE plasticity in response to fluctuations in aridity was negatively related to early life drought survival and growth.

Keywords iWUE · Carbon isotopes · Plasticity · Leaf nitrogen · Mojave Desert

Introduction

Stomatal control constrains both the rate of water loss and the rate of photosynthesis, and therefore, leaves face a trade-off between greater carbon gain and reduced water loss. Plants tend to optimize stomatal opening to minimize the costs of transpiration while also maximizing photosynthesis (Medlyn et al. 2011; Prentice et al. 2014; Wolf et al. 2016; Sperry et al. 2017). The cost of water loss increases as water supply decreases, and therefore, in arid environments plants often prioritize water conservation over carbon gain to a greater degree than those in mesic environments (Schwinning and Ehleringer 2001; Sperry et al. 2017).

Intrinsic water-use efficiency (iWUE), the ratio of photosynthetic rate (A) to stomatal conductance (g_s, Farquhar et al. 1989; Ehleringer et al. 1993), captures the carbon–water trade-offs that occur at the leaf level and can be measured at several temporal scales. $\delta^{13}C$ values can be used as seasonally integrated indicators of iWUE, reflecting the balance of A to g_s across the time period in which the carbon was assimilated. iWUE has been conceptualized as one component of an aggressive-to-conservative spectrum of water-use strategies, in which "aggressive" water-use strategies are associated with low iWUE and prioritization of carbon gain, while "conservative" strategies are associated with high iWUE and prioritization of water conservation (Schwinning and Ehleringer 2001; Gebauer et al. 2002; Prentice et al. 2014; Goud et al. 2019; Dong et al. 2020). Widespread

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increases in iWUE associated with both rising atmospheric CO_2 concentrations and increasing water stress have been documented in many species and across biomes (Battipaglia et al. 2013; Keenan et al. 2013), and have generally been expected to increase productivity. However, several studies have found that CO_2-driven increases in iWUE did not result in increased growth (Peñuelas et al. 2011; Lévesque et al. 2014; van der Sleen et al. 2015), challenging assumptions of increased productivity. Across species, iWUE has been linked to growth rates and drought tolerance, although the directions of the relationships have been mixed (Schuster et al. 1992; Morán-López et al. 2014; Altieri et al. 2015).

Spatial distributions of iWUE and other components of water-use strategy often reflect variations in aridity, with the prevalence of conservative water-use strategies increasing jointly with aridity (Ehleringer and Cooper 1988; Comstock and Ehleringer 1992; Ares et al. 2000; Schwinning et al. 2002; Zheng and Shangguan 2007; Prentice et al. 2011). The tendency of iWUE to increase with increasing aridity runs parallel to the broad trend that slow or conservative resource-use strategies are often observed in ecosystems with low resource availability because resource conservation improves the odds of survival (Schwinning et al. 2005; Wright et al. 2004; Ordoñez et al. 2009; Reich 2014; Dong et al. 2020). Variability in optimal resource-use strategies can lead to diversity in traits across resource availability gradients and to convergence of traits within a population or biome where resource availability is uniform, and has often been evoked to explain species distribution, community composition, and plant performance across spatial gradients (Wright et al. 2001, 2005; Westoby and Wright 2006; Trugman et al. 2020).

Despite the many studies relating plant traits to performance outcomes across species and functional groups, the majority neglect to consider intraspecific variability in traits, which can be large (Sandquist and Ehleringer 1998; Anderegg 2015; Siefert et al. 2015; Funk et al. 2017). Studies that have examined intraspecific variability in water-use strategies have primarily focused on identification of local adaptation across spatial resource availability gradients (Rehfeldt et al. 2002; Savolainen et al. 2007; Benito-Garzón et al. 2011), or experimental assessment of annuals (Kenney et al. 2014; Lorts and Lasky 2020). Relationships between iWUE and the growth, reproduction, and survival outcomes of perennial individuals have been infrequently assessed (Ehleringer 1993; Donovan and Ehleringer 1994), and we are unaware of any in situ studies that considered the effects of variable water-use strategies on the performance of perennials across year-to-year fluctuations in water availability.

Here, we use a long-term record of plant growth, reproduction, survival, distribution, leaf N concentrations, and foliar $\delta^{13}C$ values from an undisturbed population of *Encelia farinosa* in the Mojave Desert to address the following question: does variability in iWUE between individuals, due to either genotypic variation or phenotypic plasticity, affect reproduction or growth across temporal fluctuations in resource availability? First, we identify the degree to which precipitation, vapor pressure deficit (VPD), and competition limit plant growth and flowering within the population. Next, we evaluate any growth or reproduction benefits associated with particular water-use strategies as water availability fluctuates from year to year, with the expectation that plants with high iWUE will outperform those with low iWUE under dry conditions and the opposite will occur under wet conditions. Finally, we explore the disadvantages and benefits associated with iWUE plasticity, expecting that plants with high plasticity will be able to both take advantage of wet conditions and survive drought conditions and therefore grow larger, survive longer, and reproduce more over their lifetimes.

