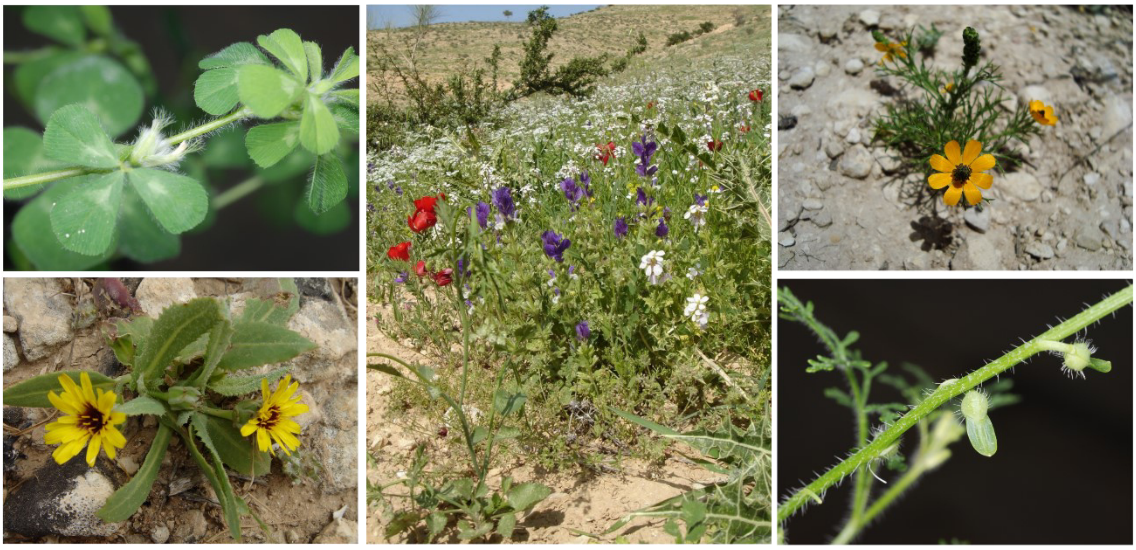
# Trait-based understanding of species' responses to drought and grazing in winter annuals from drylands



*Doctoral Thesis*

Susanne Kurze

# Trait-based understanding of species' responses to drought and grazing in winter annuals from drylands

## Doctoral Thesis

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**Susanne Kurze**

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Doctoral committee:

| | |
|---|---|
| Dr. Leonor Álvarez-Cansino | (reviewer) |
| Prof. Dr. Heike Feldhaar | (reviewer) |
| Prof. Dr. Elisabeth Obermaier | (chairman) |
| JProf. Dr. Johanna Pausch | |

Cover figure. Leaves and flower of *Trifolium pilulare** (top left), *Reichardia tingitana*[#] (bottom left), Winter annual plant community in Wadi Shuayb in Jordan[#] (middle), *Adonis dentata*[#] (top right), Fruit of *Carrichtera annua** (bottom right). © [#]Sara Bangerter, *Susanne Kurze

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# Abstract

A grand challenge in plant ecology is to identify the mechanisms underlying species' responses to the environment. Especially trait-based approaches provide these insights since traits influence plants' functioning. The knowledge of the underlying mechanisms is required to understand and project species' performance, community composition, and ecosystem services, with increasing significance under global change.

In winter annual species, characterized by a life cycle of less than 12 months (germination to plant death), the mechanisms underlying their responses to the environment remain understudied, although winter annuals exhibit a high ecological and economic importance in drylands. Drylands cover approximately 41 % of earth's terrestrial land mass, harbour a large human population, and influence global nutrient, carbon, and water cycles. In addition, they are considered to be particularly vulnerable to global change due to an expected increase of water scarcity and livestock production. Here, I investigated the mechanisms underlying species' responses to drought and grazing in winter annuals on the basis of two trait-based concepts: the *stress response strategies* and the *plant economics spectrum*, using 18 to 30 winter annuals from the southwestern Levant.

According to the concept of *stress response strategies*, three main trait syndromes (i.e. suites of coordinated traits) minimize species' fitness losses under drought and grazing: escape (to evade stress), avoidance (to minimize stress exposure), and tolerance (to maintain physiological functioning under stress). Each syndrome should be differently favoured by the environment, such as along rainfall gradients. I comparatively measured 26 traits and identified the main trait syndromes in the annuals. Species' trait syndrome strengths were linked to (i) their fitness responses (based on fecundity) to drought or grazing within the growing season under common conditions in the greenhouse, (ii) to species' abundance responses to grazing in dry and moist habitats in the field, and/or (iii) to their distribution along a large-scale rainfall gradient.

The winter annuals unexpectedly showed four instead of three main drought response syndromes: avoidance, tolerance, and two escape syndromes (a tall and small escape syndrome). Only species' strengths of the small escape syndrome were associated with their fitness responses to drought, with annuals exhibiting a pronounced small escape syndrome showing high fitness losses. Species with differing strengths of the avoidance, tolerance, and tall escape syndrome partly showed similar fitness responses to drought. This finding indicates that annuals with different trait syndromes can be similarly successful under drought. Accordingly, annual plant community composition may hardly change under (increasing) drought. In respect to grazing, the annuals exhibited an escape and tolerance syndrome, but no avoidance syndrome. Both annuals with a pronounced escape and tolerance syndrome showed low fitness losses under grazing, but only annuals with a pronounced grazing escape syndrome maintained high abundances under grazing in dry habitats. The favouring of the grazing escape syndrome in dry habitats should result from its convergence with the small drought escape syndrome, enabling the annuals to withstand grazing and to escape drought. Annuals' strengths of the drought and grazing response syndromes were (almost) independent from their distribution along the rainfall gradient. On a large scale, annuals with different trait syndromes thus co-occur in a wide range from arid to moister conditions.

The key hypothesis of the *plant economics spectrum* is an interspecific coordination of resource-use related traits along one main axis, resulting in a trade-off among acquisitive and conservative trait attributes at the whole plant level. Species' trait attribute combinations along this axis are hypothesized to influence their growth rate, fitness responses to drought, and distribution along rainfall gradients. I tested this concept based on 12 resource-use related traits in winter annuals.

Contrary to the hypothesis of the plant economics spectrum, structural and carbon gain traits were decoupled (i.e. independent) in the winter annuals. Annuals' trait attribute combinations were (predominantly) independent from their growth rates, fitness responses to drought, and distribution along the rainfall gradient. Accordingly, the plant economics spectrum is not applicable to winter annuals, cautioning to use resource-use related traits to assess their drought responses.

The explicit relations between annuals' strengths of the drought and grazing response syndromes and their fitness responses reinforce a foundational assumption of trait-based ecology, i.e. the interspecific relation between traits and species' fitness responses. The observed relations provide insight into the mechanisms that can be used to project species performance, community composition, and ecosystem functioning in winter annuals under (increasing) drought and grazing. The present findings suggest that increasing drought and grazing under global change will favour annuals with a pronounced escape syndrome (grazing escape and small drought escape syndrome, respectively) with likely pervasive consequences for ecosystem functioning. In contrast, under a hypothetical global change scenario with only rainfall decreases but no changes in grazing intensity, annuals with different trait syndromes should co-occur. Species richness and ecosystem services of annual plant communities under global change will thus strongly depend on human land-use.

# Zusammenfassung

Eine große Herausforderung in der Pflanzenökologie besteht darin, die Mechanismen zu identifizieren, die den Reaktionen von Pflanzenarten auf die Umwelt zugrunde liegen. Dies ist vor allem mit merkmalsbasierten Forschungsansätzen möglich, da die Funktionsweise der Pflanzen von ihren Merkmalen abhängt. Kenntnisse der zugrundeliegenden Mechanismen sind erforderlich, um die Vitalität von Pflanzenarten, die Zusammensetzung von Pflanzengemeinschaften und Ökosystemfunktionen zu verstehen und vorherzusagen. Der globale Wandel erhöht die Notwendigkeit solcher Vorhersagen.

