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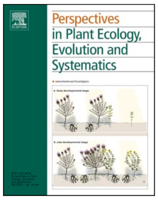

Winter annuals not only escape but also withstand winter droughts: Results from a multi-trait, multi-species approach

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ABSTRACT

Winter annual plants are a dominant life form in drylands. They evade seasonal drought through their life history, but are also exposed to drought within their growing season. Across species, winter annuals differ in traits allowing them to reproduce before a drought occurs (drought escape) as well as in traits minimizing tissue dehydration (drought avoidance) and/or maintaining functioning under drought (drought tolerance). It is yet uncertain how these traits are coordinated and influence winter annuals' performance responses to drought within the growing season and their distribution along rainfall gradients. Understanding these mechanisms is crucial to predict global change impacts in drylands. We measured 22 traits hypothesized to influence whole-plant performance responses to drought in 29 winter annuals common in the Eastern Mediterranean Basin. We examined trait syndromes and linked species' strengths of these trait syndromes with their fecundity responses to an experimental within-season drought, their maximum growth rates (in 18 species), and their distribution along a rainfall gradient. Four trait syndromes emerged: Two were largely consistent with drought avoidance and tolerance, while the other two consisted of traits considered to confer drought escape. Both escape syndromes were differently associated with plant size and therefore referred to as small and tall escape syndrome. Species with a pronounced small escape syndrome showed, albeit weakly, higher fecundity losses under experimental drought. Both species with a pronounced avoidance or tall escape syndrome exhibited higher growth rates, but only annuals with pronounced avoidance traits tended to occur in moister conditions. Our findings highlight that winter annuals, despite their common life history, exhibit several trait syndromes conferring them similar ability to cope with drought in the growing season. Consequently, increasing within-season drought with global change may hardly affect community composition of winter annuals.

1. Introduction

Drylands are considered highly vulnerable to ongoing and projected changes in precipitation regimes associated with climate change (IPCC, 2022). For most drylands, both a decrease in mean annual rainfall and an increase in inter-annual rainfall variability are expected (IPCC, 2022; Maestre et al., 2016). These changes lead to more frequent, longer, and/or intense droughts, i.e. periods of low water availability that result in soil water deficit affecting plant function (see Gilbert and Medina, 2016; Slette et al., 2019, Glossary in Supplement), within the growing season (IPCC, 2022; Maestre et al., 2016). Within-season droughts in drylands last several days to months and affect plant survival, biomass production, and ecosystem services (IPCC, 2022; Metz and Tielbörger, 2023; Ziv et al., 2014). To assess global change consequences in drylands, a comprehensive understanding of the mechanisms underlying species' responses to within-season drought is necessary.

Winter annual plants are a dominant life form in many drylands with winter rainfall, where they substantially contribute to biodiversity and

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ecosystem services (Boyko et al., 2023; Poppenwimer et al., 2023). They grow and reproduce in the favourable, rainy winter season and evade the unfavourable, dry summer season as desiccation tolerant seeds (Friedman, 2020; Kooyers, 2015). Pronounced between-year seed dormancy enables winter annuals to buffer unpredictable catastrophic events, such as drought, within the growing season (Friedman, 2020; Kooyers, 2015). However, as within-season droughts are common in drylands, annuals need to withstand drought as metabolically active plants (Gutterman, 2000; Metz and Tielbörger, 2023; Pérez-Camacho et al., 2012). They thus must exhibit high drought resistance, i.e. a pronounced ability to maintain high whole-plant performance (growth, survival, reproduction) under within-season drought (Fang and Xiong, 2015; Levitt, 1980, Glossary in Supplement). High resistance to within-season drought should be increasingly relevant for the persistence of winter annuals and their communities under global change.

Winter annuals should thus exhibit trait syndromes, i.e. suites of covarying traits (Reich et al., 2003, Glossary in Supplement), which enable them to cope with summer drought and/or rainfall unpredictability, and/or to withstand within-season drought. Interspecific studies show that traits hypothesized to confer drought escape and/or to act as bet-hedging mechanism buffering rainfall unpredictability (e.g. flowering time, seed size, between-year seed dormancy) differ across winter annuals. Species with more pronounced drought escape and/or bet-hedging mechanisms are favoured in drier and/or more unpredictable conditions (e.g. Gremer and Venable, 2014; Harrison and LaForgia, 2019; Metz et al., 2010; Tielbörger et al., 2012; Venable, 2007). Several traits relevant for plant-water relations, such as root traits or turgor loss point, also differ across winter annuals (Funk et al., 2021, 2024; Harrison and LaForgia, 2019; Kurze et al., 2021a, 2021b; Pérez-Ramos et al., 2019; Wilcox et al., 2021). However, the interplay of all these traits influencing species' resistance to within-season drought in winter annuals remains largely unexplored.

Three main trait syndromes are considered to minimize whole-plant performance losses under drought, i.e. they constitute ecologically successful plant strategies: drought escape, drought avoidance, and drought tolerance (*sensu* Levitt, 1980). The syndromes are not mutually exclusive, but functional links, trade-offs, or coordinated selection pressures preclude certain trait combinations (Levitt, 1980). *Drought escape* enables species to evade drought in time by early reproduction combined with bet-hedging mechanisms (Grime, 1977; Kooyers, 2015; Levitt, 1980, for details on traits see Table S1). *Drought avoidance* minimizes tissue dehydration by traits optimizing water uptake and water storage capacity, and minimizing transpirational water loss (Fang and Xiong, 2015; Kooyers, 2015, for details see Table S1). *Drought tolerance* enables plants to continue physiological processes under drought by maintaining cell turgor and water transport (Fang and Xiong, 2015, for details see Table S1). Both drought avoidance and tolerance can thus confer plants high drought resistance, though by different traits and mechanisms (Fang and Xiong, 2015; Levitt, 1980). In winter annuals, we are far from understanding how traits are coordinated into syndromes and how these syndromes are related to species' whole-plant performance responses to drought and their distribution along rainfall gradients. Accordingly, we do not know which trait syndromes constitute ecologically successful strategies in annuals in the face of increasing within-season drought.