Methods

Site descriptions, sample collection, and data collection

A near-monospecific stand of *E. farinosa,* located approximately 21 km southwest of Shoshone, CA and covering about 450 m^2 of a south-facing slope in Death Valley National Park was marked in 1981 for continuous annual monitoring (Ehleringer and Sandquist 2018). In the first survey year, all plants one year or older (as indicated by the presence of a woody basal stem) were tagged and their coordinates on an *X*, *Y* grid were recorded. Each year, new individuals were tagged and added to the record if they were a year old. Plants were not considered to be dead until they were entirely leafless for three consecutive years, at which point tags were removed and no further data were recorded. During annual surveys conducted in late March, we measured plant height and width at the widest and perpendicular widths, recorded any signs of flowering (including the presence of flowers, buds, or seed heads), and estimated leaf cover on a 1–4 scale (with values of 1 corresponding to leaf cover of 0–25% and values of 4 corresponding to leaf cover of 76–100%). *E. farinosa* shrubs have a hemispherical shape with leaf growth concentrated toward the ends of branches (Ehleringer and Sandquist 2018), so we calculated hemispherical surface area (HSA) as an indicator of total plant size. The plant radius used for the calculation of HSA was the mean of plant height, half of the width along the widest axis, and half of the width along the perpendicular axis. Additionally, 5–10 of the most recently produced, mature sun leaves were collected annually from each plant for carbon and nitrogen isotope analysis beginning in 1991. Leaves were not collected from plants that would be damaged by leaf collection, and not all plants had leaves in every year.

E. farinosa in this area lose their leaves each summer during the extended drought period and typically leaf out again in late fall. Several rounds of leaf turnover occur between initial leaf out and sampling, so foliar δ^{13}C values from the most recent leaves are likely to reflect only photosynthate assimilated in the current growing season rather than stored carbon. A total of 1503 unique plants were surveyed over the study period for a total of 9150 sets of annual observations over 38 years.

C isotope and N content analysis

Leaf samples were dried upon returning from the field and stored in a cool, dark, and dry place until analysis was conducted. A total of 2210 samples from 630 plants in 26 years were selected for analysis, ground, and loaded into tin capsules for analysis of carbon and nitrogen isotope ratios and concentrations using a Carlo-Erba EA-1110 elemental analyzer coupled to a Finnigan Mat Delta + IRMS via a continuous flow interface (ThermoFinnigan Conflo III; Bremen, Germany). Laboratory reference materials were calibrated using international standards USGS40 ($\delta^{13}C = -26.24‰$) and USGS41 ($\delta^{13}C = 37.76‰$), and all results are reported in delta notation on the VPDB scale. Long-term measurement uncertainty for quality control materials was ± 0.2‰ for δ^{13}C, and ± 0.3% for N concentration.

Climate, CO_2 concentration, and $\delta^{13}CO_2$ data acquisition

Monthly climate data, including total precipitation and mean daily maximum VPD, were acquired for the grid cell containing Shoshone, CA from the PRISM Climate Group datasets (4 km resolution, http://www.prism.oregonstate.edu/, accessed 15-Jan-2020). Annual surveys were conducted in late March. Because we were interested in identifying interactive effects of climate and δ^{13}C values on growth and flowering, we restricted climate data to the November–March growing season preceding each survey.

We obtained data on the $\delta^{13}C_{atm}$ value (White et al. 2015) and concentration (Dlugokencky et al. 2019) of atmospheric CO_2 in Wendover, UT from NOAA's Earth System Research Laboratory Global Monitoring Division (ESRL). Although other NOAA ESRL sites have longer-term data sets, we used data from the Wendover site as it is similar to the study sites in terms of latitude, aridity, vegetation, and proximity to urbanized areas. Data on the δ^{13}C values of CO_2 were available for 1993–2014, and data on CO_2 concentrations were available for 1993–2018. Data from missing years were extrapolated using the linear relationships between year and $\delta^{13}CO_2$ ($r^2 = 0.965$, $y = -0.028597x + 49.031911$) and year and CO_2 concentration ($r^2 = 0.995$; $y = 2.091x - 3811$).

Calculation of c_i/c_a and iWUE

The ratio of the intracellular concentration of CO_2 (c_i) to the atmospheric concentration of CO_2 (c_a) of a leaf can be derived from the δ^{13}C value of the leaf and atmospheric CO_2, where a is the constant fractionation factor associated with CO_2 diffusion ($a = 4.4‰$) and b is the constant fractionation factor associated with net carboxylase discrimination ($b = 27‰$, Farquhar et al. 1982, 1989):

$$^{13}C_{\text{leaf}} = {}^{13}C_{\text{atm}} - a - (b - a)\left(\frac{c_i}{c_a}\right) \tag{1}$$

iWUE can be calculated from c_i and c_a as shown in Eq. 2 (Ehleringer et al. 1993), where 1.6 is the ratio of the diffusivities of CO_2 to that of water vapor in air.

$$\text{iWUE}_{\text{leaf}} = \frac{A}{g_s} = \frac{c_a\left(1 - \frac{c_i}{c_a}\right)}{1.6} \tag{2}$$

Data analysis

Because very young plants are not reproductively mature and can differ substantially from adults in their patterns of growth, we constrained analyses to plants over the age of 3 (with the exception of iWUE plasticity, discussed below). We selected two binary criteria to serve as annual indicators of plant performance: the presence or absence of flowers and growth, defined as an increase in hemispherical surface area (HSA) from the previous year. For plants that grew, the magnitude of growth (current HSA minus the previous HSA) and the rate of growth (growth divided by previous HSA) were used as additional indicators of plant performance. A decrease in plant HSA is referred to throughout as canopy dieback, which we consider to be a process distinct from growth.