In einjährigen Pflanzenarten, die durch einen Lebenszyklus von weniger als 12 Monaten (Keimung bis Pflanzentod) gekennzeichnet sind, blieben die Mechanismen, die ihren Reaktionen auf die Umwelt zugrunde liegen, bisher weitestgehend unerforscht, obwohl einjährige Arten eine hohe ökologische und ökonomische Bedeutung in Trockengebieten haben. Trockengebiete bedecken weltweit etwa 41 % der Landoberfläche, sind die Lebensgrundlage für einen großen Teil der Weltbevölkerung und beeinflussen den globalen Wasser-, Nährstoff- und Kohlenstoffkreislauf. Zudem gelten sie aufgrund der erwarteten zunehmenden Intensität von Trockenheit und Viehhaltung als sehr anfällig gegenüber dem globalen Wandel. In dieser Arbeit habe ich anhand zwei merkmalsbasierter Konzepte, den *Stressreaktionsstrategien* und dem *pflanzenökonomischen Spektrum*, die Mechanismen untersucht, die den Reaktionen wintereinjähriger Pflanzenarten auf Trockenheit und Beweidung zugrunde liegen. Die Experimente fanden mit 18-30 wintereinjährigen Arten aus der südwestlichen Levante statt.

Basierend auf dem Konzept der *Stressreaktionsstrategien* minimieren drei Merkmalssyndrome (d. h. Kombinationen miteinander assoziierte Pflanzenmerkmale) Fitnessverluste unter Trockenheit und Beweidung: Flucht (zeitliches Entkommen von Stress), Vermeidung (Reduzierung der Stressbelastung) und Toleranz (Erhalt physiologischer Prozesse unter Stress). Jedes Syndrom soll durch die Umwelt, zum Beispiel entlang von Niederschlagsgradienten, unterschiedlich begünstigt werden. Ich habe 26 Merkmale an den wintereinjährigen Arten unter gleichartigen Bedingungen gemessen und die Merkmalssyndrome identifiziert. Die Ausprägung der Merkmalssyndrome in den einjährigen Arten wurde in Beziehung gesetzt zu (i) ihrer Fitnessreaktion (basierend auf ihrer Fruchtbarkeit) auf Trockenheit oder Beweidung innerhalb der Vegetationsperiode unter gleichartigen Bedingungen im Gewächshaus, (ii) ihrer Abundanzreaktion auf Beweidung im Feld in trockenen und feuchten Habitaten und (iii) ihrer Verbreitung entlang eines großräumigen Niederschlagsgradienten.

Die einjährigen Arten zeigten nicht wie erwartet drei, sondern vier primäre Trockenheitsreaktionssyndrome: Vermeidung, Toleranz und zwei Fluchtsyndrome (ein kleinwüchsiges und großwüchsiges Fluchtsyndrom). Nur die Ausprägung des kleinwüchsigen Fluchtsyndroms stand in Beziehung mit der Fitnessreaktion der Arten auf Trockenheit, wobei Arten mit einem ausgeprägten kleinwüchsigen Fluchtsyndrom hohe Fitnessverluste zeigten. Arten mit unterschiedlich stark ausgeprägtem Vermeidungs-, Toleranz- und großwüchsigem Fluchtsyndrom zeigten zum Teil ähnliche Fitnessreaktionen auf Trockenheit. Dieses Ergebnis deutet darauf hin, dass einjährige Arten mit verschiedenen Merkmalskombinationen unter Trockenheit ähnlich erfolgreich sein können, wodurch sich wahrscheinlich die Artenzusammensetzung ihrer Gemeinschaften unter (zunehmender) Trockenheit nur schwach verändert. In Bezug auf Beweidung wiesen die einjährigen Arten ein Flucht- und Toleranzsyndrom, aber kein Vermeidungssyndrom auf. Sowohl Arten mit einem ausgeprägten Flucht- als auch Toleranzsyndrom zeigten geringe Fitnessverluste unter Beweidung. Jedoch nur ein ausgeprägtes Fluchtsyndrom minimierte Abundanzverluste unter Beweidung in trockenen Habitaten. Die hohe Abundanz einjähriger Arten mit einem

Beweidungsfluchtsyndrom in trockenen Habitaten beruht wahrscheinlich auf der Konvergenz des Beweidungsfluchtsyndroms mit dem kleinwüchsigen Trockenheitsfluchtsyndrom. Diese Konvergenz ermöglicht den Arten erfolgreich mit Beweidung umzugehen und Trockenheit zu entfliehen. Die Ausprägung der Trockenheits- und Beweidungsreaktionssyndrome in den einjährigen Arten war (fast) unabhängig von ihrer Verbreitung entlang des Niederschlagsgradienten. Großräumig betrachtet kommen also einjährige Arten mit verschiedenen Merkmalssyndromen in einem weiten Spektrum von ariden bis hin zu feuchten Bedingungen zusammen vor.

Eine Hauptannahme des *pflanzenökonomischen Spektrums* ist die Koordinierung von ressourcenbezogenen Merkmalen zwischen Arten entlang einer Hauptachse, die von erwerbsorientierten zu ressourcenschonenden Merkmalsattributen auf der Ebene der gesamten Pflanze reicht. Die Merkmalsausprägung der Arten entlang dieser Achse soll ihre Wachstumsrate, Fitnessreaktion auf Trockenheit und Verbreitung entlang von Niederschlagsgradienten beeinflussen. Hier wurde dieses Konzept anhand 12 ressourcenbezogener Merkmale an wintereinjährigen Arten getestet. Entgegen der Hypothese des pflanzenökonomischen Spektrums waren strukturelle Merkmale und Merkmale der Kohlenstoffaufnahme entkoppelt (d. h. unabhängig voneinander). Die Merkmalsattribute der Arten waren (überwiegend) unabhängig von ihrer Wachstumsrate, Fitnessreaktion auf Trockenheit und ihrer Verbreitung entlang des Niederschlagsgradienten. Das pflanzenökonomische Spektrum ist daher nicht auf wintereinjährige Arten übertragbar und ressourcenbezogene Merkmale sollten nicht genutzt werden, um ihre Reaktion auf Trockenheit abzuschätzen.

Die expliziten Beziehungen zwischen der Ausprägung der Trockenheits- und Beweidungsreaktionssyndrome in den einjährigen Arten und ihren Fitnessreaktionen bekräftigen eine fundamentale Annahme der merkmalsbasierten Ökologie: die interspezifische Beziehung zwischen Merkmalsattributen und den Fitnessreaktionen der Arten. Diese beobachteten Beziehungen geben Einblick in die zugrundeliegenden Mechanismen, die genutzt werden können um die Reaktion wintereinjähriger Arten, ihrer Gemeinschaften und Ökosysteme auf (zunehmende) Trockenheit und Beweidung abzuschätzen. Die Untersuchungsergebnisse legen nahe, dass zunehmende Trockenheit und Beweidung unter dem globalen Wandel wintereinjährige Arten mit einem ausgeprägten Beweidungs- bzw. kleinwüchsigen Trockenheitsfluchtsyndrom fördern. Dies hat wahrscheinlich erhebliche Konsequenzen für das Ökosystem und seine Dienstleistungen. Unter einem hypothetischen Szenario des globalen Wandels, welches nur eine Abnahme des Niederschlags aber keine Änderung in der Beweidungsintensität umfasst, würden dagegen einjährige Arten mit verschiedenen Merkmalssyndromen koexistieren. Der Artenreichtum und die Ökosystemdienstleistungen von wintereinjährigen Pflanzengemeinschaften unter dem globalen Wandel wird also stark von der Landnutzung durch den Menschen abhängen.

