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Intrinsic water-use efficiency influences establishment in *Encelia farinosa*

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Abstract

We describe establishment of *Encelia farinosa*, a drought-deciduous shrub common to the Mojave and Sonoran Deserts, based on annual observations of two populations between 1980 and 2020. Only 11 establishment events of 50 + yearlings (0.02–0.03 individuals m^{-2}) occurred during this monitoring period; in 68% of the years fewer than 10 yearlings were established. Yearling survival to adulthood (age 4) ranged from 88 to 5% and was significantly related to cumulative precipitation. Juvenile survival rates were lowest during the current megadrought period. We calculated intrinsic water-use efficiency (iWUE) and observed the widest variations in iWUE values among the youngest plants. Among juveniles, surviving yearlings with the lowest iWUE values exhibited upward ontogenetic shifts in iWUE values, whereas those yearlings with the highest initial iWUE values exhibited little if any change. Juvenile size, higher iWUE values, and greater likelihood of surviving were all positively related with each other over the past several decades. Furthermore, iWUE and photosynthetic capacity were positively related to each other, providing a mechanistic explanation for why increased iWUE values among juveniles could lead to greater survival rates and to larger plants under water-deficit conditions. We posit that there is bi-directional selection for genotypic variations in iWUE values among *E. farinosa* and that this variation is selected for because of inter-annual environmental heterogeneity in precipitation and VPD associated with both high- and low-frequency climate cycles. Extreme drought cycles may favor plants with higher iWUE values, whereas more mesic periods may allow for greater persistence of lower iWUE genotypes.

Keywords Intrinsic water-use efficiency · Arid land dynamics · Drought · Juvenile establishment · Carbon isotope ratio · Photosynthesis

Introduction

High water deficits in arid lands pose challenges to plant water balance and to the persistence and survival of perennial plant taxa (Schulze et al. 1987). As stomata open to allow CO_2 uptake for photosynthetic carbon gain, water is simultaneously lost through stomata as transpiration. Schwinning and Ehleringer (2001) and Schwinning et al. (2004) modeled these tradeoffs in arid land perennial plants and concluded that reductions in water loss relative to carbon gain would be favored for long-term persistence. We approach this topic through intrinsic water-use efficiency (iWUE), defined as the ratio of carbon assimilation via photosynthesis (A) to leaf conductance (g) and thus a direct measure of how much photosynthetic CO_2 uptake has occurred per unit water or CO_2 movement through stomata (Ehleringer et al. 1993; Farquhar et al. 1989). Increasing iWUE values are often associated with partial stomatal closure or plants under water stress (Bowling et al. 2008; Cernusak et al. 2013; Farquhar et al. 1989). On the other hand, longer-lived plants in the desert exhibit higher iWUE values than do shorter-lived species (Ehleringer and Cooper 1988; Schuster et al. 1992b).

Exploring iWUE concepts further, photosynthesis can be viewed as a two-step process—CO_2 is consumed during photosynthetic carbon reduction while at the same time open

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stomata allow the inward diffusion of CO_2 from the atmosphere (c_a). For C_3 plants, Farquhar and Sharkey (1982) pioneered our concepts of this leaf-level relationship in terms of CO_2 "demand" and "supply" functions, with the intercellular CO_2 (c_i) levels indicating the balance between these CO_2 demand and supply processes. The term c_i/c_a describes this balance between CO_2 demand and supply functions across all atmospheric CO_2 levels and is directly proportional to iWUE which is measurable through $\delta^{13}C$ analyses (Cernusak et al. 2013; Ehleringer et al. 1993; Farquhar et al. 1982, 1989).

It can be argued that the c_i/c_a ratio is a response parameter rather than exerting top-down control, but this need not be the case. Previous studies have shown that the c_i/c_a ratio is influenced by both a genetic component and environmental conditions (e.g., Ehleringer and Cerling 1995; Ehleringer et al. 1993; Farquhar et al. 1989; Voelker et al. 2016). While much of the literature has focused on c_i/c_a ratio plasticity in response to environmental conditions (e.g., Bowling et al. 2008; Cernusak et al. 2013), genetic differences among annual crops also demonstrate large variations in c_i/c_a ratios vis-à-vis $\delta^{13}C$ values, with ranking differences among genotypes maintained over time (e.g., Condon et al. 1990; Hall et al. 1993; White et al. 1990; Zacharisen et al. 1999). Such a top-down constraint could impose adjustments to carbon and water relations necessary to achieve a particular c_i/c_a ratio. Similarly, large and heritable variations in $\delta^{13}C$ (iWUE) values at the population level have been described in perennial arid land plant species (Donovan and Ehleringer 1994c; Schuster et al. 1992a, b, 1994). What is less clear is the basis for the relative variations in c_i/c_a ratios among juveniles and adults in arid land plant species.

Driscoll et al. (2021a) evaluated interactions between climate, growth, and iWUE in the drought-deciduous shrub *Encelia farinosa*, common to the Mojave and Sonoran Deserts. That study was based on annual, long-term surveys of population size/structure and ecophysiological characteristics on individual shrubs from two populations (Driscoll et al. 2020; Ehleringer and Sandquist 2018). Driscoll et al. (2021a) concluded that there was significant interannual plasticity in iWUE values of adult plants at both the individual and population levels, as would be expected between 'wet' and 'dry' years (Bowling et al. 2008; Cernusak et al. 2013; Farquhar et al. 1989). Driscoll et al. (2021a) furthermore concluded that the probability of interannual plant growth was positively correlated with higher precipitation and lower VPD values (as would be expected), but also to higher iWUE (perhaps unexpected). Yet these data also revealed that iWUE had limited impact on the growth rates of neighboring *Encelia* in natural stands, even if they were likely competing for water (Ehleringer 1984, 1993).

iWUE may have other impacts on adult arid land plants. Fonteyn and Mahall (1978; 1981) and Fowler (1986) have shown that perennial shrubs compete for water on a regular basis (clumped distribution) or may have competed in the past (regular distribution). In this regard, *E. farinosa* populations exhibit clumped distributions and proximity to neighbors also influences the likelihood of growth limitation in *E. farinosa* associated with competition for water (Ehleringer 1984). Recently, Bitter and Ehleringer (2021) showed that in near monospecific stands of *E. farinosa* distance to the nearest neighbor was a key parameter associated with increased adult shrub mortality. Related to this, Ehleringer (1993) discovered that adult shrubs with higher iWUE values were more likely to survive an extended multi-year drought event. Whether iWUE itself is the critical parameter for drought survival is unknown, as it could be that other parameters correlated with iWUE are the relevant parameters contributing to drought survival. Nevertheless, iWUE values and interplant distances among adult plants are indicative of shrubs more likely to die or persist through extended drought events.

Although some *E. farinosa* shrubs may live for more than 50 years, the majority of the individuals die within a decade or less (Bowers et al. 2004; Bowers 2005; Ehleringer and Sandquist 2018; Goldberg and Turner 1986; Shreve and Hinckley 1937). Additionally, rates of establishment can be low. At two long-term observation plots in the Mojave Desert, few of the germinating *E. farinosa* survived from seedling to adult (defined as age four) (Bitter and Ehleringer 2021; Ehleringer and Sandquist 2018). Bitter and Ehleringer (2021) discovered that yearling plant size and leaf cover were the strongest predictors of the likelihood that an individual yearling would survive to adulthood, but provided no mechanistic basis for this pattern.

E. farinosa seeds are wind dispersed and tend to germinate in open spaces away from adult *E. farinosa*, although seedlings do germinate under other species, including *Larrea tridentata*. This spatially dispersed germination pattern likely arises because of known allelopathic effects influencing either seed germination or seedling root elongation rates under existing *Encelia* shrubs (Gray and Bonner 1947, 1948; Wright et al. 2013). Thus, emerging seedlings tend to find themselves in open, harsher microhabitats, where plant–environment interactions (e.g., soil moisture deficit, high temperatures, and VPD) are likely to be more significant driving factors affecting seedling establishment. This contrasts with plant-plant interactions among adult *E. farinosa*, where plants might be competing for soil moisture or space (Ehleringer 1993).