That traits and their syndromes influence species' performance and fitness responses to environmental factors is a fundamental assumption of trait-based ecology and the basis for using traits to project species' responses to the environment (Laughlin et al., 2020; Shipley et al., 2016). However, studies that explicitly test these relations among species are limited (Laughlin et al., 2020; Shipley et al., 2016). For perennial species (herbaceous and woody), studies linking traits to species' growth or survival under drought support the relevance of drought avoidance or tolerance traits (e.g. Álvarez-Cansino et al., 2022; Balachowski et al., 2016; Martínez-Vilalta et al., 2010; McGregor et al., 2021; Powers et al., 2020; Sun et al., 2020). However, the observed relations were often surprisingly weak and the link to species' fitness responses remained elusive.

Annuals offer a straightforward opportunity to assess species' fitness responses, since lifetime fecundity of individuals can be directly assessed as product of seed number and seed mass, comprising the number of possible offspring and probability of plant survival (Laughlin et al., 2020). Nevertheless, to date, only a few interspecific studies examined relations between traits and species' fitness responses or performance responses to drought in annuals. They suggest that mostly traits associated with drought avoidance confer annuals higher resistance to within-season drought (Harrison and LaForgia, 2019; Huxman et al., 2013; Kimball et al., 2012). However, these studies focused on a few traits and a few species, rendering generalizations difficult. The identification of syndromes requires comparative assessment of a wide range of potentially relevant traits in multiple species to avoid missing relevant trait coordinations (see Laughlin, 2014). Furthermore, to rigorously test whether emerging syndromes constitute ecologically successful strategies, species' strengths of the syndromes need to be linked to their performance responses to drought, and the effect of low water availability must be experimentally isolated from other factors that may influence plant performance under dry conditions (e.g. light, nutrients) (Gilbert and Medina, 2016; Laughlin et al., 2020; Shipley et al., 2016).

Drought resistance is widely assumed to be traded-off against maximum growth rates, since drought avoidance and tolerance traits that increase drought resistance should be associated with slow growth rates (and a conservative resource-use strategy; Levitt, 1980; Reich, 2014). A growth-drought resistance trade-off influences the ecological filtering of species along moisture gradients: species with high drought resistance but slow growth should be favoured under drier conditions, while species with low drought resistance and high growth rates, which enable them to withstand competition, should be favoured under moist conditions (Reich, 2014). The expected trade-off and its consequences for species' distributions across moisture gradients has been shown based on survival responses in perennials (Griffin-Nolan et al., 2019; Reich, 2014; Volaire et al., 2023). In winter annuals, a growth-drought resistance trade-off emerged based on fecundity responses (Huxman et al., 2013; Kimball et al., 2012). It should lead to an incompatibility (trade-off) of drought escape (associated with high growth rates to quickly achieve size for reproduction, see Kooyers, 2015) against strategies that increase drought resistance, namely drought avoidance or tolerance, i.e. annuals with a pronounced escape syndrome should be susceptible to drought before seed production.

The growth-drought resistance trade-off should influence the ecological filtering of winter annuals and their distribution along rainfall gradients. Annuals with a pronounced escape syndrome should occur under arid conditions with low, unpredictable rainfall in a short rainfall season, since escape traits enable them to finish reproduction within the short rainfall season and to buffer rainfall unpredictability (Kooyers, 2015; Manzaneda et al., 2015). Towards moister conditions, rainfall is higher and more predictable, but the longer growing season is still frequently interrupted by drought, which can cause significant mortality in annuals (Pérez-Camacho et al., 2012; Ziv et al., 2014). Thus, annuals with more pronounced avoidance or tolerance traits should be favoured under moister conditions. They should withstand drought and reach large sizes by capitalizing on the entire duration of the growing season to successfully cope with the higher competition intensity prevalent in moister conditions. Contrary to the assumed consequences of the growth-drought resistance trade-off in perennials, we therefore hypothesized an interspecific shift in winter annuals from fast-growing species with a pronounced escape syndrome to slow-growing species with a pronounced avoidance and/or tolerance syndrome with increasing rainfall.

Here, we comparatively measured 22 traits assumed or shown to influence species' whole-plant performance responses to drought in 29 winter annual species of semi-arid rangelands from the Eastern

Mediterranean Basin under common conditions. We included mechanistic traits (10 out of 22 traits), i.e. traits whose function in plant-water relations can be clearly physiologically defined (*sensu* Brodribb, 2017). These traits pertained to water uptake, storage, transport, and loss, with several of them being associated with short-term physiological responses of plants to drought (see Table S1 for details). We additionally considered more easily measurable functional traits (*sensu* Brodribb, 2017 and Violle et al., 2007), which are widely used and hypothesized to explain species' performance responses to drought but having a looser association with physiological processes, as well as life-history traits hypothesized to be relevant for drought escape (see Kooyers, 2015). We purposely considered a large trait set to gain a comprehensive insight in trait syndromes. We assessed the coordination of traits into syndromes. To evaluate the ecological relevance of the identified syndromes, we related species' strengths of the trait syndromes with their fecundity responses (as proxy for species' fitness responses) to an experimental drought during the growing season and with their maximum growth rates. In addition, we analyzed the relation between species' strengths of the trait syndromes and their distribution along a steep, regional rainfall gradient. We tested the following hypotheses:

(1) Traits relevant for whole-plant performance responses to drought in winter annuals are coordinated along three major axes, reflecting syndromes consistent with drought escape, avoidance, and tolerance.
(2) Species' fecundity losses in response to drought and their growth rates decrease with a more pronounced avoidance and/or tolerance syndrome (associated with slow growth) but increase with a more pronounced escape syndrome (associated with fast growth). Consequently, growth rates are traded-off with fecundity responses to drought (growth-drought resistance trade-off).
(3) Along a rainfall gradient, winter annuals with a more pronounced escape syndrome are associated with arid conditions, while species with a more pronounced avoidance and/or tolerance syndrome are associated with moister conditions.

2. Material and methods

2.1. Study species and plant material

The study focused on 29 winter annual species from the Eastern Mediterranean Basin, including 21 forbs (six families, including six legumes) and eight grasses (see Table S2). Species selection considered the following criteria: (1) commonness in the region, (2) coverage of different distribution ranges along rainfall gradients in Israel (based on BioGIS, 2018), (3) inclusion of several plant families, and (4) seed availability. All species had C3 photosynthesis. Traits were determined for all 29 species. Fecundity response to drought and maximum growth rate were assessed in a subset of 18 species with sufficient seeds (Table S2).