# I Synopsis

## 1 Introduction

### 1.1 Motivation: Why do we need a mechanistic understanding of (annual) plant species' responses to the environment?

Understanding the mechanisms underlying plant species' responses to the environment allows the generalization of findings and projections of plant and ecosystem responses to the environment (Funk et al., 2017; Reich et al., 2003). This mechanistic knowledge is therefore not only of scientific interest but has also a high practical relevance (Funk et al., 2017; McGill et al., 2006).

Currently, understanding and projecting species' responses, community composition, and ecosystem functioning is of increasing significance due to global change (Chapin et al., 2000; IPBES, 2019; Maestre et al., 2016; McDowell et al., 2013). Global change influences the performance and distribution of plant species at an unprecedented scale and rate with pervasive consequences for ecosystem functioning and services (Chapin et al., 2000; Choat et al., 2018; IPBES, 2019). To mitigate or prevent devastating effects on our livelihood, we need to understand and project species' responses to the environment (Chapin et al., 2000; Maestre et al., 2016; McDowell et al., 2013). However, the basis for those projections, i.e. the understanding of the underlying mechanisms, is insufficient in various species groups and ecosystems (e.g. Choat et al., 2018; Craine et al., 2013; McDowell et al., 2013), likely since gaining this understanding is laborious and requires experiments. Epistemologically, only experiments allow the identification and disentanglement of factors and processes influencing species' responses to the environment (Langstroff et al., 2022; Seebacher & Franklin, 2012; Weber, 2018). Identifying species' performance or abundance under natural (unmanipulated) conditions, in contrast, points to correlations between species' responses and the environment but not to the underlying causalities (Dunne et al., 2004; Seebacher & Franklin, 2012).

Winter annual species are one of the species groups that remain mechanistically understudied, although winter annuals exhibit a high ecological and economic importance in drylands (Friedman, 2020). Drylands are crucial for sustaining life on earth since they cover approximately 41 % of earth's terrestrial land mass, influence global nutrient, carbon, and water cycles, exhibit a high biodiversity, and harbour a large human population (Maestre et al., 2021; Safriel & Adeel, 2005). In addition, they are assumed to be particularly vulnerable to global change due to an expected increasing water scarcity and land-use intensity mainly reflected in livestock production (IPCC, 2014; Maestre, Salguero-Gómez, et al., 2012; Safriel & Adeel, 2005). Accordingly, understanding global change consequences in drylands is highly critical.

Here, I studied the mechanisms underlying winter annual species' responses to drought and grazing by using a trait-based approach and common conditions. Traits (i.e. features of a plant, see definition in Table 1) point to the mechanisms underlying species' responses to the environment (Shipley et al., 2016; Violle et al., 2007), whereas common conditions ensure the separation of relevant factors and processes (see above). Accordingly, the present trait-based findings should provide insight into the underlying mechanisms, exhibit a high predictive ability, and should be comparable to other plant communities (McGill et al., 2006; Shipley et al., 2016). This predictive ability and generality render trait-based ecology highly valuable for assessing global change consequences on species' performance or community composition (Funk et al., 2017; Webb et al., 2010). However, the discipline might be at risk since its foundational assumption that interspecific trait differences influence species' fitness responses to the environment is hardly corroborated by empirical studies (see Laughlin & Messier, 2015; Shipley et al., 2016).

The present thesis has therefore two intertwined objectives: (i) to identify the traits and mechanisms underlying species' responses to drought and grazing in winter annuals, and (ii) to test a foundational assumption of trait-based ecology by investigating the relations between species' traits and their fitness response to drought and grazing across winter annuals. Investigating both objectives has a high practical and conceptual relevance. It expands the knowledge that is necessary for assessing global change consequences in drylands, and it provides insight into the applicability, strengths, but also in possible limitations of trait-based approaches in winter annuals.

In line with the twofold objective, I give an introduction to trait-based ecology, the ecology of drylands, and the characteristics of (winter) annual plant species, before I continue to describe the trait-based concepts used in this thesis. In the section 'Results and Discussion', I explain the findings on the traits and mechanisms underlying winter annual species' responses to drought and grazing and assess the applicability of the used trait-based concepts to this species group. The 'Conclusion' is separated into two sections: one section focuses on the explanatory and predictive power of traits in winter annuals, and the other discusses global change consequences on winter annual plant communities.

## 1.2 Trait-based ecology: a tool for understanding and predicting species' responses to the environment

Trait-based ecology seeks to understand species' responses to the environment, community assembly, and ecosystem functioning by the investigation of traits (Shipley et al., 2016; Webb et al., 2010). Traits govern species' ability to grow, reproduce, and survive in a given site by influencing plants functions or mechanisms, such as carbon gain, water, and nutrient uptake, or competitive ability (Shipley et al., 2016; Violle et al., 2007). Species' ability to grow, survive, and reproduce determine their performance and fitness responses to the environment (Table 1; Shipley et al., 2016; Violle et al., 2007). Traits thus point to the mechanisms underlying species' performance and fitness responses (Shipley et al., 2016; Violle et al., 2007). The relation between traits and species' fitness responses across species is a foundational assumption of trait-based ecology (Laughlin et al., 2020; Shipley et al., 2016).

**Table 1.** Definition of terms in the context of trait-based ecology used in this thesis. Terms are ordered from lower to higher complexity.

| Term | Definition |
|---|---|
| Trait | 'Morphological, physiological, or phenological feature measurable at the individual level' (Violle et al., 2007). |
| Trait attribute | 'Value (in case of continuous traits) or modality (in case of categorical traits) taken by a trait' (Violle et al., 2007). |
| Trait axis or Trait coordination | Association of traits, here at the interspecific level. Coordinations of continuous traits form axes of trait variation. The coordinations emerge since particular trait attributes function more successfully as a combination. The single traits do not necessarily drive each other mechanically or physiologically (Reich et al., 2003). |
| Trait syndrome | Suite of coordinated trait attributes (Reich et al., 2003), i.e. side (part) of a trait axis. Species with the same trait syndrome exhibit similar trait attributes. |
| Performance | Growth rate, reproduction, and survival are measures of species' performance. They are the proximate drivers of species' fitness (Laughlin & Messier, 2015; Violle et al., 2007). Species' abundance is not a performance parameter, but it can provide insight into the ecological relevance of traits (Shipley et al., 2006; Shipley et al., 2016). |
| Fitness (response) | Species-averaged number of viable offspring produced during their life time. This definition differs from the concept of individual's fitness used in evolutionary biology (i.e. number of viable offspring produced by one individual), but is analogue (see Laughlin et al., 2020; Laughlin & Messier, 2005; Shipley et al., 2016).<br>Species' fitness response (i.e. mean changes in the number of viable offspring) indicates the success of a species under certain conditions. |
| Strategy | Trait syndrome that is associated with species' fitness responses, i.e. species' strengths of this syndrome are related to their fitness responses (see Reich et al., 2003). |

Traits are usually not independent but related to each other. They can be positively or negatively related or they interact with each other by influencing a third trait (Laughlin, 2014; Reich et al., 2003; Westoby et al., 2002). Relations among traits result from genetic linkages, coordinated selection pressures, or functional constraints due to resource allocation or biophysical limitation (Levitt 1980; Reicht et al., 2013). The relations lead to coordinations of traits into syndromes (see Table 1) and constrain possible trait attribute combinations of a species (Laughlin, 2014; Reich et al., 2003; Westoby et al., 2002). Accordingly, species cannot be the 'jack-of-all-traits' (i.e. a 'Darwinian demon[1]' does not exist; Reich et al., 2003).