While most plant studies focus on variations in iWUE among adult plants (shrubs or trees) or variations within a single individual over time (such as tree rings), there is limited information on iWUE of young perennials that have not yet matured to become adult plants. In this study, we explore relationships between iWUE, growth, and survival of juvenile *E. farinosa*. We examine three hypotheses evaluating relationships between iWUE and growth, with implications for the survival of juvenile *E. farinosa*. This study complements earlier studies on growth and survival of adult *E. farinosa* (Bitter and Ehleringer 2021; Driscoll et al. 2021a; Ehleringer and Sandquist 2018) and seeks a more mechanistic explanation for the Bitter and Ehleringer (2021) observation that yearling plant size and leaf cover were the strongest predictors of the likelihood that an individual juvenile would survive for another three years to achieve adulthood. *Hypothesis 1*: Survival rates of juveniles will be proportional to cumulative precipitation over a multi-year period. *Hypothesis 2*: Differences in iWUE values will occur among juveniles and iWUE values will be positively correlated with plant growth rates. *Hypothesis 3:* Juveniles with lower iWUE values will experience higher mortality rates than juveniles with higher iWUE values.

Materials and methods

Site descriptions, sample collection, and data collection

Two near-monospecific stand of *E. farinosa* were used in this study (Driscoll et al. 2020; Ehleringer and Sandquist 2018). The first population, hereafter referred to as PF1, is located approximately 21 km southwest of Shoshone, CA. PF1 covers about 480 m^2 of a south-facing slope in Death Valley National Park and was established in 1981 for continuous annual monitoring. The second population, hereafter referred to as PF2, is located approximately 8 km southwest of Oatman, AZ. PF2 covers 315 m^2 on a south-facing slope and was established in 1982 for continuous annual monitoring. During annual surveys conducted in March, all *E. farinosa* seedlings on each plot were counted, but not tagged. Yearlings are defined as seedlings that have persisted for an entire year and were distinguishable from seedlings on the basis of a woody stem in yearlings that is absent in seedlings. In each year, all yearling plants were identified, tagged, and their spatial locations recorded on an X–Y grid. In each year, we measured plant height and width at the widest and perpendicular widths on all tagged plants, recorded any signs of flowering (including the presence of flowers, buds, or seed heads), and visually estimated leaf cover on a 1–4 scale (with values of 1 corresponding to leaf cover of 0–25% and values of four corresponding to leaf cover of 76–100%) (Ehleringer and Sandquist 2018). *E. farinosa* shrubs exhibit a well-defined hemispherical shape with leaf growth concentrated towards the ends of branches (Ehleringer and Sandquist 2018), allowing us to calculate a projected surface area (SA) as an indicator of total plant size (cm^2). The dimensions used for the calculation of SA were the width along the widest axis and 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. *E. farinosa* shrubs are drought deciduous and may lose most of their leaves each summer during the extended dry period and typically leaf out again with late fall rains. Within the Mojave Desert, monsoonal rains are uncommon. Leaf production is continuous between initial fall leaf out and late spring sampling. Consequently, foliar $\delta^{13}C$ values from the most recent leaves sampled in March were likely to reflect only photosynthate assimilated in the current growing season rather than from previously stored carbon.

C isotope and N content analysis

Leaf samples were dried upon returning from the field and stored in a cool, dark, dry place until analysis was conducted. Not all individual plant collections were analyzed for carbon isotope ratios, because of cost constraints. In most years, a significant but random portion of the population was analyzed and in some years an effort was made to analyze all available leaf material. In hindsight and with an unlimited analytical budget, all leaf samples would have been analyzed. For those samples analyzed, leaf samples were ground and loaded into tin capsules for analysis of leaf carbon isotope ratios ($\delta^{13}C_{leaf}$, ‰) and leaf nitrogen concentrations (N, %) 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 $\delta^{13}C$, and ± 0.3% for N concentration.

Climate

Monthly climate data, including the Palmer Drought Severity Index (PDSI) and total precipitation, were acquired for the grid cell containing Shoshone, CA for the PF1 site and the grid cell containing the PF2 site from the PRISM Climate Group datasets (4-km resolution, http://www.prism.oregonstate.edu, accessed 15-May-2021). Annual surveys were conducted in late March because we were interested in identifying interactive effects of climate; annual precipitation estimates were for the cumulative 12-month period prior to our vegetation sampling.

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 $\delta^{13}C$ 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):

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

By re-arrangement, the c_i/c_a ratio can be calculated from c_i, c_a, $\delta^{13}C_{leaf}$, and $\delta^{13}C_{atm}$ values 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. To calculate iWUE (μmol mol^{-1}) from c_i/c_a values, 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 and show similar trends, we used data from the Wendover site since it is closer to the study sites in terms of latitude, aridity, vegetation, and proximity to urbanized areas. The trend lines were extrapolated using the linear relationships between year and $\delta^{13}CO_2$ ($r^2 = 0.965$, $y = -0.0286x + 49.03$) and year and CO_2 concentration ($r^2 = 0.995$; $y = 2.091x - 811$).

$$iWUE = \frac{A}{g_s} = \frac{c_a\left(1 - \frac{c_i}{c_a}\right)}{1.6} \quad (2)$$

Results

Climate trends

During the 41 years of observations, there has been a transition from multi-year cycling between "wet" and "dry" periods to a protracted period of "dry" years (referred to in the literature as a "megadrought"; Williams et al. (2020)). Annual precipitation has been below the long-term average since 2001 with the exceptions of 2005 and 2017 (Supplemental Information Figure S1). Annual precipitation values at PF1 and PF2 averaged 135 mm and 189 mm, respectively, between 1980 and 1999. However, since 2000 with the commencement of the megadrought, average precipitation at PF1 and PF2 has decreased to 95 mm and 144 mm, respectively. Focusing only on the 5-month winter/spring growing period instead of an annual basis did not change the trend, with spring-time precipitation at both PF1 and PF2 decreasing by 32% over the megadrought period. Moreover, the fraction of rainfall that occurred during the winter-spring has not changed since the commencement of the megadrought.

Consistent with the decline in precipitation, long-term drought severity has increased over the past four decades at these sites. Since the *Encelia* surveys began in 1980, summertime Palmer Drought Severity Index (PDSI) values (defined here as June-Sep.) reveal a long-term trend of decreasing values in these two Mojave Desert sites (Fig. 1). We chose to plot the rolling 3-year average instead of monthly or annual values in order to both highlight the trend, but also because plant survival may depend on longer-term drought conditions rather than the drought severity in any given month. In contrast to the earlier wet and dry cycles associated with El Niño Southern Oscillation (ENSO), the megadrought of the past two decades appears to be associated with a shift away from cyclic positive-to-negative PDSI values to sustained negative values.

Plot-scale germination and yearling establishment patterns

Germination rates of *E. farinosa* seeds varied from year to year at both Mojave Desert locations. Over the 41 years of annual surveys, a total of 41,405 and 41,636 seedlings have been observed at PF1 and PF2, respectively. Fall/winter germination was episodic and variable, ranging from 0–9670 seedlings per year, but not correlated with the amount of precipitation (Ehleringer and Sandquist 2018). Unfortunately, we have no estimate of the soil seed bank or of its dynamics over time. So, the extent to which environmental parameters versus seed bank constraints influenced the number of seedlings observed remains unresolved. In addition to sporadic germination numbers of *E. farinosa* seeds from year to year, establishment of seedlings as yearlings was low at both Mojave Desert locations, averaging 3.25% and 2.43% over

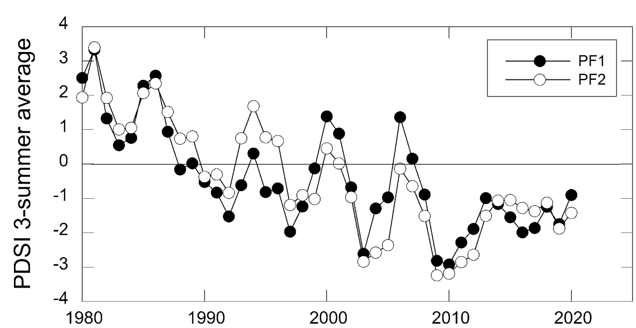

Fig. 1 Three-year running averages of the Palmer Drought Severity Index during the summer months for the *Encelia farinosa* population PF1 site (closed circles) in the southern portion of Death Valley National Park, California, and population PF2 (open circles) south of Oatman, Arizona

the entire survey period for PF1 and PF2, respectively. Over the four-decade period, 68% of the time (28 of 41 years) fewer than ten seedlings survived to become yearlings at PF1 (< 0.021 juveniles per m^2); 55% of the time (22 of 40 years) fewer than ten yearlings were added in PF2 (< 0.031 juveniles per m^2). In contrast, over the 41 years of observations there were only 11 events when 50 + seedlings survived to become yearlings and only 3 years at either PF1 or PF2 when 90 + seedlings survived to become yearlings. For 10 of these 11 events, an average of only 0.26 ± 0.13 yearlings per m^2 were added to either population. The exception was an extraordinary germination event at PF1 in 1991 when 1.78 yearlings per m^2 were added to the population in 1992. As we show next, even fewer yearlings survived through the juvenile stage and to eventually become adults (year 4).