Seeds were collected in Israel, in two sites 40 km apart from each other (Lahav and Matta, for details see Tielbörger et al., 2014), in April 2012. For trait measurements (except seed dormancy) and the drought experiment, we grew plants under common, favourable conditions (i.e. high light, nutrient, and water availability, no competition, temperature 20–26°C) in a greenhouse from F1 seeds during winter in Bayreuth, Germany (see details in Method S1). This approach enabled us to directly compare traits and fecundity responses across species, and to minimize potential uncontrolled intraspecific variation due to trait plasticity, ecotypic differentiation, or maternal effects. Trait plasticity in response to drought is commonly considerably smaller than interspecific trait differences, especially in large multi-species comparisons (Funk et al., 2021; Garnier et al., 2001; Kramp et al., 2022), as we conducted here.

2.2. Measurements of traits and maximum growth rate

We measured 22 mechanistic, functional, and life-history traits in 5–14 replicates per species under common, favourable conditions (see above and details in Method S1). We chose traits that are involved in processes in plant-water relations (i.e. water uptake, storage, loss, and transport) and/or are known or assumed to influence species' whole-plant performance response to drought (see Table 1 for an overview and Table S1 for details).

We followed standardized protocols for trait measurements (see Method S2 for details).

Maximum absolute growth rate was measured as biomass increase per day under high resource conditions (irrigated, fertilized, high light) from germination until 16 weeks after sowing on 6–9 replicates per species (see Method S3 for details). In this period, all species showed substantial vegetative growth and none stopped growing due to senescence. Maximum absolute growth rate thus indicates maximum vegetative biomass production per unit time and is not equivalent to total biomass, quantifying biomass production during the whole life cycle (Pearson correlation coefficient $R = 0.55$, $p = 0.018$, Table S4).

2.3. Drought experiment

To comparatively assess species' fecundity responses to a period of low water availability during the growing season (within-season drought), we conducted a drought experiment. Given the highly variable nature of drought in our study region (see 2.4.), we did not attempt to simulate a specific drought. We though exposed all plants to the same soil water content to induce soil drying independently of plants' individual transpiration rate, reflecting natural conditions.

Plants were exposed to a drought treatment for 46 days (i.e. about 6.5 weeks) or were maintained under irrigated control conditions. Each treatment included 8–10 individuals per species. To apply a within-season drought, the drought treatment started 16 weeks after sowing when approximately half of the species had started flowering, but none had produced ripe seeds (i.e. none escaped the experimental drought), i.e. species were affected in their vegetative and/or start of reproductive phase. After the drought period, the plants were re-watered and received the same amount of water as control plants for ca. 9–12 weeks until they were harvested at the end of their life cycle (indicated by leaf senescence in most species).

In the drought treatment, we took special care that drought intensity was equivalent across species, i.e. all species were dried out at a similar rate through differential watering and were then maintained at non-lethal soil water contents of 3–4 % (compared to 10 % in the control group) by a gravimetric method (see Method S4 and Figure S1 for details; Sack, 2004). Soil water content was determined by weighing the pots every day. This approach avoided that species with higher transpiration rates dry out faster and assured the comparability of fecundity responses to drought across species (Sack, 2004). All species showed strong signs of wilting (e.g. leaf rolling, folding) during the drought, with approximately half of them showing some leaf necrosis.

To assess species' fecundity responses to drought, we measured total seed weight of each plant (TSW, TSW = seed number * seed mass, see Method S3) at the end of its life cycle. The few (6 %) individuals that died before reproduction were included in fecundity calculations (as TSW = 0). Fecundity response (FR) of each species was calculated as response ratio (Hedges et al., 1999) of mean total seed weight between drought-stressed and control plants ($FR = \log [\text{mean } TSW_{drought}/\text{mean } TSW_{control}]$). A more negative value indicates a stronger negative response of species' fecundity to drought. We consider species' fecundity response a solid proxy for species' fitness response to drought (and reciprocally for their drought resistance), since it comprises both the number of possible offspring (i.e. seed number) and the probability of plant survival, which is related to seed mass (Metz et al., 2010).

Table 1

Traits considered in this study with their abbreviations and units. They are categorized as mechanistic traits, i.e. traits whose function in plant-water relations can be clearly physiologically defined (*sensu* Brodribb, 2017), functional traits (*sensu* Brodribb, 2017 and Violle et al., 2007), which are widely used and hypothesized to explain species' whole-plant performance responses to drought, and life-history traits hypothesized to be relevant for drought escape (see Kooyers, 2015). For each trait, we indicate whether it is considered to confer drought avoidance, tolerance, or escape (*sensu* Levitt, 1980) based on prior knowledge of their function in plant-water relations or for whole-plant performance responses to drought. + or - indicates whether a high or low trait attribute is considered favourable for whole-plant performance under drought. We did not make any *a priori* assumption for the coordination of traits into syndromes. Detailed information on the traits, their function in plant-water relations, and their measurements are given in Table S1 and Method S2.

Trait	Abb.	Unit	Escape	Avoidance	Tolerance
Mechanistic traits					
Turgor loss point	TLP	MPa		+	-
Minimum leaf conductance	gmin	mmol/ (m^{2} * s)		-	
Leaf xylem vessel diameter	XVdiam	µm			-
Leaf tissue density	LTD	g/cm^{3}			+
Root tissue density	RTD	g/cm^{3}			+
Relative leaf water content	LWC	-		+	
Relative root water content	RWC	-		+	
Instantaneous water-use efficiency	WUEinst	µmol CO$_{2}$ /mmol H$_{2}$O		+	
Leaf carbon isotope ratio (integrated WUE)	WUEint	‰		+	
Specific root length	SRL	m/g		+	
Functional traits					
Photosynthetic rate	Photo	µmol/ (m^{2} * s)	+		
Specific leaf area	SLA	mm^{2}/ mg	+	-	
Leaf area	LA	cm^{2}			-
Leaf thickness	Lthick	mm		+	
Leaf mass fraction	Leaf MF	g/g	+	-	
Root mass fraction	Root MF	g/g	-	+	
Life-history traits					
Seed dormancy	Sdormancy	-	+		
Age at flowering onset	Flower Onset	days	-		
Leaf number at flowering	Leaf Number	count	-		
Reproductive mass fraction	Rep. MF	g/g	+		
Height at end of the life cycle	Height	cm	-		
Total biomass	Tot. Biomass	g	-		

2.4. Species' distribution across rainfall gradients

Israel comprises steep rainfall gradients with a 40-fold increase from low and unpredictable rainfall in a short rainy season in winter (summer rain is almost missing) in arid (desert) areas in the south and near the Dead Sea (east) (20 mm/year ± 55 %, mean ± CV, December/January-March) to higher and more predictable rainfall in a longer rainy season in mesic-Mediterranean areas in the north and west (up to 800 mm/year ± 18 %, rainy season October/November-April/May, Ziv et al., 2014). Rainfall frequently, but unpredictably, subsides for days or weeks within the rainfall season along the whole gradient, imposing drought that differs in timing, intensity, and length, with pervasive consequences on plant performance (Saaroni et al., 2015; Ziv et al., 2014).