Due to their constrained trait attribute combinations, species should reach their maximum fitness only under certain environmental conditions (Reich et al., 2003; Shipley et al., 2006; Shipley et al., 2016). Species are thus expected to be differently favoured by the environment, as described by the concept of species' ecological filtering (Figure 1; Keddy, 1992). This concept assumes the environment as a metaphorical 'sieve' that only permits species with particular trait attributes to persist in a given environment (Keddy, 1992; McGill et al., 2006). Species that do not exhibit these trait attributes are outperformed (Keddy, 1992). The concept of species' ecological filtering is at the interspecific level the analogue to the concept of natural selection at the intraspecific level (Keddy, 1992; Shipley et al., 2006). Natural selection favours the individuals that are, based on their traits, best adapted to the environment since these individuals reach the highest fitness (Latta, 2010; Violle et al., 2007). At the interspecific level, ecological filtering favours the species to which these better adapted individuals belong (Keddy, 1992). The ecological filtering of species leads to interspecific relations between traits and the environment and is reflected in the differing distribution of species along environmental gradients (Figure 1; Keddy, 1992; Shipley et al., 2006).

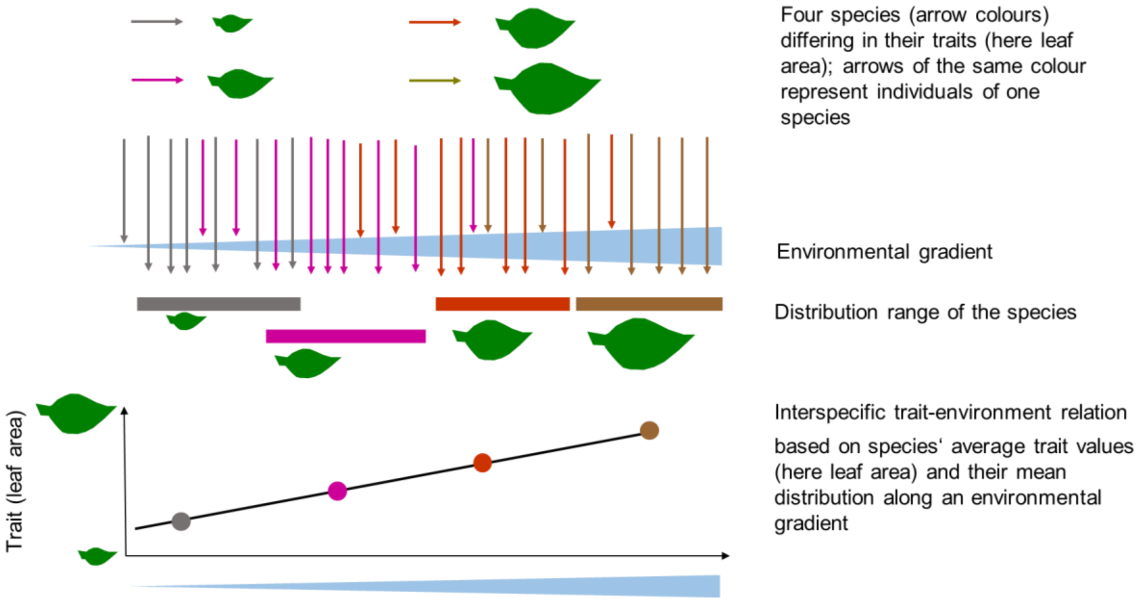

**Figure 1.** Conceptual scheme of the ecological filtering of species along an environmental gradient with leaf area as an exemplified trait. Each species passes the filter under different conditions, i.e. is favoured under certain environmental conditions, depending on its trait attributes (here leaf area). The ecological filtering leads to interspecific trait-environment relations.

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[1] A 'Darwinian demon' is a hypothetical organism that simultaneously maximises all aspects of fitness in all environments. It would exist if there are no physiological, biophysical, or resource-associated constraints (Laughlin, 2018).

The focus on traits provides not only a mechanistic understanding of species' responses to the environment but also enables comparisons of findings across geographical locations or plant communities since traits are independent of species' taxonomic affiliation (Laughlin, 2014; McGill et al., 2006; Shipley et al., 2016). Furthermore, species' traits influence processes at higher biological levels, such as community assembly or ecosystem functioning, i.e. trait-based findings can be scaled up from species to ecosystem processes (Laughlin, 2014; Lavorel & Garnier, 2002; Shipley et al., 2016). The mechanistic understanding, predictive ability, generality, and transferability should enable trait-based ecology to discover 'general laws' in plant ecology (Lawton, 1999; McGill et al., 2006; Verberk et al., 2013). Trait-based ecology holds the promise of transforming plant ecology from 'messy' (see Lawton, 1999) descriptive taxon-based studies into a predictive science (Verberk et al., 2013).

The premises of mechanistic insight, generality, and predictive ability of trait-based ecology rely at the interspecific level on the assumption that traits influence species' fitness responses across species (Laughlin & Messier, 2015; Shipley et al., 2016). In theory, virtually every trait should, although with differing strength, influence species' fitness responses in almost every environment (Shipley et al., 2016). However, this foundational assumption that interspecific trait differences influence species' fitness responses is understudied (Laughlin et al., 2020; Shipley et al., 2016; Swenson et al., 2020). Relations between traits and fitness responses have been shown across individuals (intraspecific level; Latta, 2010; Violle et al., 2007) but hardly studied across species (interspecific level). Most of the few available interspecific studies, focusing on relations between traits and species' responses, quantify performance responses rather than fitness responses and point to weak or even missing relations between traits and performance or fitness responses (e.g. Adler et al., 2014; Garnier et al., 2018; Harrison & LaForgia, 2019; Medeiros et al., 2019; Poorter et al., 2008; Visser et al., 2016). This weak empirical base of a foundational assumption of trait-based ecology undermines the whole discipline and questions its conclusions (Shipley et al., 2016; Swenson et al., 2020). Accordingly, empirical studies testing interspecific relations between traits and fitness responses are urgently needed (Laughlin & Messier, 2015; Shipley et al., 2016). Considering the enormous number of plant species, life forms, and ecosystems, an adequate evaluation of interspecific relations between traits and fitness responses requires studies in various species (Shipley et al., 2016). This thesis contributes to this evaluation by investigating relations between traits and species' fitness responses in winter annuals. Working with annuals facilitates the establishment of these relations since species' fitness responses can be assessed by their life time fecundity (i.e. the product of seed mass and seed number), a parameter which is hard to assess or even elusive in perennial species (see Laughlin et al., 2020).

## 1.3 Drylands: ecosystems assumed to be highly vulnerable to global change

Drylands, i.e. areas with an aridity index[2] of less than 0.65, are characterized by water scarcity and seasonal drought (Safriel & Adeel, 2005). Rainfall is restricted to a maximum of six months (i.e. rainfall season), is highly variable in amount and frequency within and across years, and does not compensate for the annual evaporative demands due to the intense solar radiation and high

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[2] Aridity index is defined as the ratio between mean annual rainfall and mean annual potential evapotranspiration. An aridity index of less than 0.65 indicates that mean annual potential evapotranspiration is at least 1.5 higher than mean annual rainfall (Safriel & Adeel, 2005).

temperatures (Safriel & Adeel, 2005). Other abiotic conditions, such as bedrock, soil type, or nutrient availability, differ among drylands (Maestre, Salguero-Gómez, et al., 2012).

Due to the chronic water scarcity, drylands do not sustain a continuous cover by vascular plants like mesic ecosystems (Maestre, Salguero-Gómez, et al., 2012). The vegetation typically consists of a mosaic with discrete patches of vascular plants and a matrix of bare ground or biological soil crusts with lichens, mosses, and cyanobacteria (Figure 2; Maestre, Salguero-Gómez, et al., 2012). Nevertheless, drylands harbour a substantial proportion of the global biodiversity including an outstanding richness of soil microbes (Fierer & Jackson, 2006; Maestre, Salguero-Gómez, et al., 2012; Safriel & Adeel, 2005). Twenty percent of the global hotspots of plant diversity are located in drylands (White & Nackoney, 2003). The high biodiversity confers drylands a high multifunctionality, i.e. drylands simultaneously provide multiple functions and services, such as biomass production, carbon storage, water regulation, and climate regulation (Maestre, Quero, et al., 2012).