All 11 cohorts of 50 + yearling cohorts in both PF1 and PF2 over the past four decades were followed until they reached adulthood at age four (and then followed subsequently as adults). On average, there was a tendency for cohort survival to be higher at PF1 than at PF2 (Supplemental Information, Figure S2). Yet there was large variability in year-to-year survival rates of juveniles at both sites, with juvenile survival to adulthood rates below 40% in the 2003–2012 time period, coincident with the steepest declines in PDSI values. Juvenile survival rates were below 20% for the 2005- and 2008-cohorts when PDSI values were at their lowest values in the four decades of observations. Yet during the wettest period, 88% of the yearlings survived to become adults.

In support of *Hypothesis 1*, juvenile survival to adulthood was positively correlated with cumulative precipitation (Fig. 2). Only 11 cohorts at PF1 and PF2 over the past four decades contained sufficient numbers of yearlings for analyses of cohort-establishment. In these cohorts, juvenile survival was positively correlated with accumulated precipitation amounts after two ($r = 0.504$, $p = 0.056$), three ($r = 0.668$, $p = 0.012$), and four ($r = 0.604$, $p = 0.025$) years.

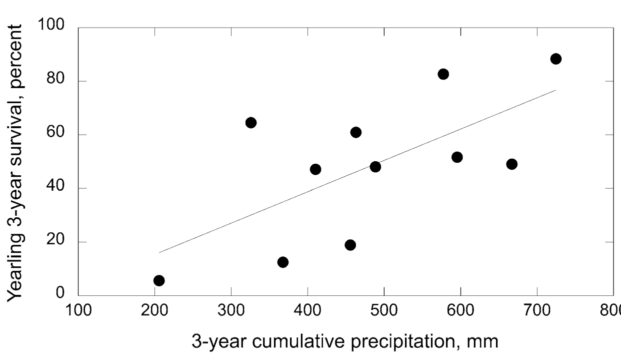

Fig. 2 The three-year survival rate of tagged yearling *E. farinosa* from both PF1 and PF2 populations as a function of the cumulative precipitation over that three-year period. The regression is $y = 0.117x - 8.0$ ($r^2 = 0.447$, $p = 0.012$)

There were simply insufficient numbers of yearlings in other years to conduct similar analyses.

What role does iWUE play in juvenile establishment?

It is easy to imagine that in a bare-soil environment in the desert away from any potential nurse-plant effects, the physical environment likely imposes a greater constraint on initial seedling establishment than potential biotic interactions, such as competition for water (Donovan and Ehleringer 1992, 1994b; Donovan et al. 1993; Sandquist et al. 1993). Assuming hot soils with limited soil moisture to be the major challenge for seedlings in the Mojave Desert, we hypothesized that iWUE played a role in successful establishment. There is strong genetic evidence that carbon isotope ratio values (a proxy for iWUE) span a large range of values within field populations and are highly heritable (Farquhar et al. 1989; Schuster et al. 1992a, 1994). However, uni-directional selection for specific iWUE values may be unlikely since *Encelia* are self-incompatible, obligate outcrossers (Kyhos 1967, 1971; Kyhos et al. 1981), and Ehleringer (1993) has shown that in adult shrubs released from neighbor competition, those shrubs with low iWUE values grew faster and flowered more intensively than those individuals with high iWUE values.

Evaluating the initial claim of *Hypothesis 2* was challenging, because large seedling establishment events were a sufficiently rare phenomenon. There have only been three events over the past four decades (1981–2020) that were large enough (> 90 yearlings) to explore iWUE variations among yearlings (PF1 = 1991, 1992; PF2 = 1991). In each of these events, the juvenile variations in iWUE were large, ranging from 20 to 120 µmol mol^{-1} and consistent with *Hypothesis 2* (Fig. 3). iWUE values of juveniles were significantly lower than those of adults in both PF1 and PF2 populations (Table 1). In fact, average iWUE values were 8–11% lower in juveniles when compared to adults and these iWUE differences were significantly different as follows: PF1 (ANOVA, $p = 0.043$) and PF2 (ANOVA, $p < 0.0001$). In PF1 1993, the mean and standard deviation of iWUE values of juvenile and adult plants were 64.9 ± 11.1 and 70.1 ± 6.0 µmol mol^{-1}, respectively, which is statistically significant ($F = 4.23$, $p = 0.04$). In 1993, the mean iWUE values of juvenile and adult PF2 plants were 59.5 ± 9.7 and 65.9 ± 8.4 µmol mol^{-1}, respectively, which is also statistically significant ($F = 26.27$, $p < 0.0001$).

Later when surviving juvenile plants were resampled as new adults in 1998, those PF1 juveniles that had survived and transitioned to adults still had significantly lower iWUE values than older adults (Table 1). Here the mean iWUE values of juvenile and adult plants were 80.9 ± 9.2 and 86.6 ± 6.4 µmol mol^{-1}, respectively, which is statistically significant ($F = 5.02$, $p = 0.026$). However, in PF2 by 1998