We characterized species' distribution along the rainfall gradient in Israel by their mean annual rainfall niche provided by the database BioGIS (2018). Species' mean annual rainfall niche was calculated as the average of mean annual rainfall across all occurrences (based on presence/absence data) of a species based on independent biological records (BioGIS, 2018).

Mean annual rainfall is positively related to rainfall season length (corresponding to growing season length), and negatively associated to inter-annual rainfall variability and the length of drought periods in the rainfall season (Kurze et al., 2017; Ziv et al., 2014). Species' mean annual rainfall niche thus reflects species' distribution with respect to various metrics of rainfall patterns.

2.5. Statistical analyses

We identified the main axes of trait variation to assess continuous trait syndromes, and evaluated if species' scores along these axes, representing the strength of the respective trait syndrome, are related to their fecundity responses to drought, their maximum growth rates, and their mean annual rainfall niches.

Species differences in each of the 22 traits and in growth rate were tested with F-tests on linear models (LM). Several traits were natural log-transformed (see details in Table S3) to improve normality and homoscedasticity.

We evaluated the coordination of traits across all species with a principal component analysis (PCA) based on centred and standardized species' mean trait values using the prcomp function. Leaf tissue density was excluded from the PCA due to its high correlation (Table S4) and functional similarity to leaf water content. Excluding this trait did not qualitatively influence the trait coordinations. The emerged trait coordinations along the principal components (PC) were *a posteriori* compared to the trait syndromes considered to confer the strategies of drought escape, avoidance, and tolerance according to Levitt (1980) (see Table S1 and Table 1 for an overview), and in case of consistency named accordingly. To facilitate the interpretation of emerged trait coordinations, we also conducted an orthogonal axis rotation of PC 1 to PC 3 using the varimax function. A PCA with the subset of 18 species with growth rate and fecundity response measurements as well as a PCA with phylogenetic independent contrasts (see Method S5 for details) gave similar species' scores along the PCs as the PCA with the full set of 29 species without phylogenetic correction (Pearson correlation coefficients for PC 1-PC 3 $|R| \geq 0.49$). Therefore, we consistently used species' scores based on the PCA with the entire species set without phylogenetic correction for all following analyses.

The effect of the experimental drought on fecundity, seed number, and seed mass was tested with F-tests on LMs, and the effect on the proportion of reproducing individuals with Chi^{2}-tests on a generalized linear model (GLM) with binomial error distribution (logit link). In all models, we considered species, treatment (drought *vs.* control), and their interaction as explanatory variables. To improve normality and homoscedasticity, fecundity and seed number were natural log-transformed after adding 0.5 and 100, respectively.

We evaluated whether species' fecundity responses to drought, their maximum growth rates, or their mean annual rainfall niches were related to their scores along the PCs, i.e. the strengths of their trait syndromes, with F-tests on separate LMs. Each LM comprised one response variable (i.e. species' mean values of fecundity response, growth rate, or mean annual rainfall niche) and species' scores along the first three PCs as explanatory variables. Interactions between species' scores along the PCs were not significant and were excluded from final models to avoid overfitting. To directly test for a growth-drought resistance trade-off, we evaluated the relation between maximum growth rates and fecundity responses with a F-test on a LM. We also tested for relationships between mean annual rainfall niches, growth rates, and fecundity responses with F-tests on separate LMs. Species' minimum and maximum rainfall niches (based on BioGIS, 2018) were also considered, but no significant relation emerged (results not shown).

Pairwise correlations between single traits (species' average trait values), species' fecundity responses, maximum growth rates, or mean annual rainfall niches were assessed with Pearson correlation coefficients.

All analyses were conducted with R 3.6.1 (R Core Team, 2019).

3. Results

3.1. Interspecific trait differences and trait syndromes

All 22 traits and maximum growth rate differed across species (all traits $p < 0.001$, up to 52-fold variation, Table S3). Pairwise trait correlations were mostly weak (Table S4). Some significant relations, mainly between life-history and functional traits and between mechanistic traits, emerged (Table S4).