All data analyses were conducted in R version 3.6.1 (R Core Team). At the population scale, we tested for the effects of total precipitation and the average daily maximum VPD on the proportion of the population that grew (beta regression; Cribari-Neto and Zeileis 2010), the average change in plant HSA from the previous year (linear regression, including both growth and dieback), the average growth rate of the population (linear regression), and the probability of flowering in a given year (logistic regression). We also tested the relationships between the 5-month March Standardized Precipitation Evaporation Index, a commonly used drought metric (Vicente-Serrano et al. 2010), and these population-scale growth and flowering variables using same methods. However, we found that it was a weaker predictor of plant growth and flowering than either VPD or precipitation and therefore did not use it for subsequent analyses (Table S1).

At the individual scale, multivariate logistic models were used to examine the impact of plant and environmental factors on the presence or absence of growth and flowering, and a multivariate linear model was used to understand drivers of the magnitude of growth. All full models included the following centered and scaled predictors: leaf cover, leaf nitrogen content by mass (N_{mass}), precipitation, VPD, and interactions between iWUE and VPD, iWUE and precipitation, and iWUE and N_{mass}. Additionally, the growth models included HSA from the previous year and the flowering model included HSA from the current year. Model selection was conducted by sequentially adding and removing variables to minimize the AIC value (function "step"). This model selection process automatically retained main effects for significant interaction terms, so we manually removed main effects that were not meaningful and did not improve model fit via stepwise elimination.

To further understand interactive effects of iWUE and water availability on plant growth and flowering, we grouped years into high, intermediate, and low levels of water availability corresponding to VPD and precipitation quartiles. Years were classified as having high water availability if VPD was within the first quartile (Q1) or precipitation was in the fourth quartile (Q4) of values over the study period, as intermediate if VPD or precipitation were in the second or third quartiles (Q2–Q3), and as low moisture availability if VPD was in the fourth quartile (Q4) or precipitation was in the first quartile (Q1). Within these climate bins, we tested for relationships between iWUE and growth (linear regression), for differences in iWUE values between plants that flowered and those that did not (*t* tests), and for relationships between N_{mass} and iWUE and c_i/c_a ratios (linear regressions). We omitted an analysis of plant survival from this manuscript because we analyzed relatively few leaf samples from plants that died within the following year (see Figure S1 for the available data).

iWUE plasticity, which we define as the slope of the linear relationship between iWUE and VPD (Lande 2009; Chevin et al. 2010), was quantified for 65 plants from the 1991 cohort for which δ^{13}C values were measured in every possible year. We chose to use plasticity to VPD instead of precipitation or an alternative climate variable because iWUE values were most closely correlated to VPD in this population (Driscoll et al. 2020), possibly because VPD directly influences stomatal opening, whereas precipitation is an imperfect proxy for soil moisture availability. Additionally, iWUE plasticity in response to VPD change is very closely correlated with plasticity in response to precipitation change (Figure S2, $r^2 = 0.89$, $P < 0.0001$). Thirty-seven of the 65 plants died in 1997 or 1998, following severe droughts, while the remaining 28 plants were still alive as of the 2019 survey. To enable comparison between the group of plants that survived and the group of plants that died, we first measured iWUE plasticity across the 1992 to 1998 period and analyzed relationships between iWUE plasticity and lifetime plant outcomes, including drought survival (Mann–Whitney *U* test), maximum HSA by 1998 (linear regression), and the number of years in which a plant flowered by 1998 (one-way ANOVA). For the group of plants that survived until 2019, we also analyzed the relationship between lifetime plasticity and maximum HSA (linear regression) and the number of years in which the plant flowered (one-way ANOVA).

Results

Moisture availability affects growth and flowering

Growth can be slow in arid regions, such as Death Valley. On average, only 55% of the adult population grew in any given year. The remaining plants either remained the same size or experienced a reduction in area associated with canopy dieback. Because water is the primary limiting factor in most arid ecosystems, we expected both the ability of plants to grow and the magnitude of plant growth to be related to precipitation (representing water supply) and VPD (representing atmospheric water demand). Growing season precipitation and VPD were moderately correlated over the study period ($r^2 = 0.66$, $P < 0.0001$).

Growing season VPD (Fig. 1a; $P < 0.0001$, pseudo-$r^2 = 0.34$) and precipitation (Fig. 1b; $P < 0.0001$, pseudo-$r^2 = 0.37$) were related to the proportion of plants that were able to grow in a given year, with more plants growing when water availability was higher. Similarly, the mean rate of change in plant surface area was related to VPD ($P = 0.0002$, $r^2 = 0.31$) and precipitation ($P < 0.0001$, $r^2 = 0.36$) if considering all plants, including those that experienced canopy dieback. When only plants that grew were considered, there was a weaker relationship between the mean growth rate and VPD (Fig. 1c; $P = 0.009$, $r^2 = 0.15$ for VPD) and precipitation (Fig. 1d; $P = 0.006$, $r^2 = 0.17$) than when dieback was included. Thus, in this population, moisture availability more strongly dictated whether or not plants were able to grow than how much they grew.