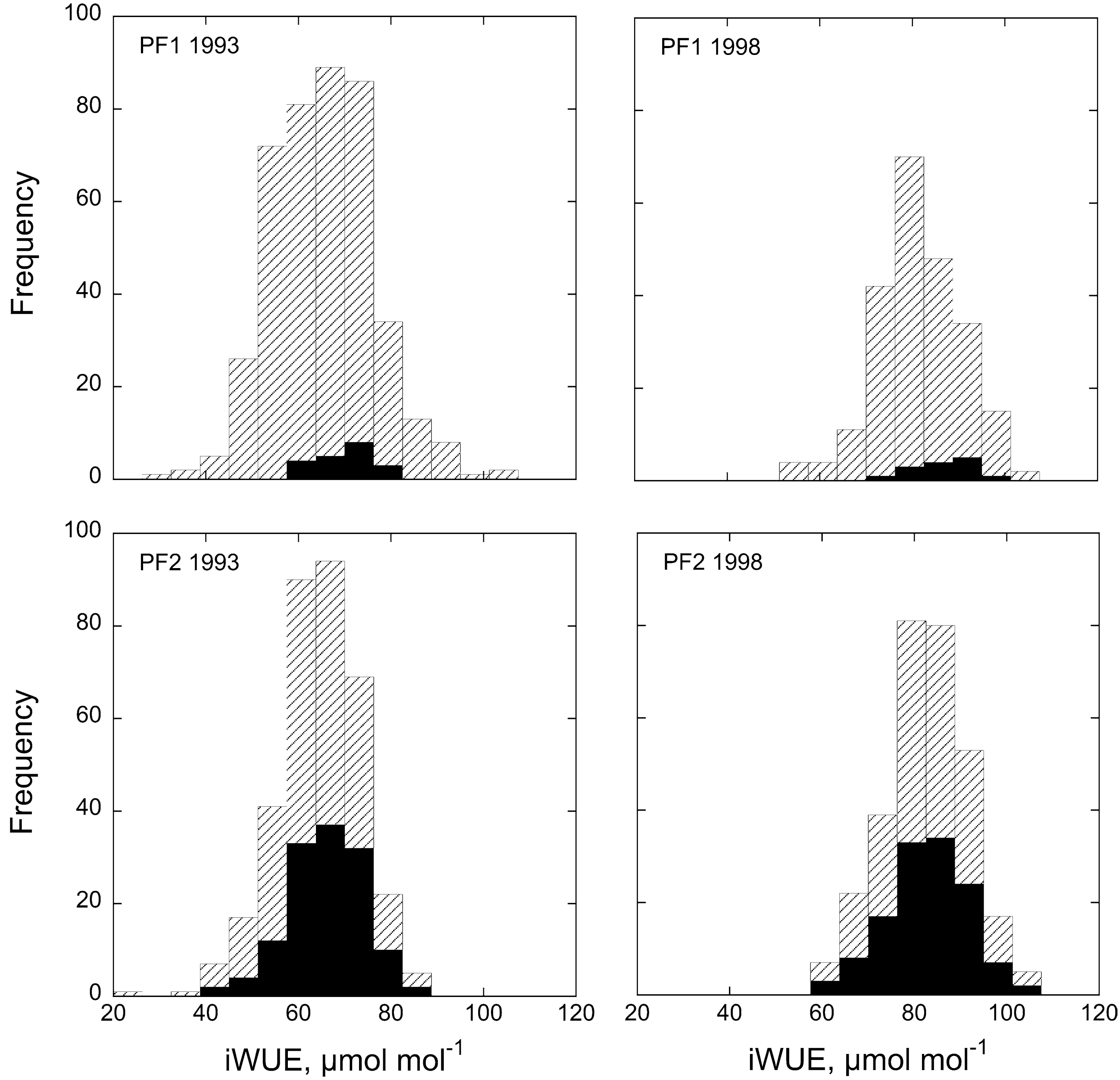

Fig. 3 Frequency histograms of the intrinsic water-use efficiency values for juvenile (hashed values) and adult (solid values) *E. farinosa* measured in 1993 and again in 1998

there were no longer significant differences in iWUE values between newer and older adults (ANOVA, $p=0.24$).

While there were large differences in iWUE values among juveniles in both PF1 and PF2 as shown in Fig. 3, that variation appeared to be randomly distributed across each of the two plots and not related to measures of the density of neighboring plants in the vicinity of individual plants. As a first measure to assess this random distribution of iWUE values, we measured proximity of a juvenile to its nearest neighbor (either adult or juvenile). There were no significant relationships between iWUE values of juveniles and the distance to the nearest neighboring plant: PF1 1991 cohort ($r=-0.061$, $n=72$, $p=0.307$), PF1 1992 cohort ($r=-0.232$, $n=14$, $p=0.212$), and PF2 ($r=-0.085$, $n=83$, $p=0.44$). As a second assessment, we measured the total number of neighboring *E. farinosa* within 1.5 m (both juveniles and adults), which ranged from 0 to 26 plants. Again, there were no significant relationships between juvenile iWUE values and the number of neighbors within 1.5 m to suggest that biotic interactions

Table 1 A comparison of the intrinsic water-use efficiency (iWUE) values of juvenile and adult *Encelia farinosa* sampled at both populations PF1 and PF2 in both 1993 and 1998

Population	Year	Category	iWUE (μmol mol^{-1})	Sample size
PF1	1993	Juvenile	64.9 ± 11.1	379
PF1	1993	Adult	70.1 ± 6.0	20
PF1	1998	Juvenile	80.9 ± 9.2	201
PF1	1998	Adult	86.6 ± 6.4	14
PF2	1993	Juvenile	59.5 ± 9.7	83
PF2	1993	Adult	65.9 ± 8.4	132
PF2	1998	Juvenile	80.8 ± 9.0	48
PF2	1998	Adult	82.5 ± 8.8	128

were influencing the following juvenile iWUE values: PF1 1991 cohort ($r = 0.000$, $n = 72$, $p = 1.0$), PF1 1992 cohort ($r = 0.276$, $n = 14$, $p = 0.170$), and PF2 ($r = 0.189$, $n = 83$, $p = 0.0998$). As a third assessment, we considered the spatial area that might be conceivably "controlled" by a juvenile through negative belowground root interactions. Here we calculated Thiessen polygon areas associated with each of the juvenile plants. Again, there were no significant relationships between the Thiessen polygon area "occupied" by a juvenile plant and its iWUE value: PF1 1991 cohort ($r = -0.033$, $n = 72$, $p = 0.392$), PF1 1992 cohort ($r = 0.396$, $n = 14$, $p = 0.08$), and PF2 ($r = -0.186$, $n = 64$, $p = 0.14$). Our conclusion is that iWUE differences among juvenile *E. farinosa* were either associated with inherent genetic differences among juveniles or to undetected soil micro-gradients that might have retained water differentially. As the soils appeared uniformly rocky across both sites, spatial soil moisture gradients were a less likely explanation and it was more likely that inherent genetic differences were largely responsible for variations in iWUE values across the populations of juvenile plants.

During the transition from yearling to adult (age four) stages, not all yearlings survived. Among the surviving juveniles, there were detectable ontogenetic adjustments in iWUE values among surviving juveniles that were proportional to its initial iWUE value. The trend was that juveniles with high iWUE values exhibited little or no adjustments in iWUE values between the first iWUE observation and the follow-up adult observation, whereas surviving juveniles that had relatively low iWUE values increased their iWUE values significantly and proportionally to their baseline iWUE values (Fig. 4). Figure 4 plots the iWUE values of individuals in the cohorts born in 1991 and in 1992 versus the adjustments in iWUE values between 1993 and 1998, 2 years in which extensive stable isotope sampling occurred. The relationships were significant for both cohorts: PF1 1991 cohort ($r^2 = 0.389$, $n = 201$, $p < 0.0001$) and PF1 1992 cohort ($r^2 = 0.336$, $n = 31$, $p = 0.0006$). Similarly, in PF2 the

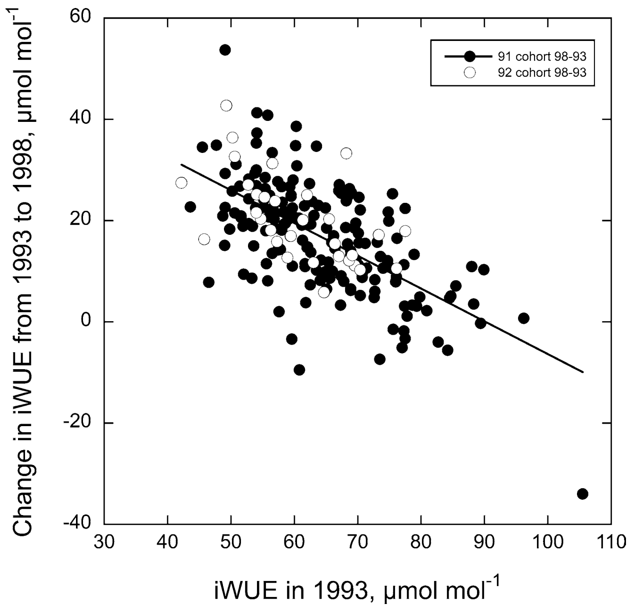

Fig. 4 A plot of the decrease in intrinsic water-use efficiency values of individual *E. farinosa* juveniles in PF1 between 1993 and 1998 as a function of the initial measurement in 1993. For individuals in the 1991 cohort, the relationship is y = 58.3 – 0.647•iWUE ($r^2 = 0.392$, $n = 201$, $p < 0.001$) (linear relationship shown). For individuals in the 1992 cohort, the relationship is y = 54.7– 0.568•iWUE ($r^2 = 0.336$, $n = 31$, $p = 0.003$)

iWUE values of individuals born in 1991 versus the adjustments in iWUE values between 1993 and 1998 was also significant (ΔiWUE = 44.5 – 0.40•iWUE, $r^2 = 0.153$, $n = 26$, $p = 0.024$). A mechanistic basis for these apparent ontogenetic adjustments is unknown. What seems evident is that the lower the iWUE values during early stages in life, the great the upward adjustments in iWUE values among surviving individuals.

While juvenile plants exhibited changes in iWUE from 1993 to 1998 (ΔiWUE), no similar adjustments were observed in adult plants within either PF1 or PF2 during that time period. That is, in contrast to juvenile plant behavior, for adult plants there were no significant relationships between iWUE values in 1993 versus the change in iWUE values between 1993 and 1998: PF1 ($r^2 = 0.0027$, $n = 15$, NS) and PF2 ($r^2 = 0.0002$, $n = 6$, NS).