The main trait coordinations emerged along three axes (PC 1 to PC 3,

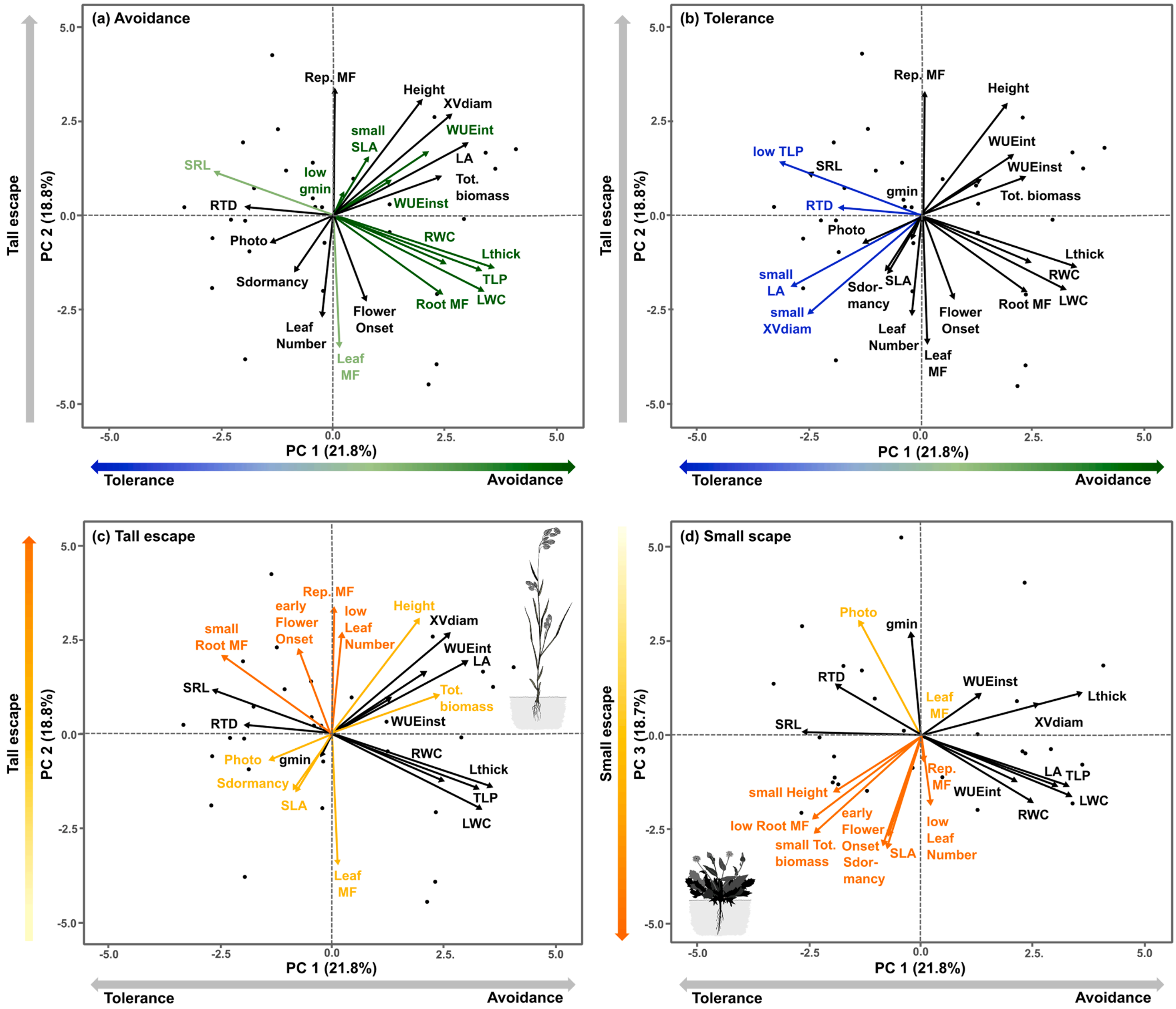

Fig. 1. Coordination of 21 traits hypothesized to influence species' whole-plant performance responses to drought in 29 winter annuals along PC 1 to PC 3 of a principal component analysis. In a, b, and c PC 1 and PC 2 and in d PC 1 and PC 3 are shown. Trait arrows in each panel were coloured according to the assumed association of traits with the strategies of drought avoidance (a, green), drought tolerance (b, blue) and drought escape (c, d, orange) and trait arrows point to the direction of expected minimized fecundity losses under drought in the respective syndrome. In a, c, and d, trait attributes whose association emerged contrary to general expectation are depicted in a lighter shade. Traits not considered to be associated with the respective syndrome are shown in black (assumptions followed Kooyers 2015 and Levitt 1980, see Table S1 for details). In c and d exemplary species for both syndromes are shown (c, *Briza maxima*; d, *Hedypnois rhagadioloides*), drawn by DharmaBeren Studio (https://www.dharmaberen.com/). Table 1 gives trait abbreviations, Fig. 2 trait loadings on PC 1-PC 3, Fig. S4 and S6 species identities and trait coordination along PC 2 and PC 3.

each explaining >18 % of variation, Fig. 1). Species with high scores on PC 1 (Fig. 1a, Fig. 2a, Figures S4-S5) exhibited thick leaves, high tissue water content, high turgor loss point, high root mass fraction, and high water-use efficiency, i.e. traits considered to confer drought avoidance. Additionally, these species exhibited large size (height and biomass). Species with low (negative) scores on PC 1 exhibited low turgor loss point, small leaf area, small xylem vessel diameter, and high root tissue density, i.e. traits considered characteristic for drought tolerance, but also high specific root length (Fig. 1b, Fig. 2a, Figures S4-S5). Thus, avoidance and tolerance traits were associated with the opposite sides of PC 1, indicating that annuals ranged along a continuum from more pronounced drought avoidance to more pronounced drought tolerance. In the following, we refer to PC 1 as the avoidance-tolerance axis and termed the respective trait syndromes at the opposite sides of this axis as drought avoidance and drought tolerance.

Species with high scores on PC 2 and low scores on PC 3 were mainly characterized by life-history traits. They exhibited early flowering onset at a low leaf number combined with low root mass fraction (Fig. 1c, d, Fig. 2b, c, Figures S4-S6), i.e. traits considered characteristic for drought escape. Species with high scores along PC 2 additionally exhibited high reproductive mass fraction as characteristic trait of drought escape, but also several trait attributes usually not considered to be associated with escape, such as low leaf mass fraction, large height, low seed dormancy, large xylem vessels, and large leaves (Fig. 1c, Fig. 2b, Figures S4-S6). Species with low scores on PC 3 exhibited several additional traits considered characteristic for escape, such as high seed dormancy, high specific leaf area, small size, but unexpectedly combined with low photosynthetic rate (Fig. 1d, Fig. 2c, Figures S4-S6). We *a posteriori* refer to PC 2 and PC 3 as the tall escape and the small escape axis/syndrome, respectively, based on their different association with plant size (total biomass and height).

3.2. Drought effects on species' fecundity

The experimental within-season drought reduced species' fecundity, with the response size varying across species (Figure S3, LM statistics: species $F_{17,320} = 98.22$, $p < 0.001$; treatment $F_{1,320} = 8.84$, $p = 0.003$; interaction $F_{17,320} = 1.62$, $p = 0.057$, $R^2 = 0.82$). The response of individual species ranged from fecundity reductions by 50 % in drought-stressed compared to control plants to no significant response (equal fecundity of drought-stressed and control plants, no overyielding was observed). Fecundity declines were due to decreases in seed number and seed mass, while the few individuals (6 %) that died before reproduction had no effect (see Figure S3 for details).