The proportion of plants that flowered in a given year was variable and skewed toward the extremes, with flowering rates below 5% in 14 of the 39 survey years and above 90% in 9 of the 39 years. Both growing season precipitation and VPD influenced the probability of flowering (multiple logistic regression, $P < 0.0001$, Tjur's $R^2 = 0.35$; see Table S2 for full statistics). The probability of flowering increased rapidly as VPD decreased from about 18 to 16 hPa (Fig. 2a) and as precipitation increased from about 40 to 100 mm (Fig. 2b), leveling off as moisture availability increased beyond those

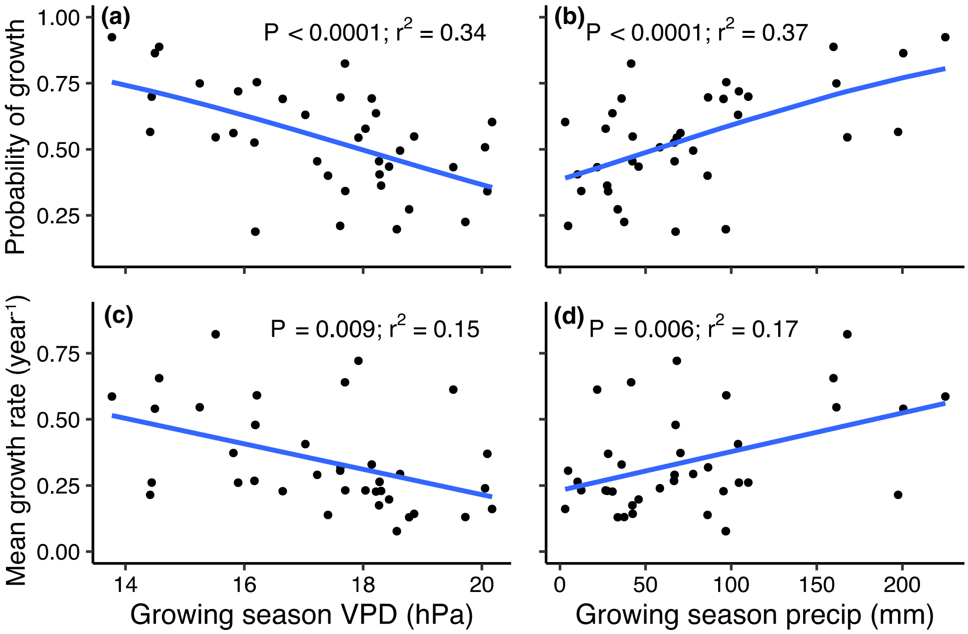


Fig. 1 The probability of growth and the mean growth rate among *E. farinosa* shrubs as a function of **a**, **c** growing season vapor pressure deficit (VPD) and **b**, **d** precipitation, respectively. Blue lines represent significant beta regressions (**a**, **b**) and linear regressions (**c**, **d**) (color figure online)

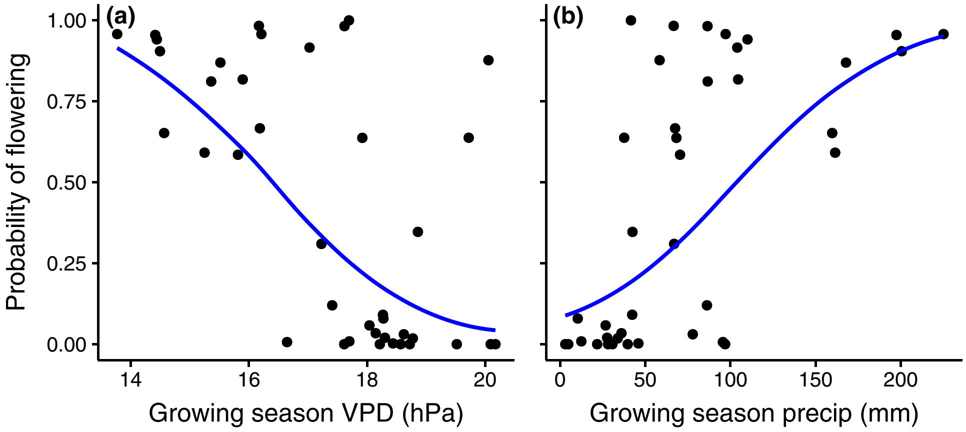


Fig. 2 The annual probability of *E. farinosa* flowering as a function of **a** growing season vapor pressure deficit (VPD; $P < 0.0001$, Tjur's $r^2 = 0.35$) and **b** growing season precipitation ($P < 0.0001$; Tjur's $r^2 = 0.27$). Blue lines represent the mean predicted probability of flowering based on single logistic models of flowering status by precipitation and VPD (color figure online)

values. The relationships between water supply, evaporative water demand, plant growth, and flowering confirm that water was a critical limiting input for the surveyed population of *E. farinosa*.

Relationship between competition and plant performance

Our previous experimental study demonstrated that competition affected growth among *E. farinosa* individuals where neighbors had been removed (Ehleringer 1984). However, in this undisturbed population the number of neighbors within 1.5 m and the distance to the nearest neighbor were insignificant predictors of growth rate ($P = 0.67$ and 0.24, respectively) after controlling for plant age and VPD. By these measures, competition-related limitations on growth were negligible, and therefore, we did not dwell further on plant density or distribution.