Once surviving *E. farinosa* juveniles in the three cohorts became adults, there were no further adjustments in interannual ΔiWUE values among individuals as a function of initial iWUE values. For example, when iWUE values of plants from the 1991 and 1992 PF1 cohorts were examined later in life as adults, there was no significant relationship between the initial adult measurement in 1998 and the difference in iWUE between 1998 and 2010 (ΔiWUE): 1991 cohort ($r^2 = 0.0042$, $n = 16$, NS) and 1992 cohort ($r^2 = 0.062$, $n = 9$, NS). A similar pattern was observed in the 1991 PF2 cohort ($r^2 = 0.0002$, $n = 6$, NS). Thus, it appears that an ontogenetic adjustment occurred during the juvenile stage, whereby surviving juveniles with lower iWUE values exhibit increased values, resulting in a decreased range of iWUE values observed in the adult population. Once these juveniles had matured to become adults, no further differential iWUE adjustments occurred.

Could there be a relative fitness advantage associated with a high iWUE value?

Given (a) that there was juvenile mortality between the yearling stage and adulthood (Figure S2) and (b) that changes in iWUE values appeared to pivot around an iWUE value of ~ 90 µmol mol^{-1} during this juvenile stage (Fig. 4), we next evaluated *Hypothesis 3* and tested to determine if there were patterns that related to juvenile mortality using observations from the large establishment events in 1991 at both PF1 and PF2. Indeed, size differences among juveniles had emerged by the second year of life, and these related to the odds of survival to adulthood (Table 2). Larger juveniles were more likely to survive to adulthood. In addition, iWUE was positively related to the odds of juvenile survival when tested independently (Table 3). However, the effect of iWUE on the odds of survival was mediated by plant size. Larger plants had higher iWUE values, and we found that iWUE was not a significant predictor of survival odds after controlling for plant size (Table 3).

Consistent with the latter assertion of *Hypothesis 2*, yearling size and iWUE values were associated with the likelihood of surviving another 3 years to become adults. PF1 yearlings that survived to become adults had an average size of 69.3 ± 54.1 cm^2 ($n = 245$) as yearlings, whereas those yearlings which did not survive were already significantly smaller (34.6 ± 40.4 cm^2) ($p < 0.0001$, $n = 85$). A similar size pattern was observed at PF2, where yearlings that survived to adulthood were larger (62.2 ± 60.6 cm^2) than those that died (19.2 ± 14.9 cm^2) ($p = 0.019$, $n = 83$). In PF1, the iWUE values of yearlings surviving to adulthood were significantly higher than those yearlings that died before maturing, 65.9 versus 62.7 µmol mol^{-1}, respectively ($p = 0.025$, $n = 85$). However, in PF2, the iWUE values of yearlings surviving to adulthood were not quite significantly higher than those yearlings that died before maturing, 60.3 versus 55.5 µmol mol^{-1}, respectively ($p = 0.099$, $n = 83$).

We next evaluated relationships between flowering, iWUE, and plant size among juveniles within the 1991 PF1 cohort that did not survive long enough to reach adulthood. Juveniles that flowered at least once and died were much larger (45.1 ± 46.3 cm^2, $n = 55$) than juveniles that died without any flowering event (15.4 ± 12.1 cm^2, $n = 30$) ($p = 0.001$). Not only were non-flowering juveniles that died during this stage smaller, but their iWUE values were also significantly lower than juveniles that flowered prior to death (54.9 ± 10.6 µmol mol^{-1} *vs*. 67.0 ± 10.2 µmol mol^{-1}, $p < 0.0001$). When plant size was regressed against iWUE for all juveniles that died by their fourth year, the relationship was significant and positive (SA = 0.00130•iWUE – 0.047, $r^2 = 0.145$, $n = 85$, $p = 0.0003$). The smallest juveniles were not only non-reproductive, but also had the lowest iWUE values. A logistic regression of the 1991 cohort confirmed that iWUE ($\beta = 0.037$, $p = 0.006$) and plant size ($\beta = 41.0$, $p < 0.0001$) were significant predictors of flowering status in 1993 after controlling for population.

There was a significant positive relationship between juvenile iWUE values and plant size for the 1991 cohort

Table 2 Observations of the intrinsic water-use efficiency (iWUE) and plant size values for the 1991 cohorts of *Encelia farinosa* in 1993 (age 2) at both populations PF1 and PF2, divided into those juveniles that survived to attain adulthood and those that did not survive to 1995

	Died during juvenile stage	Survived to reach adulthood	*P* value
iWUE PF1 (µmol mol^{-1})	62.7 ± 11.8 (85)	65.9 ± 10.9 (245)	0.025
iWUE PF2 (µmol mol^{-1})	55.5 ± 9.9 (13)	60.3 ± 9.7 (70)	0.099
Plant size PF1 (cm^2)	34.6 ± 40.4 (85)	69.3 ± 54.1 (245)	< 0.001
Plant size PF2 (cm^2)	19.2 ± 14.9 (13)	62.2 ± 60.1 (70)	0.0133

Data are means ± 1 standard deviation, with sample sizes in parentheses

Table 3 Effect of iWUE and plant size on the odds of juvenile survival to adulthood from three logistic regressions

Predictors	Coefficient for iWUE (*p* value)	Coefficient for plant size (*p* value)	Pseudo-R^2
Plant size, population	NA	23.14 ± 4.62 (< 0.001)	0.173
iWUE, population	0.027 ± 0.01 (0.014)	NA	0.048
Plant size, iWUE, population	0.007 ± 0.01 (0.53)	22.35 ± 4.74 (< 0.001)	0.175

Nagelkerke's pseudo-R^2 is reported as an indicator of model fit

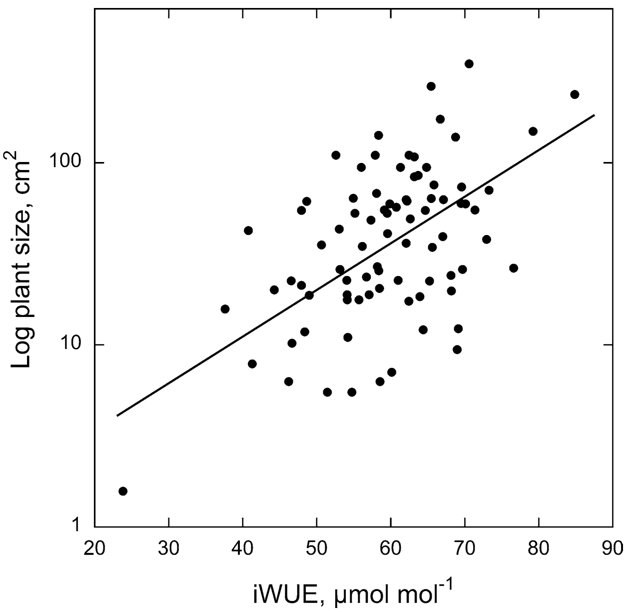

Fig. 5 A plot of the relationship between intrinsic water-use efficiency values versus log plant size for PF2 *E. farinosa* juveniles in the 1991 cohort measured in 1993. The relationship is statistically significant (log SA = 0.231•iWUE + 0.18, $r^2 = 0.273$, $n = 69$, $p < 0.001$)

Table 4 Correlation coefficients between juvenile intrinsic water-use efficiency (iWUE, µmol mol^{-1}) value and plant size (projected surface area, cm^2) for *Encelia farinosa* 1991 cohorts from populations PF1 and PF2

Population cohort	Year	*r*	*n*	*p* value
PF1 1991	1993	0.26	330	0.0001
PF1 1991	1998	0.25	232	0.0001
PF1 1991	2001	0.15	193	0.036
PF1 1992	1993	0.44	47	0.001
PF2 1991	1993	0.43	97	0.0001
PF2 1991	1994	0.52[a]	10	0.013
PF2 1991	1995	0.80	12	0.002
PF2 1991	1998	0.27[a]	47	0.034

[a]Correlation coefficient calculation was conducted following removal of one data point based on a Dixon outlier test

at both PF1 and PF2. Figure 5 shows this pattern for the PF2 1991 cohort for plants sampled in 1993. Since higher iWUE values are typically associated with water stressed plants with partially closed stomata, the pattern in Fig. 5 reveals the opposite pattern. Instead, individuals exhibiting higher iWUE values attained larger sizes; they also exhibited a higher likelihood of surviving to adulthood. Fewer iWUE observations were collected in the two successive years for this cohort, but similar positive and significant relationships were observed between iWUE and plant size at PF1 in both the 1991 and 1992 cohorts (Table 4).