**Figure 2.** Winter annual plant community in a dryland in Wadi Shuayb in Jordan in spring. © Sara Bangerter

The high multifunctionality of drylands enables their intensive use by humans (Safriel & Adeel, 2005). Approximately 40 % of the global human population lives in drylands (White & Nackoney, 2003). Most households depend on the provision of ecosystems services from vegetation, with livestock production being the main land-use form (Koohafkan & Stewart, 2008; Safriel & Adeel, 2005). Approximately 65 % of drylands are rangelands, sustaining about 50 % of the global livestock population (Safriel & Adeel, 2005). Livestock production is traditionally associated with a (semi-) nomadic or transhumant lifestyle, i.e. the herders follow the irregular distribution of rainfall to supply their animals with fodder and water (Koohafkan & Stewart, 2008; Safriel & Adeel, 2005). In recent decades, this traditional land use has been increasingly replaced by private tenure and sedentary livestock production (Davies et al., 2012).

Global change threatens the high biodiversity and multifunctionality of drylands since both water scarcity and human land use are predicted to increase (IPCC, 2014; Maestre, Quero, et al., 2012). The increasing water scarcity is expected to result from changes in mean annual rainfall by -30 % to

+25 %[3], increasing rainfall variability, and higher mean annual temperatures of 3-6°C until 2100 (Bates et al., 2008; IPCC, 2014; Maestre et al., 2016). Even in areas with increasing rainfall, water is expected to become scarcer since the higher temperatures will increase evapotranspiration (Maestre, Salguero-Gómez, et al., 2012). Human population is expected to increase by 1.5-2.0 % per year in drylands from 2000 to 2050, resulting in a higher demand for water, food, and fuel (Bongaarts, 2009; Clawson, 2009; Safriel & Adeel, 2005). Together the climatic changes and growing human population increase the risk that land use exceeds the carrying capacity of vegetation, soil, and water resources (Koohafkan & Stewart, 2008; Safriel & Adeel, 2005). A depletion of natural resources results in the degradation of dryland ecosystems with substantial and virtually irreversible reductions of biological and economic productivity (Maestre, Salguero-Gómez, et al., 2012; Maestre et al., 2016). Currently, 10-20 % of drylands are already considered degraded with pervasive consequences for the livelihood of approximately 250 million inhabitants (Reynolds et al., 2007).

## 1.4 Annual plant species: an important life-history strategy in drylands

Annual plant species reproduce once within their life cycle (Friedman, 2020). Their vegetative and reproductive phase, i.e. their phase as metabolically active plant, takes less than twelve months, but their seeds can remain viable for several years in the soil seed bank (Facelli et al., 2005; Friedman, 2020; Saatkamp et al., 2011). This life history enables annuals to grow and reproduce in periods of high resource availability and to endure unfavourable conditions as seeds (Friedman, 2020; Grime, 1977).

Annuals' life history has evolved as adaptation to unpredictable environments with high and variable risk to die before reproduction (Friedman, 2020). Accordingly, annuals are a dominant life form in drylands, where they grow and reproduce in the rainfall season and evade the seasonal drought as desiccation-tolerant seeds (Friedman, 2020). In the drylands of the southwest of the USA, in the Mediterranean Basin, the Middle East, and in Australia annuals can account for 50-90 % of species diversity and for 50-90 % of net primary production (Facelli & Temby, 2002; Tielbörger et al., 2014; Wheeler et al., 2021). Depending on the timing of the rainfall season, annuals grow in winter (winter annuals) or summer (summer annuals), with both groups differing in phenology and physiology (Mulroy & Rundel, 1977). This thesis explicitly focused on winter annuals, which is the dominant group of annuals in drylands of Eurasia (Saatkamp et al., 2011; Tielbörger et al., 2014).

Traditionally, annuals (including winter annuals) have been pooled in one homogeneous functional group of species escaping stress or disturbance (i.e. 'escapers', 'ruderals'; Grime, 1977; Levitt, 1980) due to their common life history and differences from perennials (herbaceous and woody species). Annuals exhibit higher reproductive allocation, shorter life span, higher growth rates, and more acquisitive trait attributes (e.g. high specific leaf area, high specific root length, low tissue density) than perennials (Garnier et al., 1997; Grime, 1977; Kooyers, 2015; Roumet et al., 2006). However, the high diversity of winter annuals and their interspecific abundance differences across rainfall, nutrient, and land-use gradients (Bilton et al., 2016; Sternberg et al., 2015; Wheeler et al., 2021) indicate that they widely differ in their traits. Furthermore, winter annuals are frequently exposed to stress, such as dry spells or grazing, within their growing season (Noy-Meir, 1973; Sternberg et al.,

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[3] The proportional changes in mean annual rainfall refer to the period 2080–2099 relative to 1980–1999 (Bates et al., 2008).

2015). Accordingly, they should withstand stress within the growing season, in addition to evading it as seeds. Considering annuals as one homogenous functional group of 'escapers' is likely too simplistic. However, interspecific trait differences and their consequences for species' performance or fitness responses have been hardly explored in winter annuals (see details in 1.5.1.2). Winter annuals' ability to withstand drought and grazing within the growing season and the underlying mechanisms are thus unsolved.

At the community level, some, but not all, of the few available studies indicate negligible changes in winter annual species composition under drought and/or grazing (Carmona et al., 2012; Harrison et al., 2015; Miranda et al., 2009; Peralta et al., 2019; Rota et al., 2017; Sternberg et al., 2015; Tielbörger et al., 2014). These studies did not address the underlying mechanisms. They assume that the negligible compositional changes result from annuals' pronounced between-year seed dormancy rather than their ability to withstand drought and/or grazing within the growing season (DeMalach et al., 2021; Sternberg et al., 2015; Tielbörger et al., 2014). Between-year seed dormancy buffers reproductive failure and compositional changes in aboveground vegetation by spreading germination across years (DeMalach et al., 2021; Tielbörger et al., 2012). The buffering ability of the seed bank though should diminish in the long-term due to seed loss and species' differences in seed production (DeMalach et al., 2021; Sternberg et al., 2003). Accordingly, a thorough understanding of the traits and mechanisms influencing species' ability to withstand and escape drought and grazing is necessary to assess global change consequences on winter annual plant communities.

## 1.5 Trait-based concepts to assess annual species' responses to drought and grazing

This thesis addressed the mechanisms underlying winter annual species' responses to drought and grazing on the basis of two trait-based concepts: the stress response strategies (Levitt, 1980) and the 'fast-slow' plant economics spectrum (Reich, 2014). Both concepts encompass hypotheses on trait syndromes and their relations to species' performance or fitness responses to drought (i.e. periods of low water availability; see Gilbert & Medina, 2016) or grazing, and to species' distribution along moisture gradients.

In perennials (perennial herbaceous and woody species), both concepts have been shown to be suitable to identify the mechanisms underlying species' performance responses to drought, grazing, and/or distribution along moisture gradients (e.g. Adler et al., 2004; Bartlett et al., 2012; Damhoureyeh & Hartnett, 2002; Milchunas et al., 1988; Reich, 2014, Sun et al., 2020). The applicability of both concepts to annuals is unknown and should not be taken for granted. Annuals differ in their traits from perennials (see 1.4) and may underlie other physiological, biophysical, or resource-use related constraints than perennials. We therefore developed hypotheses for winter annuals within the framework of both concepts considering their life history and the few interspecific studies in this species group.

Below, I present the theoretical framework and hypotheses of both concepts, before I summarize corresponding findings in perennials and explain our hypotheses on winter annuals.

### 1.5.1 Concept of stress response strategies

Based on the concept of stress response strategies, three main strategies increase species' stress resistance, i.e. minimize performance and fitness losses under stress (Levitt, 1980):

- the escape strategy enables species to evade stress in time;
- the avoidance strategy reduces species' stress exposure;
- the tolerance strategy enables species to maintain physiological functioning under stress.