Impacts of iWUE on growth

iWUE varied widely between years in response to changes in climate and CO_2 concentration, with population mean values ranging from a low of 66 μmol mol^{-1} in a wet year (2005) to a high of 126 in a dry year (2014). Additionally, iWUE values varied from 40 to 145 μmol mol^{-1} between individuals, including large variability within each year not attributable to climate (Fig. 3). The average difference between the minimum and maximum iWUE value in the population within a given year was 40 μmol mol^{-1}. In order to evaluate the effects of these widely variable iWUE values on plant performance, we first fit a logistic model to identify variables that affected the likelihood that a plant

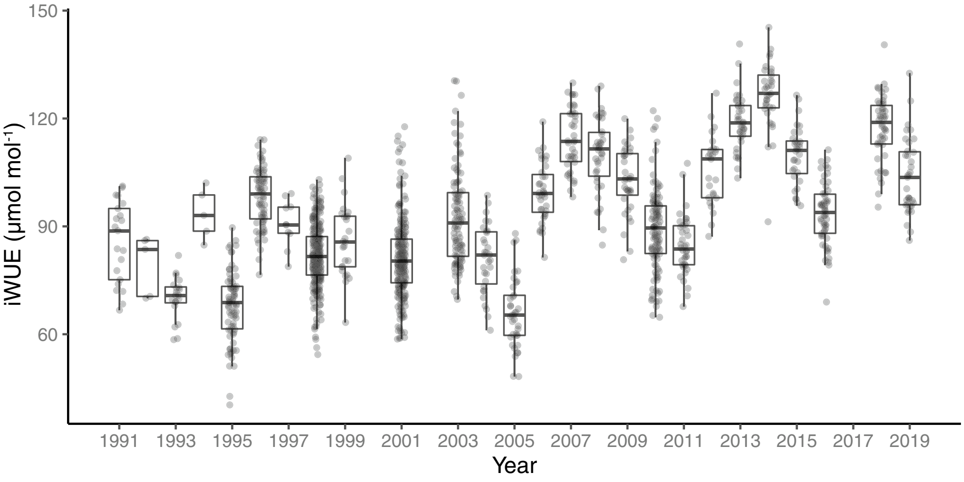


Fig. 3 The intrinsic water-use efficiency (iWUE) values of individual *E. farinosa* shrubs across the duration of the study. Data points represent all individual plants measured in each year. Boxes indicate the first quartile, median, and third quartile, and whiskers indicate Q1 and Q3 ± 1.5*IQR

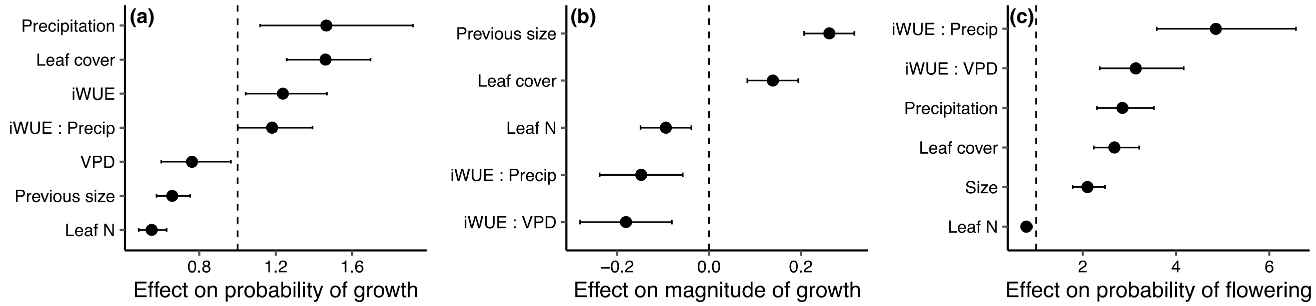


Fig. 4 The **a** odds ratios for variables in the optimized logistic model of growth, **b** standardized coefficients for variables in the optimized linear model of the magnitude of growth, and **c** odds ratios for variables in the optimized logistic model of flowering. Odds ratios represent the change in **a** the odds of growth or **c** the odds of flowering associated with a 1-standard deviation change in the predictor variable, and **b** standardized coefficients represent the change in the magnitude of growth associated with a 1-standard deviation change in the predictor variable. Dashed vertical lines represent no effect on the response variable, and whiskers represent 95% confidence intervals of each odds ratio or standardized coefficient

grew over the preceding year (Fig. 4a; Tjur's $R^2 = 0.19$, $n = 1466$). The optimized model showed that greater leaf cover ($P < 0.0001$), higher precipitation ($P = 0.0056$), higher iWUE ($P = 0.015$), lower VPD ($P = 0.024$), lower N_{mass} ($P < 0.0001$), and smaller plant size in the previous season ($P < 0.0001$) were associated with increased odds of growth. Additionally, an interaction between iWUE and precipitation significantly influenced the odds of growth ($P = 0.048$).