The PF2 population had not experienced a significant mortality event prior to 1993 and thus it was possible to explore these same iWUE-size relationships among adult *E. farinosa*. Perhaps surprisingly, positive relationships between iWUE and adult plant size were also observed in PF2 adults in 1993 ($r = 0.273$, $n = 132$, $p = 0.0002$), 1998 ($r = 0.263$, $n = 125$, $p = 0.001$), and 2010 ($r = 0.153$, $n = 76$, $p = 0.09$). These were the only years with sufficient iWUE observations to allow for such analyses. The PF1 population had experienced significant mortality prior to the 1991 cohort establishment (Ehleringer and Sandquist 2018), greatly restricting the potential for a similar analysis. Nevertheless, 21 adults had survived and there was also a positive trend between iWUE and plant size ($r = 0.350$, $n = 21$, $p = 0.12$). Together these data suggest that a positive relationship persists between iWUE and plant size in adult *E. farinosa* in both PF1 and PF2. As previous studies have shown that adult *E. farinosa* compete for limited soil moisture (Ehleringer 1984), that plant size and survival are positively correlated (Bitter and Ehleringer 2021), and that plant proximity increases the probability of plant mortality (Bitter and Ehleringer 2021), these observations suggest that there may be a survival and fitness advantage associated with high iWUE values.

Leaf iWUE values are positively correlated with photosynthetic capacity

Among the most consistent ecophysiological trait characteristics in plants is leaf nitrogen content, which is proportional to leaf maximum photosynthetic capacity (Ehleringer and Cook 1984; Evans 1989; Field and Mooney 1986; Peterson et al. 1999). We also measured leaf nitrogen content on each *E. farinosa* sample analyzed for carbon isotope ratios at PF1 and PF2. The overall correlations between leaf nitrogen content (N) and iWUE were positive and highly significant for PF1 ($r = 0.177$, $n = 2092$, $p < 0.0001$) and PF2 ($r = 0.087$, $n = 1780$, $p < 0.0001$). However, when individual years were analyzed separately, the relationship between N and iWUE was typically much stronger (e.g., Fig. 6), because much of the overall variation in the larger dataset was associated with year-to-year variations in the slope of the relationship between N and iWUE.

Discussion

Encelia farinosa as a model species - population ecology, ecophysiology, and systematics

Over the past five decades, *Encelia* has emerged as the archetypal drought-deciduous shrub in the North American southwestern deserts for population biology,

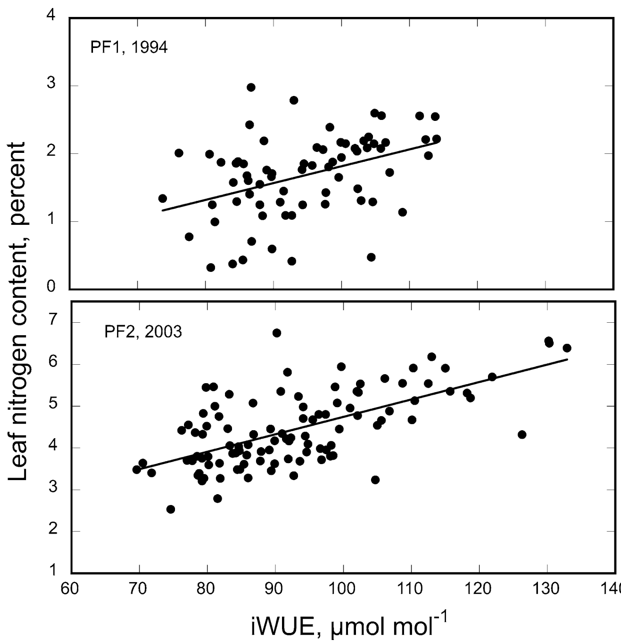

Fig. 6 Examples of the relationships between leaf nitrogen content and intrinsic water-use efficiency for leaves from different individual *E. farinosa* plants. Top: PF1 in 1994 ($N = 0.025 \cdot \text{iWUE} + 0.66$; $r^2 = 0.164$, $n = 71$, $p = 0.0005$). Bottom: PF2 in 2003 ($N = 0.042 \cdot \text{iWUE} + 0.57$; $r^2 = 0.407$, $n = 103$, $p < 0.0001$)

ecophysiology, and systematic studies (Smith et al. 1997) and thus it is important to not only understand adult behavior but also that of juveniles as they establish in this arid environment. While population biology studies across both the Mojave and Sonoran Deserts have found *E. farinosa* to have maximum life spans of 20–50 years (Bitter and Ehleringer 2021; Bowers et al. 1995, 2004; Bowers 2005; Ehleringer and Sandquist 2018; Goldberg and Turner 1986), there has been limited detailed attention addressing shrub establishment. Adult *E. farinosa* shrubs exhibit clumped distributions predisposing them to intraspecific competition, with strong growth responses observed when shrubs are released from competition (Ehleringer 1984, 1993). Distance to nearest neighbor among adults is also a factor influencing the likelihood of death (Bitter and Ehleringer 2021). However, our casual observations suggested that seedling spacing patterns appeared random early in the plant's life history, suggesting that clumped distributions must arise as individuals age and compete among themselves for water. It is evident that decreases in *E. farinosa* population size occur in response to prolonged drought (Ehleringer and Sandquist 2018). The current megadrought (Williams et al. 2020) is having even broader landscape level impacts on shrub mortality and overall decreased shrub biomass across the Mojave and Sonoran Deserts (Hantson et al. 2021; McAuliffe and Hamerlynck 2010).

Earlier ecophysiological studies of *E. farinosa* focused on interactions among energy balance, photosynthesis, and transpiration, especially in how these features changed in coordinated ways as plants were exposed to seasonal dry periods and/or prolonged droughts (e.g., Cunningham and Strain 1969; Ehleringer 1980; Ehleringer and Björkman 1978a, b; Ehleringer et al. 1976; Ehleringer and Cook 1984; Ehleringer and Mooney 1978; Smith and Nobel 1977, 1978; Werk and Ehleringer 1983). Leaves become highly pubescent which results in high reflectances, maintain reduced leaf temperatures in response to water deficits, and possess meristematic tissues that retain memory of the status of the current seasonal drought (Ehleringer 1982; Ehleringer and Mooney 1978; Sandquist and Ehleringer 1997, 1998). The advantages of leaf pubescence were verified through field, laboratory, and transplant garden studies involving mutant and wild type *E. farinosa* (Ehleringer 1983, 1985; Ehleringer and Cook 1990). Relevant to the results of this study, these earlier publications revealed that features prolonging activities into the dry season allowed plants to achieve larger sizes.

After water limitations, availability of soil nitrogen is thought to be the second major constraint on desert plant growth. In *Encelia*, older shrubs are associated with greater soil nitrogen availability, with the potential to influence both vegetative and reproductive production (Driscoll et al. 2021b). A positive nutrient feedback relationship exists between plant size and age resulting in islands of fertility as shrubs mature. Soil N values are four times higher in the upper 20 cm under mature shrubs than occur in open spaces where seedlings germinate. The higher soil nitrogen levels under mature shrubs may be a consequence of elevated soil organic matter, allowing for greater abundances of free-living nitrogen fixing bacteria (Driscoll et al. 2021b). Whatever the driver is that results in an island of fertility, *E. farinosa* seedlings do not germinate into this environment, but instead germinate in open microsites with low soil N values.

While much of the ecological research has focused on *E. farinosa*, evolutionary and phylogenetic studies have revealed broader insights into the rapid evolution within this genus across arid landscapes of southwestern North America (Clark 1998, 2019; Ehleringer and Clark 1988; Fehlberg and Fehlberg 2017; Fehlberg and Ranker 2007, 2009; Singhal et al. 2021). Changes in leaf sizes, leaf spectral characteristics, and trichome structures have coevolved as these shrub species appear in distinct habitats across the precipitation range of southwestern arid land sites. At the interface zones associated with climatic or wash/slope boundaries, hybridization is common (Clark et al. 1988; DiVittorio et al. 2020; Kyhos et al. 1981).