Each strategy is characterized by a certain suite of coordinated trait attributes, i.e. a trait syndrome (see Table 1; Levitt, 1980). The trait attributes determine the ecological filtering of each strategy by the environment (see ecological filtering concept in 1.2; Briske, 1996; Levitt, 1980). Coordinated selection pressures, functional linkages, or trade-offs among the traits do not render the strategies mutually exclusive but favour some trait combinations and preclude others (Levitt, 1980).

The concept is applicable to different environmental factors (Levitt, 1980), but this thesis focused on the three strategies in respect to drought and grazing.

#### 1.5.1.1 Conceptual drought and grazing response strategies and their ecological filtering

The *drought escape strategy* and *grazing escape strategy* are similar. Both strategies increase the probability of reproduction before grazing or drought occur by an early start of reproduction, small plant size, and trait attributes conferring high growth rates (Grime, 1977; Kooyers, 2015; Levitt, 1980). High reproductive allocation and pronounced between-year seed dormancy should buffer reproductive failure in these strategies (Grime, 1977; Philippi & Seger, 1989; Tielbörger et al., 2012). Both strategies are favoured in habitats with a short growing season and an unpredictable risk of drought and grazing, respectively (Friedman, 2020; Philippi & Seger, 1989).

*Dehydration avoidance* enables plants to maintain high water status even under drought. The strategy encompasses trait attributes that minimize transpirational water loss, maximise water uptake, and/or water storage (Comita & Engelbrecht, 2014; Kooyers, 2015). Species with a pronounced *dehydration tolerance strategy*, in contrast, continue physiological processes under drought by trait attributes that maintain water transport and cell turgor despite low tissue water potentials (Bartlett et al., 2012; Comita & Engelbrecht, 2014; Fang & Xiong, 2015). Both strategies, dehydration tolerance and avoidance, are associated with low growth rates and are favoured under dry conditions (i.e. low water availability; Lambers & Poorter, 1992; Levitt, 1980; Reich, 2014).

*Grazing avoidance* minimizes tissue loss by trait attributes that reduce the accessibility of the plant tissue or the food intake by herbivores and trait attributes that deter herbivores by lowering the palatability or digestibility of the plant tissue (Briske, 1996; Díaz et al., 2001; Herms & Mattson, 1992). The strategy is favoured under resource-poor (i.e. dry) conditions, where tissue replacement is costly (Briske, 1996). The favouring of the grazing avoidance strategy under resource-poor conditions should be especially pronounced along moisture gradients since several trait attributes of grazing avoidance, such as low leaf allocation and small specific leaf area, concomitantly confer dehydration avoidance (Coughenour, 1985; Milchunas et al., 1988). The convergent favouring of avoidance traits by grazing and drought is a key hypothesis of the generalized grazing model (Milchunas et al., 1988).

The *grazing tolerance strategy* is characterized by a high ability to compensate tissue loss through regrowth. High compensation ability results from high photosynthetic rate, high growth rate, and/or from high biomass allocation to roots for carbon storage (Briske, 1996; Rosenthal & Kotanen, 1994; Strauss & Agrawal, 1999). The strategy is favoured under resource-rich (i.e. moist) conditions since high resource availability facilitates high compensation ability and the high growth rates enable the species to withstand the more intense competition in resource-rich conditions (Briske, 1996; Strauss & Agrawal, 1999).

#### 1.5.1.2 Drought and grazing response strategies and their distribution along moisture gradients in perennials and annuals

In this section, I summarize previous interspecific findings on drought and grazing response syndromes and their relations to species' performance responses, fitness responses, or distribution along moisture gradients in perennials and, if available, in winter annuals and present our hypotheses on winter annuals.

**Drought and grazing response strategies in annuals and perennials**

Perennials have been shown to exhibit an avoidance and tolerance strategy with respect to drought and grazing. Drought and grazing response-related traits are coordinated into the expected syndromes in these species, and perennials with a more pronounced avoidance or tolerance syndrome maintain higher performance or abundance under drought and grazing, respectively (e.g. Adler et al., 2004; Álvarez-Cansino et al., 2022; Damhoureyeh & Hartnett, 2002; Fischer et al., 2019; Kursar et al., 2009; Powell et al., 2017; Sun et al., 2020).

Winter annuals have been shown to differ in escape traits (e.g. flowering time, seed dormancy; Aronson et al., 1992; Pearse et al., 2020; Tielbörger et al., 2012) as well as in traits of dehydration and grazing avoidance and tolerance (e.g. rooting depth, water-use efficiency, turgor loss point, specific leaf area, leaf nitrogen content; Funk et al., 2021; Ge et al., 2019; Harrison & LaForgia, 2019; Kraft et al., 2015; Wilcox et al., 2021). The coordinations of the traits remain virtually unexplored (but see Angert et al., 2009; Harrison & LaForgia, 2019). The interspecific differences in escape, avoidance, and tolerance traits though suggest that winter annuals exhibit all three syndromes with respect to drought and grazing in line with the hypotheses of the stress response strategy concept.

Interspecific relations between traits and species' performance or fitness responses in winter annuals have been only investigated in respect to drought but not in respect to grazing. Annuals with pronounced dehydration avoidance trait attributes (e.g. deep roots, high water use-efficiency) maintain higher fecundity or survival under drought (e.g. Harrison & LaForgia, 2019; Huxman et al., 2013; Kimball et al., 2012). However, these relations are based on single traits and have been partly investigated under natural conditions, i.e. they can be confounded by co-occurring factors. The consequences of interspecific differences in escape, avoidance, and tolerance traits and their syndromes for species' performance or fitness responses to drought and/or grazing in winter annuals are thus far from being solved.

**Distribution of drought response strategies in perennials and annuals along moisture gradients**

In perennials, species with both a pronounced dehydration avoidance and tolerance strategy have been shown to be associated with drier conditions, as expected since they maintain high performance under drought (Griffin-Nolan et al., 2019; Kursar et al., 2009; Lopez-Iglesias et al., 2014; Reich, 2014). In moister conditions, perennials with both strategies are outperformed due to their lower growth rates, which decrease their ability to withstand the more intense competition in moister conditions (Li et al., 2018; Lopez-Iglesias et al., 2014; Martínez-Vilalta et al., 2010; Reich, 2014).

In winter annuals, the ecological filtering of drought response strategies should differ from perennials. Rainfall gradients in drylands usually range from arid conditions with low, unpredictable rainfall in a short rainfall season to higher, more predictable rainfall in a longer rainfall season, which is still interrupted by occasional dry spells (Noy-Meir, 1973). Since winter annuals generally escape the dry season, species with a pronounced escape strategy should be favoured under arid conditions. The escape strategy should enable the annuals to grow and reproduce in the short rainfall season and to buffer reproductive failure in the unpredictable environment (Kooyers, 2015; Tielbörger et al., 2012). Winter annuals associated with arid conditions have been observed to exhibit pronounced escape trait attributes (Manzaneda et al., 2015; Pearse et al., 2020). Annuals with a pronounced dehydration avoidance or tolerance strategy are expected to be favoured under moister conditions due to their ability to withstand occasional dry spells in the growing season. These annuals thus utilize the whole length of the growing season and reach large sizes to withstand the more intense competition in moister conditions (Liancourt & Tielbörger, 2009; Schiffers & Tielbörger, 2006). Accordingly, we expected an interspecific strategy shift from drought escape to dehydration avoidance and/or tolerance with increasing rainfall in winter annuals.

#### Distribution of grazing response strategies along moisture gradients in perennials and annuals

In perennials, species with a pronounced grazing tolerance strategy have been shown to be favoured under moister and species with a pronounced grazing avoidance strategy under drier conditions (Figure 3a; Adler et al., 2004; Díaz et al., 2007; Quiroga et al., 2010). This interspecific shift agrees with the generalized grazing model that assumes a convergent favouring of avoidance traits by grazing and drought (see 1.5.1.1; Milchunas et al., 1988).