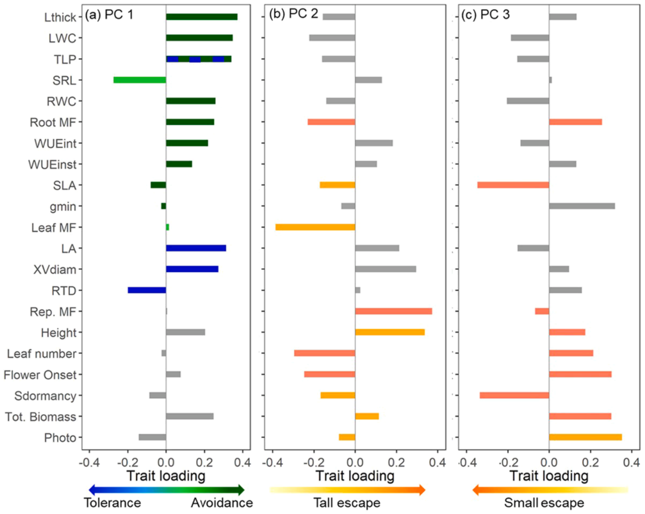

Fig. 2. Loadings of the 21 traits hypothesized to influence species' whole-plant performance responses to drought on the first three axes of a principal component analysis (compare Fig. 1). PC 1 (a) was mainly associated with traits considered to confer drought avoidance (green) and tolerance (blue), and PC 2 (b) and PC 3 (c) with escape traits (orange). Traits coordinated contrary to general expectation are depicted in a lighter shade. Traits not considered to be associated with the respective syndrome are grey (assumptions followed Kooyers 2015 and Levitt 1980, see Table S1 for details). Traits are ordered based on their association with the syndromes and loadings on PC 1, for trait loadings on rotated axis see Fig. S5.

3.3. Relations between species' scores along the axes, their fecundity responses to drought, their maximum growth rates, and their distribution along the rainfall gradient

Species' scores along the small escape axis (PC 3) were marginally significantly related with their fecundity responses to drought in the growing season ($p = 0.051$): annuals with a more pronounced small escape syndrome exhibited higher fecundity losses (Fig. 3c, Table S5). Species' fecundity responses were independent from their scores along the tall escape axis (PC 2) and the avoidance-tolerance axis (PC 1) (Fig. 3a-b, Table S5).

Species' maximum growth rates were related with both their scores along the avoidance-tolerance axis (PC 1) and the tall escape axis (PC 2), with species with a pronounced avoidance or tall escape syndrome exhibiting higher growth rates (Fig. 4a, b, Table S5). Species' scores along the small escape axis (PC 3) were independent from growth rate (Fig. 4c, Table S5). Species' maximum growth rates were also unrelated to their fecundity responses to drought, i.e. no growth-drought resistance trade-off emerged (Fig. 4d, Table S5). Consistently, growth rate and fecundity response were correlated with different traits (Table S4). Growth rate was not traded-off with any single trait but positively associated with four traits (total biomass, leaf area, xylem vessel diameter, integrated water-use efficiency), while fecundity response was positively correlated with photosynthetic rate, and negatively with specific leaf area and root water content (Table S4).

Species' mean annual rainfall niches were marginally significantly related to their scores along the avoidance-tolerance axis (PC 1, $p = 0.06$), indicating an interspecific shift from drought tolerance under arid conditions to avoidance towards moister conditions (Fig. 5a, Table S5). However, species' mean annual rainfall niches were independent from species' scores along both escape axes (PC 2, PC 3), fecundity responses to drought, maximum growth rates, and all single traits (except leaf area and root tissue density, Fig. 5b, c, Figure S7, Tables S4-S5).

4. Discussion

In our multi-trait, multi-species approach, we measured for the first time a comprehensive set of mechanistic traits directly related to plant-water relations alongside functional and life-history traits across winter annuals. This analysis of a broad trait set identified four main trait syndromes. Two syndromes aligned with strategies for drought avoidance and tolerance, while the other two reflected traits considered to confer drought escape (small and tall escape syndrome) (see Kooyers, 2015; Levitt, 1980). Species' strengths of the small escape syndrome were related to their fecundity responses to experimental drought, and species' strengths of the tall escape, avoidance, or tolerance syndrome were associated with their maximum growth rates and/or their distribution along the rainfall gradient. The relations to species' fecundity responses and growth rates highlight that the emerging trait syndromes are ecologically relevant strategies in winter annuals.

4.1. Syndromes of avoidance, tolerance, and escape traits in winter annuals

The drought avoidance and tolerance syndromes in our study annuals aligned with trait combinations that allow perennial herbaceous

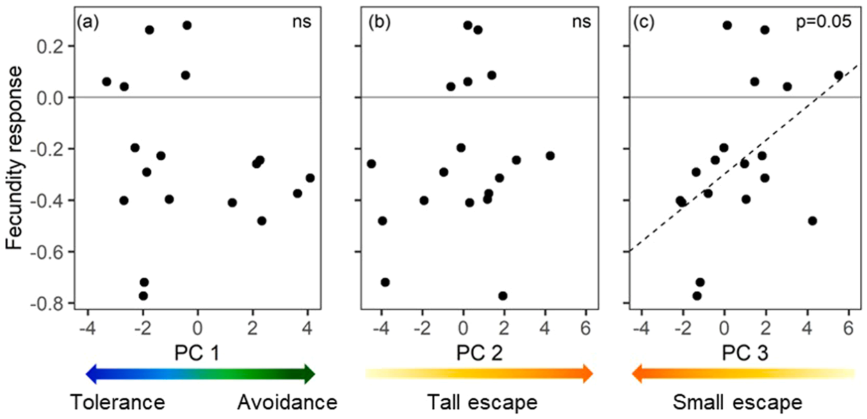

Fig. 3. Relations between species' fecundity responses to experimental drought in the growing season and their scores along the (a) avoidance-tolerance axis (PC 1), (b) tall escape axis (PC 2), and (c) small escape axis (PC 3) in 18 annual species. Significances (ns not significant, dashed line for marginal significance) are given, for statistical details see Table S5.

and woody species to withstand drought (e.g. Kramp et al., 2022; Martínez-Vilalta et al., 2010; Powers et al., 2020; Sun et al., 2020). Drought avoidance and tolerance syndromes traded-off against each other across our study annuals, a pattern also observed among populations in a perennial grass (Bristiel et al., 2018).

In addition, the winter annuals stood out as presenting not only one but two drought escape syndromes. The tall escape syndrome encompassed key traits of drought escape (i.e. early reproduction, high reproductive allocation, low root allocation, see Kooyers, 2015), but also several trait attributes that are opposite to the direction usually expected to confer escape (e.g. large height, low seed dormancy), and some traits not previously considered in this context (e.g. large xylem vessels). The small escape syndrome was consistent with the widely recognized trait combination that confers drought escape (Kooyers, 2015; Levitt, 1980).