Different variables were associated with the magnitude of a plant's growth (Fig. 4b; $R^2 = 0.18$, $n = 939$) than with the likelihood of a plant growing. Plant size in the previous year ($P < 0.0001$) and leaf cover ($P < 0.0001$) were positively related to growth, and N_{mass} was negatively related to growth ($P = 0.00090$). Interactions between iWUE and VPD ($P = 0.00040$) and between iWUE and precipitation ($P = 0.0014$) were also significantly related to growth, indicating that the effect of iWUE on growth was dependent on water availability. Grouping data by VPD and precipitation quantiles provided some understanding of how the relationship between iWUE and growth rate fluctuated depending on moisture availability. Notably, years were not always classified in corresponding VPD and precipitation quartiles (Table S3). Rather, some years with low precipitation (Q1) did not have high VPD (Q4), and some years with low VPD (Q1) did not have high precipitation (Q4). In years with high (VPD in Q1 or precipitation in Q4) or average (VPD or precipitation in Q2–Q3) moisture availability, growth rates were not significantly correlated with iWUE ($P > 0.05$ and $r^2 < 0.01$ for all; see Table S4 for full results). In years with low moisture availability (VPD in Q4 or precipitation in Q1), iWUE was negatively, but weakly, related to growth rates ($P < 0.01$ and $r^2 = 0.07$ when grouped by either VPD or precipitation).

Impacts of iWUE on flowering

Both climate and plant characteristics influenced the odds of flowering (Fig. 4c; Tjur's $R^2 = 0.37$, $n = 1466$). Plant size ($P < 0.0001$), leaf cover ($P < 0.0001$), and precipitation ($P < 0.0001$) were positively associated with the odds of flowering. N_{mass} ($P = 0.0010$) was negatively associated with flowering, possibly because flowering plants allocated available N away from leaves to reproductive structures. Additionally, interactions between iWUE and VPD ($P < 0.0001$) and iWUE and precipitation ($P < 0.0001$) significantly affected the odds of flowering, indicating that iWUE had different effects on flowering status depending on water availability.

To better understand the nature and direction of the interactions between iWUE and water availability, we examined the relationship between iWUE and flowering after grouping data by VPD (Table S5). During years in which water availability was high (VPD in Q1), there was no significant difference between the iWUE of plants that flowered and those that did not flower ($P = 0.90$). During years in which water availability was average (VPD in Q2 or Q3), the iWUE of plants that flowered was significantly lower than the iWUE of plants that did not flower ($P < 0.001$). This pattern reversed in dry years (VPD in Q4), during which the iWUE of plants that flowered was significantly higher than plants that did not flower ($P < 0.001$).

Relationships between iWUE and leaf nitrogen content

Population mean N_{mass} fluctuated annually, ranging from 1.4 to 4.4% across the study period, but was not significantly correlated with either growing season precipitation or VPD ($P > 0.35$ for both). There was also large variation in N_{mass} among individuals, with the range of values spanning up to 4.8% between plants. N_{mass} and c_i/c_a were negatively related, but the strength of the relationship varied with water availability. The relationship between N_{mass} and c_i/c_a ratio was strongest in years with low VPD (Fig. 5a) and weaker in years with typical VPD (Fig. 5b) and high VPD (Fig. 5c). As a result of the relationship between N_{mass} and c_i/c_a, there was a positive relationship between N_{mass} and iWUE in wet years ($P < 0.0001$, $r^2 = 0.14$), that was negligible in years with average ($P = 0.10$, $r^2 < 0.01$) and low ($P = 0.004$, $r^2 = 0.028$) water availability. The relationships between N_{mass}, c_i/c_a, and iWUE appeared to be driven by between-plant differences rather than interannual changes in individuals, as there was not a consistent relationship between iWUE and N_{mass} for individual plants.

iWUE plasticity and its implications for plant performance

The degree to which the iWUE of individuals responded to fluctuations in VPD was variable, and values of iWUE plasticity ranged from 1.6 to 9.5 μmol mol^{-1} hPa^{-1} among the 65 plants from the 1991 cohort for which iWUE plasticity was measured over the 1992–1998 time period. Plasticity values were positive for all plants, indicating that water-use efficiency increased as expected with increasing water stress.

The average plasticity value of plants that died following the 1996–1997 droughts (6.8 μmol mol^{-1} hPa^{-1}) was significantly higher than that of plants that survived the droughts (5.0 μmol mol^{-1} hPa^{-1}, Fig. 6a, Mann–Whitney *U* test, $P < 0.0001$). Plasticity values of plants that died during drought also spanned a wider range than values for plants that survived (1.6 to 9.5 vs 2.0 to 7.5 μmol mol^{-1} hPa^{-1}). iWUE plasticity between 1992 and 1998 was negatively related to maximum plant size (Fig. 6b; linear regression, $P = 0.0040$, $r^2 = 0.11$), but was not significantly related to the number of flowering events ($P = 0.093$). Plasticity explained a small but significant portion of the variability in plant growth and drought survival over this period, and plants with very high plasticity tended to die during the drought period and attain smaller maximum sizes.

Among plants that were still alive in 2019, we controlled for the effect of rising CO$_2$ concentrations on iWUE to calculate iWUE plasticity to VPD. iWUE plasticity over the 1992–2019 time period was comparable to the 1992 to 1998 time period, with an average of 6.1 μmol mol^{-1} hPa^{-1}, and a range of 4.8 to 8.1. For these long-lived plants, plasticity over the plant's lifetime was not significantly related to maximum plant size ($P = 0.80$) nor the number of flowering events ($P = 0.68$).