Winter annuals, in contrast, escape seasonal drought (see 1.4 and above; Kooyers, 2015). Grazing avoidance (e.g. high root allocation, high tissue density) associated with low growth rates should thus decrease rather than increase annuals' performance under arid conditions due to a higher risk to be affected by seasonal drought before reproduction (see Carvajal et al., 2019 for shrubs). Accordingly, the ecological filtering of grazing response strategies in annuals should differ from perennials. We suggest two scenarios for the ecological filtering of grazing response strategies along rainfall gradients in winter annuals (Figure 3b-c).

In the first scenario, the escape strategy minimizes the probability to be affected by both drought and grazing before reproduction. In this scenario, grazing and drought act as convergent ecological filters in winter annuals, but favour the escape instead of the avoidance strategy in arid conditions. In the following, this scenario is called *convergence scenario* (Figure 3b). It is especially likely if grazing allows successful escape, for example, by being infrequent and/or occurring late in the growing season.

In the second scenario, winter annuals with an escape strategy exhibit high performance losses under grazing in the vegetative and reproductive phase, i.e. if escape is not successful. The performance losses emerge since escape trait attributes, such as high growth rate and low root allocation, are traded-off (i.e. incompatible) with grazing avoidance or tolerance. The escape strategy thus does not confer annuals a high resistance to grazing within the growing season as avoidance or tolerance do. In this scenario, grazing and aridity do not act as convergent ecological filters in winter annuals. Instead, both factors favour strategies that are traded-off: arid conditions favour escape (see above), whereas grazing favours avoidance or tolerance, with the avoidance strategy expected to be favoured under drier conditions due to its lower resource demand (see 1.5.1.1). However, unlike in perennials, grazing avoidance does not confer annuals a high resistance to drought in arid conditions (see above). Winter annuals are thus either characterized by high resistance to drought in arid conditions (escape strategy) *or* grazing resistance (avoidance or tolerance strategy). This scenario is called *trade-off scenario* (Figure 3c). It should be most likely when high grazing intensity precludes successful grazing escape. The few available studies on grazing responses of winter annual communities are consistent with the trade-off scenario. They indicate lower grazing resistance of annuals under arid conditions (Carmona et al., 2012; Carmona et al., 2015; Osem et al., 2002).

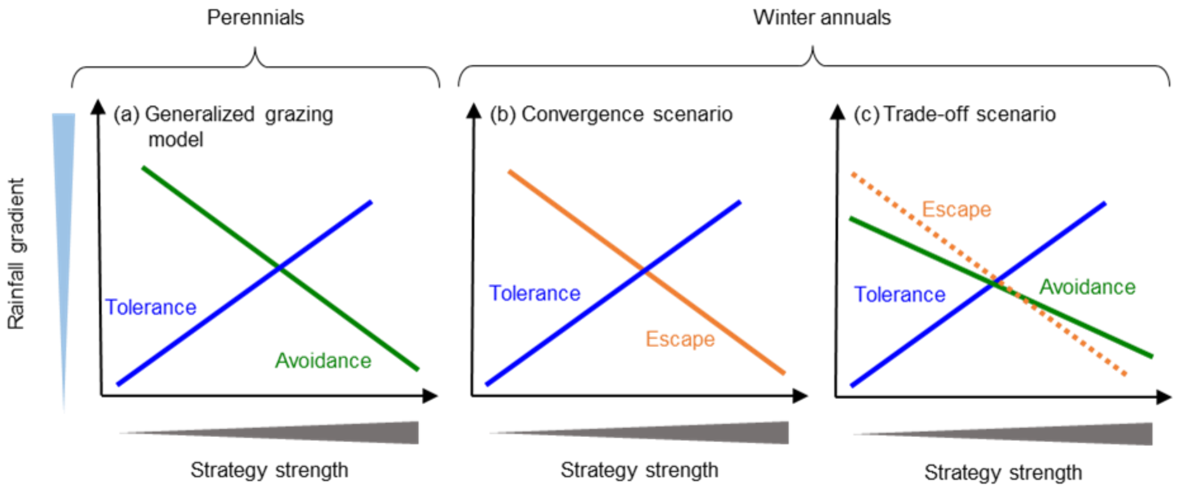

**Figure 3.** Conceptual scheme of the ecological filtering of grazing response strategies along a rainfall gradient in (a) perennials and (b, c) in winter annuals, with (b) showing the convergence scenario and (c) the trade-off scenario. The convergence scenario does not consider grazing avoidance. To indicate the trade-off in (c), the dashed line for escape shows the favouring of this strategy if grazing would be absent.

In both scenarios (convergence and trade-off scenario), winter annuals with a grazing tolerance strategy are favoured under moister conditions (Figure 3b-c). This strategy should enable annuals, similarly as perennials, to successfully cope with the more intense competition in moister conditions.

### 1.5.2 The 'fast-slow' plant economics spectrum

All vascular plants use the same main resources, light, water, carbon dioxide, and mineral nutrients, and underlie the struggle for existence, which is expected to lead to an economic use of resources to avoid shortage and excess (Chapin, 1980; Reich et al., 1997; Westoby et al., 2002; Wright et al., 2004). An economic use of the same main resources should constrain species' trait attribute combinations and result in a coordination of resource-use related traits across species (Reich et al., 1997; Wright et al., 2004). This interspecific coordination of resource-use related traits is a key assumption of the 'fast-slow' plant economics spectrum (Reich, 2014).

Below, I explain the hypotheses of this concept, before I describe corresponding findings in perennials (perennial herbaceous and woody species) and annuals and our hypotheses on winter annuals.

#### 1.5.2.1 Hypotheses of the 'fast-slow' plant economics spectrum

According to the plant economics spectrum, resource-use related leaf, stem, and root traits are coordinated across species, forming one axis of trait variation (Figure 4; Reich, 2014). This axis, referred to as fast-slow plant economics spectrum, ranges from trait attributes inferring rapid resource acquisition (acquisitive or fast attributes) to those conserving resources (conservative or slow attributes, Figure 4; Reich, 2014). Acquisitive and conservative trait attributes are assumed to be traded-off across species at the whole plant level (Reich, 2014).

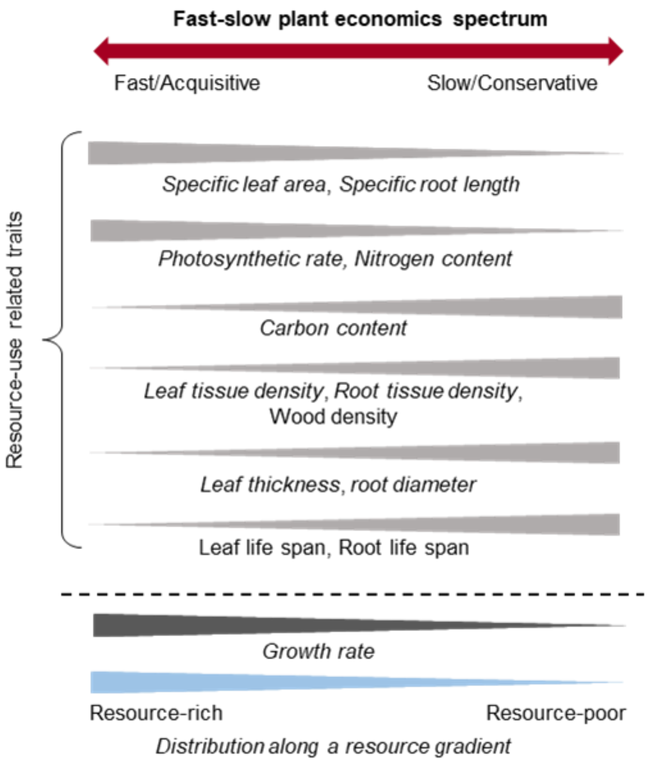

**Figure 4.** Conceptual scheme of the plant economics spectrum with some exemplary traits based on Reich (2014) and Wright et al. (2004). Traits considered in this thesis are depicted in italics.