Juvenile survival and climate

Since multi-year cumulative precipitation amounts were less during the megadrought period than prior to that time, the current megadrought has been associated with lower juvenile establishment rates and contributed to decreased adult population sizes (Driscoll et al. 2021a; Ehleringer and Sandquist 2018). Based on four decades of annual surveys, Ehleringer and Sandquist (2018) noted that many of the major seedling germination events followed periods of high adult mortality, where overall population size had shrunk significantly. Whether or not adult mortality pre-disposes the potential for *E. farinosa* seeds to germinate is unclear and perhaps unlikely. However, it was well established earlier that organic compounds from adult *E. farinosa* leaves exhibited an allelopathic effect, reducing seed germination rates (Gray and Bonner 1947, 1948; Wright et al. 2013). In field observations at PF1 and PF2, neither *E. farinosa* seedlings nor those of other species have been observed under adult *E. farinosa* shrubs, although seedlings occasionally established under the long-lived evergreen shrub *Larrea tridentata*. However, seedlings have been observed under the skeletons of dead *E. farinosa*. While allelopathic effects might provide insights into why *E. farinosa* seedlings are limited to open spaces and not under *E. farinosa* shrubs, that explanation does not provide any insights into factors critical to *E. farinosa* seedling establishment and survival.

Hypothesis 1 predicts that survival rates through those years of the juvenile stage will be proportional to the cumulative precipitation received over that period of time. Indeed, field observations support this hypothesis at both PF1 and PF2, whether evaluated over 2-, 3-, or 4-year periods. Perhaps this hypothesis is not so insightful, since most would expect that plant survival is related to water availability. But to the contrary, it is a non-trivial expectation when swings in interannual precipitation amounts during successful establishment events were large, such as the interannual decrease from the mean of + 112% to − 60% between 1993 and 1994. This may be because in 1995 annual precipitation was again above average (Figure S1). This and similar observations noted in this study may point to the importance of integrating drought impacts over multi-year periods, such as the PDSI trends shown in Fig. 1, rather than focusing on observations in any single year. Unlike the observed juvenile survival pattern, it appears that survival in adult plants is influenced by both precipitation patterns and proximity to neighboring shrubs (Bitter and Ehleringer 2021; Ehleringer 1984; Ehleringer and Sandquist 2018).

There is no doubt though that the 2000–2020 megadrought period described by Williams et al. (2020) had its impact on *E. farinosa* through low juvenile survival, especially in the 2005–2012 time interval. Here it seems that ENSO-related events may have been associated with seedling germination (Ehleringer and Sandquist 2018), but the subsequent low precipitation amounts in years following the germination event resulted in high mortality rates at both PF1 and PF2. Not only has the megadrought negatively impacted *E. farinosa* recruitment rates, but overall plant density has diminished across numerous Mojave Desert sites (Ehleringer and Sandquist 2018; Hantson et al. 2021; Miriti et al. 2007). Over the long term, drier conditions are predicted for much of the southwestern arid lands of North America (Cook et al. 2015; Udall and Overpeck 2017; Wang and Kumar 2015), leading to the possibility that successful *E. farinosa* establishment rates may diminish further in the future unless there are favorable runs of wet years.

Juvenile mortality and iWUE relationships

Ehleringer and Clark (1988) showed that, under natural field conditions, viable seed output by *E. farinosa* shrubs was proportional to plant size over all size classes, from the smallest through the largest plants. This is because flowers are located at the tips of stems on all *Encelia* species. No further vegetative growth occurs once that stem transitions into a reproductive mode (subsequent vegetative growth is axillary). Thus, from a simplistic sense, achieving larger plant size could be viewed as contributing to improved plant fitness. While flowering could occur among juveniles, it tended to occur infrequently and only among larger juveniles. Having at least one stem produce flowers was no guarantee of longer-term success, as some juveniles flowered at least once, but died before reaching adulthood.

Plant establishment and mortality have been explored for many decades (Harper 1977; Harper and White 1974; Silverton and Charelsworth 2009), but there have been few contributions from the perspective of how iWUE might influence establishment of perennials. Some of the most relevant contributions emerge from observations that seedlings and juvenile plants have lower iWUE values than observed in adults (Donovan and Ehleringer 1991, 1992, 1994a; Sandquist et al. 1993) and the results presented here are consistent with those observations. Each of these studies implied that higher iWUE values in adult plants may be the consequence of differential juvenile mortality, but those annual-frequency data were not available to explore that possibility until this study. However, supporting such a possible explanation, population-level iWUE comparisons of long- versus short-lived shrubs in warm and cold deserts had indicated that higher iWUE values were associated with longer-lived perennials (Schuster et al. 1992b). The explanation that has been proposed is that individuals within a population with lower iWUE values may have a tendency to die earlier in response to a drought resulting in changes in the frequency distribution of iWUE values (Ehleringer 1993; Sandquist and Ehleringer 2003a, b). One possible mechanism is that subtle variations in both xylem cavitation and iWUE values may be associated with each other.

One surprising observation was of a significant ontogenetic shift in iWUE values among *E. farinosa* juveniles with no subsequent shifts as adult plants. Surviving juveniles with the lowest initial iWUE values increased their values by the time they became adults and did not adjust further in subsequent years (recall Fig. 4). However, statistically, those juveniles with the lowest iWUE did not survive, while those juveniles with the highest iWUE values exhibited little ontogenetic adjustment. Ontogenetic changes in gas exchange characteristics have been described before (Bond 2000; Mason and Donovan 2015; Mason et al. 2013; Palow et al. 2012), but this is the first description we are aware of showing that iWUE ontogenetic shifts can occur as well. Perhaps the most unexpected trend here was that individuals with high iWUE values did not exhibit an ontogenetic shift, while the magnitude of the adjustment in other juveniles was inversely proportional to the initial iWUE value. Whether or not the adjustments in iWUE values during this juvenile stage were associated with decreased stomatal conductance or increased photosynthetic rate is unknown. However, the significant positive correlations observed between iWUE values and leaf nitrogen content (a measure of photosynthetic capacity) suggest that increasing iWUE values were likely associated within increasing photosynthetic capacity. The value of the ontogenetic adjustment may be that gaining size is more critical for young plants in terms of survival and competition than at later stages in life. While modeling results from Bitter and Ehleringer (2021) did confirm that yearling plant size was the strongest predictor of the likelihood to survive to adulthood, that study did provide any mechanistic basis for ontogenetic effects or potential genotypic differences among yearlings.

iWUE, juvenile size, and an unexpected iWUE-N relationship

The basis of *Hypothesis 2* was twofold: model results from Bitter and Ehleringer (2021) that larger yearlings were more likely to survive to adulthood combined with field observations by Driscoll et al. (2021a) that adult size and iWUE were positively correlated. While observations of (a) a positive relationship among adult *E. farinosa* shrub size and precipitation (Driscoll et al. 2021a) and (b) a positive relationship between juvenile survival and precipitation (recall Fig. 2) agree with fundamental concepts of productivity and growth, the connections between juvenile size and iWUE may at first seem counterintuitive. That is, until one recognizes that not all juveniles had the same leaf N content and that leaf N and iWUE were positively correlated with each other. Although the basis for this relationship may not be universally agreed upon, positive correlations between leaf N and iWUE have been observed by others, implying that this relationship might be widespread (Adams et al. 2016; Cornwell et al. 2018; Gebauer and Ehleringer 2000; Prentice et al. 2011).

The consequences of positive relationships between *E. farinosa* leaf N and iWUE values have direct implications for photosynthesis and possibly plant size. Ehleringer and Cook (1984) and Comstock and Ehleringer (1984) showed that both photosynthetic rate (*A*) and the slope of the photosynthesis versus intercellular CO_2 concentration relationship (*A vs.* c_i/c_a) in *Encelia* were linearly related to leaf N values. This would imply that juvenile *E. farinosa* with higher iWUE values would tend also to have higher photosynthetic capacities. Consequently, high iWUE values could lead to higher photosynthetic rates for these short-lived drought-deciduous leaves, resulting in larger juveniles by the end of the growing season.