Both escape axes were independent of the drought avoidance-tolerance axis, i.e. winter annuals ranged along a continuum of trait combinations pertaining to more or less pronounced drought escape (tall or small escape syndrome) combined with more or less pronounced avoidance or tolerance. This finding suggests that winter annuals differ in both their ability to escape summer drought and to withstand within-season drought. Our study annuals are also a functionally diverse group with trait variation comparable to that found in similar-sized species groups of perennials (see also Angert et al., 2009; Harrison and LaForgia, 2019; Kurze et al., 2021a).

4.2. *Relations of species' trait syndrome strengths with their fecundity responses to drought and their maximum growth rates*

Species with a pronounced small escape syndrome (including pronounced between-year seed dormancy) exhibited high fecundity losses when exposed to within-season drought in our experiment, as expected. This negative relation highlights the importance of pronounced between-year seed dormancy buffering reproductive failure in the small escape strategy. The importance of between-year seed dormancy for species' population dynamics in the long term (i.e. across years) has been previously shown (DeMalach et al., 2021; Huang et al., 2016; Kimball et al., 2012; Venable, 2007). Our findings emphasize that the small escape strategy influences fecundity responses to drought *even* within the growing season.

Species' fecundity responses to the experimental drought were unexpectedly not related to the emerging drought avoidance or tolerance trait syndromes. Both syndromes may become relevant under longer, more intense within-season drought when species die before reproduction (see Harrison and LaForgia, 2019) and/or when drought interacts with biotic interactions. Here, we purposely applied a non-lethal drought to assess fecundity responses independent of plant mortality and separated the effect of low soil water availability from other factors affecting plant's performance.

In accordance with the growth-stress resistance hypothesis (Reich, 2014), we expected that drought avoidance and tolerance are associated with low growth rates and that the widely considered escape syndrome (i.e. the small escape syndrome in our study species) is associated with high growth rates. Instead, annuals with a more pronounced avoidance or tall escape syndrome exhibited higher growth rates and growth rates were independent of the small escape syndrome. Consistently, but contrary to the expected growth-drought resistance trade-off, species' maximum growth rates were independent of fecundity responses to drought. A growth-drought resistance trade-off based on fecundity responses thus does not generally emerge in winter annuals. Also in perennial herbaceous species, a few studies found no support for the growth-drought resistance trade-off (Fernández and Reynolds, 2000; Jung et al., 2020). These findings caution against generalizing this trade-off within and across life forms.

4.3. *Relations of species' trait syndrome strengths with their distribution across rainfall gradients*

We hypothesized an interspecific strategy shift from escape in arid conditions to drought avoidance and tolerance in moister conditions. Instead, annuals with pronounced escape traits were distributed across the whole gradient in our study system. Only a weak shift from tolerance under drier to avoidance under moister conditions occurred. Species with a pronounced avoidance syndrome were large and exhibited high maximum growth rates, likely enabling them to outcompete tolerators towards moister conditions, where competition is more intense (Schiffers and Tielbörger, 2006). Species' rainfall niche differed more towards the moister than drier end of the gradient (BioGIS, 2018). Accordingly, biotic factors like competition or pest pressure should influence species' distribution more than drought intensity or unpredictability. This likely explains the independence between species' rainfall niches and fecundity responses to drought in our study annuals.

4.4. *Weak relations between the strengths of species' trait syndromes and their fecundity response to drought and distribution*

We identified strategies in winter annuals based on a wide range of mechanistic, functional, and life-history traits assumed or known to influence whole-plant performance responses to drought. However, the relations between species' strengths of several strategies and their fecundity responses or distribution along the rainfall gradient were weak (maximum explained variance $R^2 = 0.16$). The weak relations