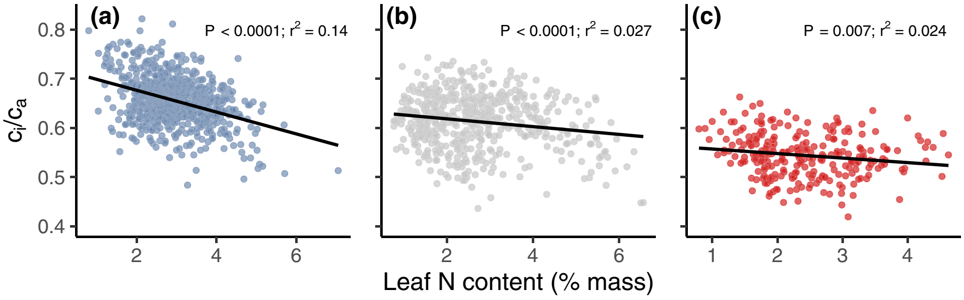
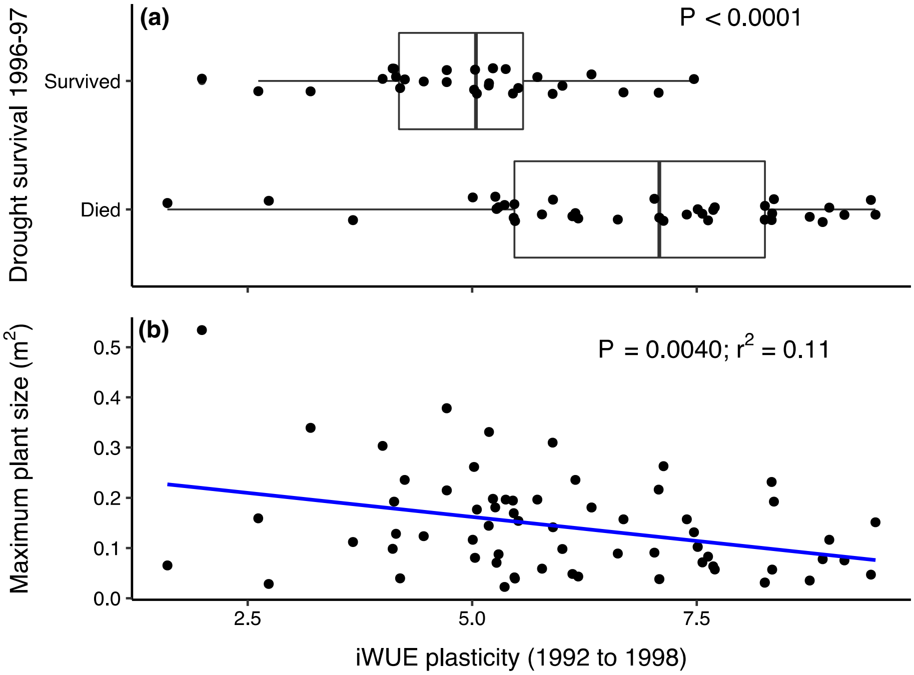


Fig. 5 The relationship between an individual's leaf nitrogen content by mass (N_{mass}) and its c_i/c_a ratio, grouped by **a** low growing season vapor pressure deficit (VPD in Q1), **b** intermediate growing season VPD (Q2–Q3), and **c** high growing season VPD (Q4)

Fig. 6 Relationships between the intrinsic water-use efficiency (iWUE) plasticity of *E. farinosa* over the 1992–1998 time period and **a** survival through the 1996–1997 droughts and **b** maximum plant size. On-plot statistics show results of **a** a Mann–Whitney *U* test for differences between the iWUE plasticity of plants that died and those that survived, and **b** the linear regression of maximum plant size by iWUE plasticity (blue line) (color figure online)



Discussion

Over the past three decades, a 53% increase in average iWUE has been observed within this *E. farinosa* population in response to rising VPD and CO_2 concentrations (Driscoll et al. 2020). This population average increase in iWUE is approximately within the between-plant variability in any given year, underscoring the importance of considering intraspecific variability in water-use strategy. Precipitation and VPD strongly drove growth and reproduction among *E. farinosa* in Death Valley, and the effects of iWUE on plant performance tended to be mediated by interannual weather conditions. Interactions between iWUE and precipitation affected the odds of new growth, and interactions between iWUE and both VPD and precipitation affected the magnitude of growth and the odds of flowering (after controlling for other plant and climate variables). These significant interactions are consistent with the suggestion that diverse water-use strategies persist within the population because different strategies differentially improve plant performance under contrasting moisture conditions (Ehleringer 1993).

Assuming that differences in iWUE were driven primarily by changes in the degree of stomatal limitation to photosynthesis (Farquhar and Sharkey 1982; Comstock and Ehleringer 1984), we expected "aggressive" plants with lower iWUE values to grow more rapidly under wet conditions, but then to show limited-to-no growth under dry conditions. In contrast, "conservative" plants with higher iWUE values would grow more slowly and perhaps more consistently. In some cases, these contrasting patterns were supported by the data: higher iWUE values were associated with increased odds of growth regardless of water availability, and the iWUE of flowering plants was higher than those that did not flower in dry years. In these cases, mapping iWUE variability onto an aggressive-to-conservative spectrum of water-use strategies improved our understanding of the growth and reproductive outcomes of individuals. Other studies have documented notable differences in plant responses to atmospheric water demand versus water supply (Sulman et al. 2016; Novick et al. 2016), and, at this site, the temporal trend in VPD is stronger than the temporal trend in precipitation (Driscoll et al. 2020). We found that the effects of VPD were generally consistent with the effects of precipitation, with the exceptions that VPD was not a significant independent predictor in the multivariate model of flowering probability and that VPD did not interact with iWUE to significantly influence the probability of growth.