Figure 7 captures what is known based on our understanding of the observed patterns of juvenile leaf N and iWUE values based on an *A vs.* c_i analysis and makes predictions as to when low versus high iWUE values might be favored. The *A vs.* c_i/c_a curve is referred to as the "demand" function

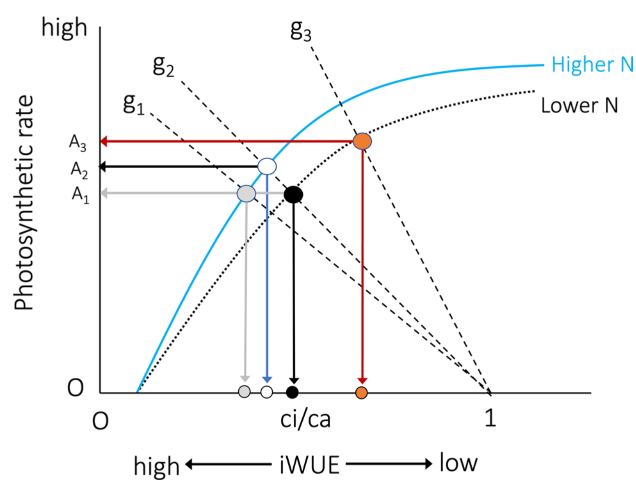

Fig. 7 A plot of the expected relationships between photosynthetic rate and the ratio of intercellular-to-ambient CO_2 levels for two *E. farinosa* leaves differing in nitrogen content: a higher leaf nitrogen content (blue line) and a lower leaf nitrogen content (black line). Farquhar and Sharkey (1982) describe this A vs c_i/c_a curve as the "demand function" of leaf photosynthesis. The three dashed lines represent different leaf conductance values: g_1 is the lowest and g_3 is the highest. Farquhar and Sharkey (1982) describe this as the "supply function" of leaf photosynthesis. The intersection of the "supply" and "demand" functions is the operational c_i/c_a value for that leaf under those conditions. The gray, white, black, and red circles represent different combinations of A vs c_i/c_a curves and g values and project down to different c_i/c_a values or across to different photosynthetic rates. Note that low iWUE values are associated with high c_i/c_a values and vice versa

(Farquhar and Sharkey 1982). Two contrasting *A vs.* c_i/c_a curves are presented. The blue *A vs.* c_i/c_a curve represents a plant having a higher N value; the black dotted *A vs.* c_i/c_a curve represents a leaf having a lower N value. In an *A vs.* c_i/c_a graphic, the dashed line represents the leaf conductance to CO_2 diffusion (*g*) and emerges from the x-axis at the point where $c_i/c_a = 1$ (i.e., the ambient CO_2 concentration). The leaf conductance is directly proportional to the slope of that line such that at an infinite conductance c_i/c_a should approach a value of 1. Obviously leaf conductance values are lower and are known to decrease as water stress increases. The leaf conductance line is referred to as the "supply" function, with the intersection of the "supply" and "demand" functions being the operational point and resulting in a specific photosynthetic rate (y-axis) and specific c_i/c_a value (x-axis) (Farquhar and Sharkey 1982). Four possible c_i/c_a values are shown in Fig. 7, representing different combinations of *A vs.* c_i/c_a curves and leaf conductances.

Figure 7 also captures what might be conjectured based on our understanding of the positive correlations between juvenile leaf N and iWUE values (recall Fig. 6). Here the higher iWUE plant is represented by the blue *A vs.* c_i/c_a curve, while the lower iWUE plant is represented by the dotted *A vs.* c_i/c_a curve. Recall that the c_i/c_a value is directly related to the iWUE value (Eq. 2). At any equivalent leaf conductance value (e.g., g_2), leaves with higher iWUE values will always have higher photosynthetic rates (e.g., A_2 versus A_1). That higher iWUE values would be associated with higher photosynthetic capacities may seem counterintuitive, given the extensive carbon isotope and water stress literature (Bowling et al. 2008; Cernusak et al. 2013; Farquhar et al. 1989). Given that literature, one might have expected lower iWUE leaves to have higher photosynthetic rates, but as shown in Fig. 7 that could only happen in juveniles if leaves with lower iWUE values also exhibited higher leaf conductances (e.g., g_3 versus g_2).

Consider differences in photosynthetic rate as a contributing mechanism that allows high iWUE juvenile plants to grow larger than low iWUE plants. As one possibility, both leaves could have the same *g* value (e.g., g_2). If so, then the leaf with a higher iWUE value would also be operating at a higher photosynthetic rate (A_2 versus A_1). That is, a leaf with a higher iWUE value also achieves a higher *A* value at the same *g* value. As a second possibility, if leaves with different iWUE values have the same *A* value (A_1), then the leaf with a higher iWUE value would be operating at a lower leaf conductance (compare black versus gray circles). That is, a leaf with a higher iWUE value could achieve a similar *A* value but at a lower *g* value. Based on the available data, we cannot distinguish between the two possibilities. We can only conclude that (a) leaves with higher iWUE values have lower c_i/c_a values (consistent with either possibility 1 or 2) and (b) juveniles with higher iWUE values either operate at higher photosynthetic rates or at lower leaf conductances than juveniles with lower iWUE values. Both options allow for the possibility that juveniles with higher iWUE values could grow larger either as a consequences of higher carbon gain rates or through a capacity to sustain carbon gain for a longer time period into the dry season if transpiration rates were lower.

Inherent in this model is that leaf-level photosynthetic capacity is greater in high iWUE plants than low iWUE plants, which is a testable assumption. Figure 6 provides strong support for this assertion, as does the multi-decadal record of nearly 4,000 PF1 and PF2 observations indicating a positive relationship between iWUE and leaf N values. In addition, Driscoll et al. (2021a) showed that in adult *E. farinosa* photosynthetic capacities (as measured by N content) were also greater in high iWUE plants, suggesting that these plants may have achieved both a greater rate of carbon gain while experiencing a lower rate of water loss. Lastly, several additional studies that did not include *Encelia* have also noted positive correlations between N and ^{13}C content among different taxa. These include a study on photosynthetic-stem species in the Mojave and Sonoran Deserts (Avila-Lovera et al. 2019) and global syntheses of ^{13}C observations in angiosperm and gymnosperm species (Adams et al. 2016; Cornwell et al. 2018; Prentice et al. 2011). However, these studies did not include growth observations at any stage of development that might provide insights into the broader connections between iWUE and aspects of plant growth. Thus, the generality of an iWUE-N pattern is unclear, but intriguing and worth further evaluation.

On the potential significance of variations in iWUE in E. farinosa

We posit that there is bi-directional selection for genotypic variations in iWUE values among *E. farinosa* shrubs and that this variation is favored because of interannual environmental heterogeneity in precipitation and VPD associated with high-frequency cycles, such as ENSO, and/or lower-frequency cycles such as the current megadrought. That genetic variation to support bi-directional selection is maintained by an obligate out-crosser pollination requirement, which results in a wide range of iWUE values among germinating seedlings. From earlier studies of carbon isotope ratio values, it is clear that *E. farinosa* populations are highly diverse (Sandquist and Ehleringer 1997, 2003a, b; Schuster et al. 1994). The results of this study support the Schwinning and Ehleringer (2001) concept that high iWUE values should be favored under many arid environmental conditions, perhaps even among drought-deciduous plants such as *E. farinosa* that only maintain leaves during favorable water balance conditions. That trend is supported by the long-term increases in iWUE associated with a warming climate among adult *Ambrosia salsola*, *E. farinosa,* and *E. frutescens* (Driscoll et al. 2020; Kannenberg et al. 2021).

At the same time, selection for low iWUE individuals may persist, because it is these individuals that are most responsive in terms of growth and flowering when wetter spatial micro-environments appear, whether it be the result of competing neighbors removed experimentally, a consequence of natural drought-induced mortality events, or greater precipitation (Comstock and Ehleringer 1993; Ehleringer 1984). That is, when soil water is abundant, increases in leaf conductance, leaf size, and canopy leaf area, were proportionally more responsive in low iWUE plants than in high iWUE plants (Ehleringer 1993). In Fig. 7, we interpret this as indicating that while the *A vs.* c_i/c_a curve differences between low and high iWUE plants persisted, the low iWUE plants achieved higher photosynthetic rates as leaf conductances in low iWUE plants shifted from g_2 to g_3.

While the future dynamics of *E. farinosa* populations are unknown, the results of this study suggest that population scale variations in iWUE values and juvenile recruitment will be influenced by both long-term aridity trends and by the nature of future ENSO cycles. As juvenile recruitment rates ultimately influence adult population densities and ecosystem-scale processes, achieving an understanding of both recruitment and adult survival probabilities is essential for predicting future community composition. It appears that ecophysiological plasticity and genetic variations in parameters such as iWUE will influence long-term viability of *E. farinosa* (and perhaps other drought-deciduous shrubs) in response to increasing aridity, and will ultimately influence the persistence of this species across Mojave and Sonoran Desert landscapes.

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Author contribution statement JRE conceived and designed the observations. JRE and AWD analyzed the data and wrote the manuscript.

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Declarations

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

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