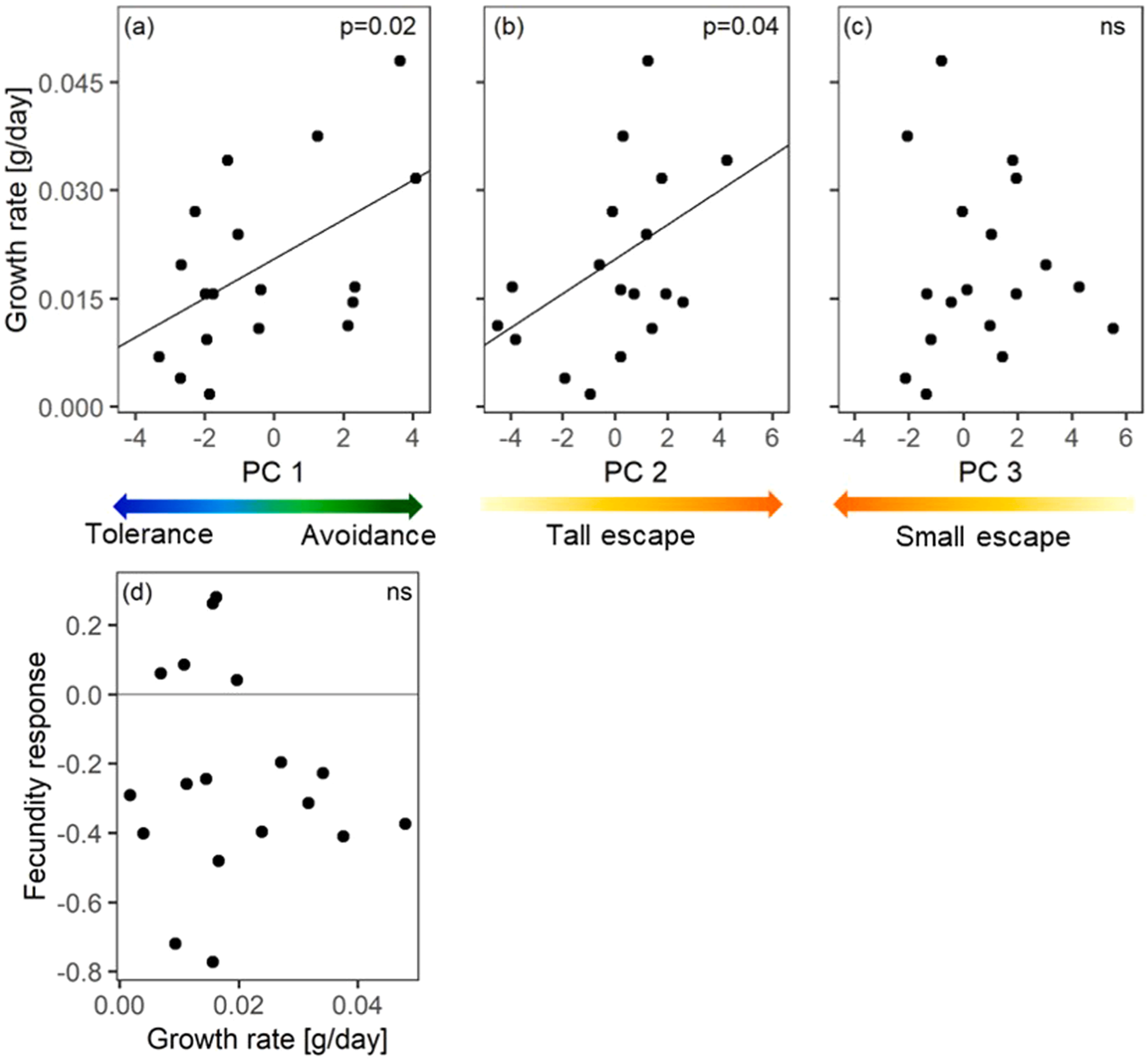

Fig. 4. Relations between species' maximum growth rates and their scores along the (a) avoidance-tolerance axis (PC 1), (b) tall escape axis (PC 2), and (c) small escape axis (PC 3); and (d) the relation between species' fecundity response (proxy for drought resistance) and maximum growth rate in 18 annual species. Significances (ns not significant) are given, for statistical details see Table S5.

indicate that annuals with a wide range of trait combinations showed similar fecundity responses to drought or distribution, i.e. they can co-occur under similar conditions. These results align with theoretical models and findings in perennials (Marks and Lechowicz, 2006; Sun et al., 2020; Zwicke et al., 2015) as well as observations in annuals of our study region (García-Camacho et al., 2017). In annuals, observed co-occurrence of species with different trait combinations has been attributed to stabilizing niche differences, small-scale variability, and/or temporal variability of environmental factors (mainly rainfall), with often seed traits mediating this co-occurrence (Angert et al., 2009; Chesson et al., 2004; Kimball et al., 2012; Kraft et al., 2015). Our results extend these previous findings by showing that annuals with different trait combinations can perform equally well during within-season drought or under specific rainfall regimes. The species may nevertheless be filtered by the environment based on their seed or seedling traits.

Our findings are based on traits measured under common, favourable conditions. This approach does not explicitly consider trait plasticity that may improve the explanatory power of traits on species' performance responses and allows classifying species according to further trait-based concepts (Couso and Fernández, 2012; Larson et al., 2020; Volaire, 2018). However, trait plasticity in response to drought is often considerably smaller than interspecific differences (Funk et al., 2021; Garnier et al., 2001; Kramp et al., 2022), as also observed in morphological root traits in our study species (Kurze et al., unpublished data). Additionally, several of the traits we included are closely associated with physiological processes and trait plasticity in response to drought. Our approach also did not address adaptation of populations to local (moisture) conditions, small-scale variation of soil moisture in time and space, or changes in species' abundance, which can be relevant for detecting species' ecological filtering (Anderegg, 2023; Bruelheide et al., 2018). Yet, similar datasets as ours have revealed relations between species' trait syndromes and performance responses to drought or

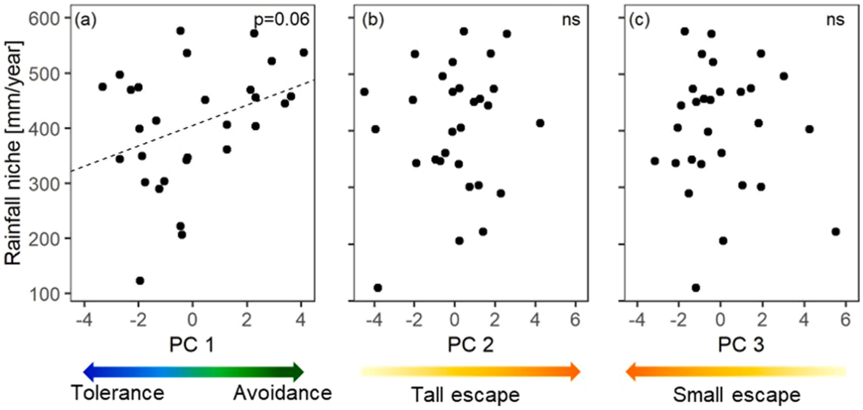

Fig. 5. Relations between species' mean annual rainfall niches, i.e. species' distribution along the rainfall gradient, and their scores along the (a) avoidance-tolerance axis (PC 1), (b) tall escape axis (PC 2), and (c) small escape axis (PC 3) in 29 annual species. Significances are given (ns not significant, dashed line for marginal significance), for statistical details see Table S5.

distribution in different ecosystems (e.g. Álvarez-Cansino et al., 2022; Funk et al., 2024; Griffin-Nolan et al., 2019; Powers et al., 2020; Thuiller et al., 2004). Thus, it is unlikely that we overlooked strong interspecific relations between species' trait syndrome strengths and their fecundity responses to drought or distribution. Regardless of the reasons for the weak relations, our findings join a growing body of literature challenging the premise of trait-based ecology that species' responses to the environment can be inferred solely and directly from "simple" trait measurements under favourable conditions (see Anderegg et al., 2023; Kraft et al., 2015).

5. Conclusions

Winter annuals exhibit, despite their common life-history strategy, syndromes of drought avoidance and tolerance, and two escape syndromes. A wide range of trait attribute combinations conferred annuals similar drought resistance and distribution along rainfall gradients. This finding aligns with prior observations of negligible compositional changes in annual plant communities under intensified drought in field experiments in our study system (Tielbörger et al., 2014). Our trait-based approach thus provides insights into the mechanisms that likely underlie plant community composition. It suggests that increasing drought in the growing season with global change (see IPCC, 2022) has limited impact on community composition of winter annuals in the Eastern Mediterranean Basin.

CRediT authorship contribution statement

Bilton Mark C.: Investigation, Conceptualization. **Engelbrecht Bettina M. J.:** Writing – review & editing, Conceptualization. **Álvarez-Cansino Leonor:** Writing – review & editing, Project administration, Funding acquisition, Conceptualization. **Tielbörger Katja:** Project administration, Funding acquisition, Conceptualization. **Kurze Susanne:** Writing – original draft, Methodology, Investigation, Conceptualization.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.ppees.2025.125849.

Data availability

Data will be made available on request.

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