Not all relationships between plant performance and iWUE were intuitive. For instance, there was a negative relationship between iWUE and growth in dry years, and no relationship between iWUE and growth in wet years. Additionally, "aggressive" plants did not flower more frequently than "conservative" plants in wet years. These exceptions, and the relatively low R^2 values of the generalized linear models, could be explained in part by a lack of precision in growth measurements, which only reflected changes in surface area and not, for example, changes in stem width or density. Likewise, our binary indicator of flowering status did not capture the intensity of flowering or the viability of seeds. Trade-offs among resource allocation to flowering, growth, and survival can vary between plants and over time (Villellas and García 2018; Lauder et al. 2019), and changes in allocation may obscure trends if, for example, plants prioritized carbon allocation toward root growth rather than woody growth in dry years (Brunner et al. 2015). Additionally, relatively small differences in rooting distribution, location, or soil quality could create meaningful differences in access to moisture or nutrients. These sources of heterogeneity in combination with the stochasticity inherent in *E. farinosa* growth and flowering patterns may obscure the effects of iWUE, especially in very dry years. A more holistic measure of total carbon assimilation (including above and belowground biomass) and total transpiration at the whole-plant scale may reveal clearer relationships between water-use strategy and productivity than can be captured by the leaf-level trade-offs reflected by iWUE.

Leaf N content, which is commonly used as a proxy for potential photosynthetic carboxylation capacity (Field and Mooney 1986; Evans 1989, but see also Croft et al. 2017), is usually considered a species-level trait with limited intraspecific variability. However, we identified substantial variability in N_{mass} among individuals that was related to both plant performance and iWUE. N_{mass} was negatively related to the odds and magnitude of growth after controlling for other variables, counter to an expected positive coordination between N_{mass}, photosynthetic rate, and growth rate (Field and Mooney 1986; Wright et al. 2004; Funk et al. 2017). In addition to the direct relationship between N_{mass} and plant growth, there was also a positive relationship between iWUE and N_{mass} in wet years. Increased leaf N content has been identified as a drought-tolerance strategy as it allows for an increased photosynthetic capacity to draw down internal CO_2 concentrations, possibly resulting in an equivalent photosynthetic rate at lower c_i/c_a values (Wright et al. 2001, 2005; Prentice et al. 2014). Across populations and species, leaf N concentrations tend to increase as aridity increases and covary with iWUE (Sparks and Ehleringer 1997; Prentice et al. 2011). Here, we found that increased N_{mass} was associated with higher iWUE in wet years even when comparing individuals within a single population. Notably, this relationship weakened in drier years. Despite significant relationships between N_{mass} and iWUE, the two variables did not interact to affect plant performance.

Plants are known to exhibit plasticity in iWUE in response to a number of environmental triggers (Heschel et al. 2004), and trait plasticity can be heritable (Kleunen and Fischer 2005; Lande 2009). Several studies have noted that trait plasticity could confer both benefits, as it allows for rapid adaptation to current conditions, and costs, as frequently switching strategies could reduce effectiveness (Chevin et al. 2010; Nicotra et al. 2010; Liancourt et al. 2015). Although several studies have documented shifts in iWUE between juveniles and adults (Donovan and Ehleringer 1992; Sandquist et al. 1993), interannual iWUE plasticity has been infrequently studied in adult plants. *E. farinosa* exhibited substantial iWUE plasticity in response to interannual variations in water stress, with the average plasticity of long-lived individuals (6.1 µmol mol^{-1} hPa^{-1}) corresponding to a 39 µmol mol^{-1} span of iWUE values over the plant's lifespan. iWUE plasticity could either be adaptive, resulting from active optimization of rates of photosynthesis and stomatal conductance to current conditions, or non-adaptive, resulting from a passive response to varying water limitation. High early life iWUE plasticity was associated with increased drought mortality and small maximum size. In contrast, iWUE plasticity was not significantly correlated with either lifetime growth or flowering outcomes among long-lived plants, possibly because only plants with plasticity values within an optimal range achieved old age. The presence and variability of iWUE plasticity suggest that the iWUE values of individuals were not strictly fixed and that some plants adjusted between "conservative" and "aggressive" water-use strategies from year to year.

A better understanding of individual-level relationships between iWUE and plant performance may help us anticipate the consequences of widespread iWUE increases on population-scale productivity. Higher iWUE values appeared to offer minor performance benefits, including increased odds of growth under all conditions and slightly increased odds of flowering under particularly dry conditions, but we also observed a negative relationship between iWUE and the magnitude of plant growth in dry years. Overall, these results do not provide strong support for the suggestion that increasing iWUE values will confer large growth or reproductive benefits under increasingly arid conditions. While consideration of intraspecific trait variability in arid land plants has been largely neglected, we demonstrated here that there was large variability in iWUE, iWUE plasticity, and leaf N content within a single population of *E. farinosa*, and that this variability meaningfully impacted plant growth and reproduction.

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Author contribution statement JRE conceived, designed, and conducted the study, AWD and NQB analyzed the data, AWD wrote the initial draft of the manuscript, and all authors contributed to subsequent versions.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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