Species' trait attribute combinations along the fast-slow plant economics spectrum are assumed to influence their maximum growth rates and resistance to abiotic factors, such as drought (Figure 4; Reich, 2014). Species with acquisitive trait attributes should exhibit high maximum growth rates under high resource availability, but their higher resource demand lower their performance under resource-poor conditions. In contrast, species with conservative trait attributes should maintain high performance under resource-poor conditions, i.e. they exhibit a high stress resistance, at the cost of lower maximum growth rate (Figure 4; Reich, 2014). The interspecific trade-off between growth rate and stress resistance should result in species' ecological filtering along resource gradients: Species with acquisitive trait attributes are favoured under resource-rich (e.g. moist) conditions, whereas species with conservative trait attributes are favoured under resource-poor (e.g. dry) conditions (Figure 4; Reich, 2014).

According to the plant economics spectrum, resource-use related traits can be used as proxy for species' drought resistance and distribution along moisture gradients (Reich, 2014). The measurement of a few resource-use related traits is less laborious than of the various traits necessary to identify species' stress response strategies (see Table 2). The plant economics spectrum may thus allow rapid assessments of species' drought resistance and distribution along moisture gradients, which should facilitate projections of global change consequences.

#### 1.5.2.2 Plant economics spectrum in perennials and annuals

The plant economics spectrum has been mainly developed for perennials and tested in those (Reich, 2014). Perennials show the hypothesized coordination of resource-use related traits along one axis (including the growth-stress resistance trade-off) and the expected relations between traits and species' distributions along resource gradients (reviewed in Reich, 2014). Findings contrary to the hypotheses of this concept in perennials exist but are rare (Baraloto et al., 2010; Carvajal et al., 2019; Fortunel et al., 2012; Rodríguez et al., 2022).

In annuals, to my knowledge, only two *intraspecific* studies address the hypotheses of the plant economics spectrum: one study focuses on leaf traits and their changes along a rainfall and nutrient gradient in an annual desert forb (*Helianthus anomalus*; Brouillette et al., 2014) and the other on whole plant traits and their changes along a rainfall and temperature gradient in *Arabidopsis thaliana* (Sartori et al., 2019). In both species, the populations show the expected trait coordination (Brouillette et al., 2014; Sartori et al., 2019). However, only in *Arabidopsis thaliana* the trait-environment relations agree with the hypotheses of the plant economics spectrum (Sartori et al., 2019), whereas in *Helianthus anomalus* trait attributes change from acquisitive (instead of conservative) to conservative (instead of acquisitive) with increasing resource availability (i.e. moister, nutrient-rich conditions; Brouillette et al., 2014). The applicability of the plant economics spectrum to inter- and intraspecific trait differences in annuals is thus unclear.

Here, I tested the hypotheses of the plant economics spectrum on *interspecific* differences in winter annuals. In the following, I describe my expectations, which hypotheses of this concept apply to interspecific differences in winter annuals or which need to be adapted to this species group.

Despite their different life history, winter annuals should, similar to perennials, underlie the constraints of resource economics. Therefore, they should show the interspecific coordination of resource-use related traits along one axis, as expected by the plant economics spectrum. The growth-drought resistance trade-off should also apply to winter annuals, when drought affects them in their vegetative and reproductive phase (i.e. when drought precludes successful escape). Fast-growing annuals (with acquisitive trait attributes) should show high performance or fitness losses under drought within their vegetative or reproductive phase since their escape traits are traded-off with dehydration avoidance and tolerance, which minimize performance or fitness losses under drought (see 1.5.1.1 and 1.5.1.2). In contrast, annuals with slow growth rates (associated with conservative trait attributes) should maintain high performance or fitness under drought in their vegetative or reproductive phase, as known from perennials (see 1.5.1.1 and 1.5.1.2), since they can exhibit pronounced dehydration avoidance or tolerance trait attributes.

The consequences of the growth-drought resistance trade-off for species' ecological filtering along moisture gradients should differ between perennials and winter annuals. Acquisitive (fast-growth) trait attributes enable winter annuals to escape seasonal drought and therefore should be favoured under more arid conditions (see 1.5.1.2; Carvajal et al., 2019 in shrubs; Kooyers, 2015). Annuals with conservative (i.e. slow-growth) trait attributes are expected to be favoured under moister conditions due to their ability to withstand occasional dry spells in the growing season. They thus utilize the whole length of the growing season and reach large sizes to successfully cope with the more intense competition (see 1.5.1.2). Consequently, ecological filtering in winter annuals should favour species with acquisitive (instead of conservative) trait attributes under more arid conditions and species with conservative (instead of acquisitive) attributes under moister conditions. This expected interspecific shift is opposite to the hypothesis of the plant economics spectrum (Reich, 2014) but consistent with intraspecific trait variation in an annual desert forb (see above, Brouillette et al., 2014).

# 2 Objectives and Hypotheses

This thesis aimed to elucidate the mechanisms underlying species’ responses to drought and grazing in winter annuals. To accomplish this objective, I comparatively measured a large number of traits, assumed to influence species’ drought and grazing responses, in winter annuals from the southwestern Levant under common conditions in a greenhouse. I identified the main trait syndromes and related traits and their syndromes (i) to species’ fitness responses (based on fecundity responses) to experimental drought and grazing under common conditions, (ii) to species’ abundance responses to grazing under dry and moister conditions in the field (natural conditions), and (iii) to their distribution along a large-scale rainfall gradient. Relating traits and their syndromes to species’ fitness responses under common conditions minimizes the influence of confounding factors (see Langstroff et al., 2022; Weber, 2018). This enabled me to identify the mechanisms underlying species’ fitness responses to drought and grazing and to rigorously test a foundational assumption of trait-based ecology, namely the relation between traits and fitness responses across species (see Shipley et al., 2016). The relations between species’ strengths of the trait syndromes and their abundance responses or distribution under natural conditions provide insight into the ecological relevance of the trait syndromes in intact communities (see Cornwell & Ackerly, 2009; Dunne et al., 2004). Similar broad and ecologically highly relevant approaches of assessing trait functionality in large species sets are, to my knowledge, missing in annuals and scarce in perennials (Garnier et al., 2018; Medeiros et al., 2019; Wright et al., 2010).

The syndromes of drought and grazing response-related traits and their relations to species’ fitness responses, abundance responses, and/or distribution are presented in separate manuscripts, with Manuscript 1 focusing on drought response syndromes and Manuscript 2 on grazing response syndromes. Both manuscripts focused on the following main hypotheses (see details in Figure 5 and in Manuscript 1, p. 76 and Manuscript 2, p. 118):

(1) Traits relevant for species’ drought responses (Manuscript 1) and species’ grazing responses (Manuscript 2) are coordinated along three major axes. The axes reflect the escape, tolerance, and avoidance strategy in respect to drought and grazing, respectively.

(2) Species’ strengths of the drought escape, dehydration tolerance, and avoidance syndrome, i.e. their positions along the trait axes, are related to their fitness responses to drought in the growing season and their distribution along a rainfall gradient (Manuscript 1).

(3) Species’ strengths of the grazing escape, tolerance, and avoidance syndrome, i.e. their positions along the trait axes, are related to their fitness responses to (simulated) grazing, their abundance responses to (natural) grazing, and their distribution along a rainfall gradient (Manuscript 2).

Additionally, I tested the hypotheses of the plant economics spectrum in winter annuals (see details in Figure 5, Manuscript 1, p. 76 and Manuscript 3, pp. 155-156) since this concept might be an avenue to rapidly assess their drought resistance and global change consequences:

(4) Resource-use related leaf and root traits in winter annuals are coordinated along one main axis, reflecting a trade-off between acquisitive and conservative attributes. Species’ positions along this axis influence their growth rates and drought resistance (i.e. fitness response to drought).

(5) Fast-growing winter annuals with acquisitive trait attributes are favoured under arid conditions, whereas slow-growing winter annuals with conservative trait attributes are favoured under moister conditions along a rainfall gradient.

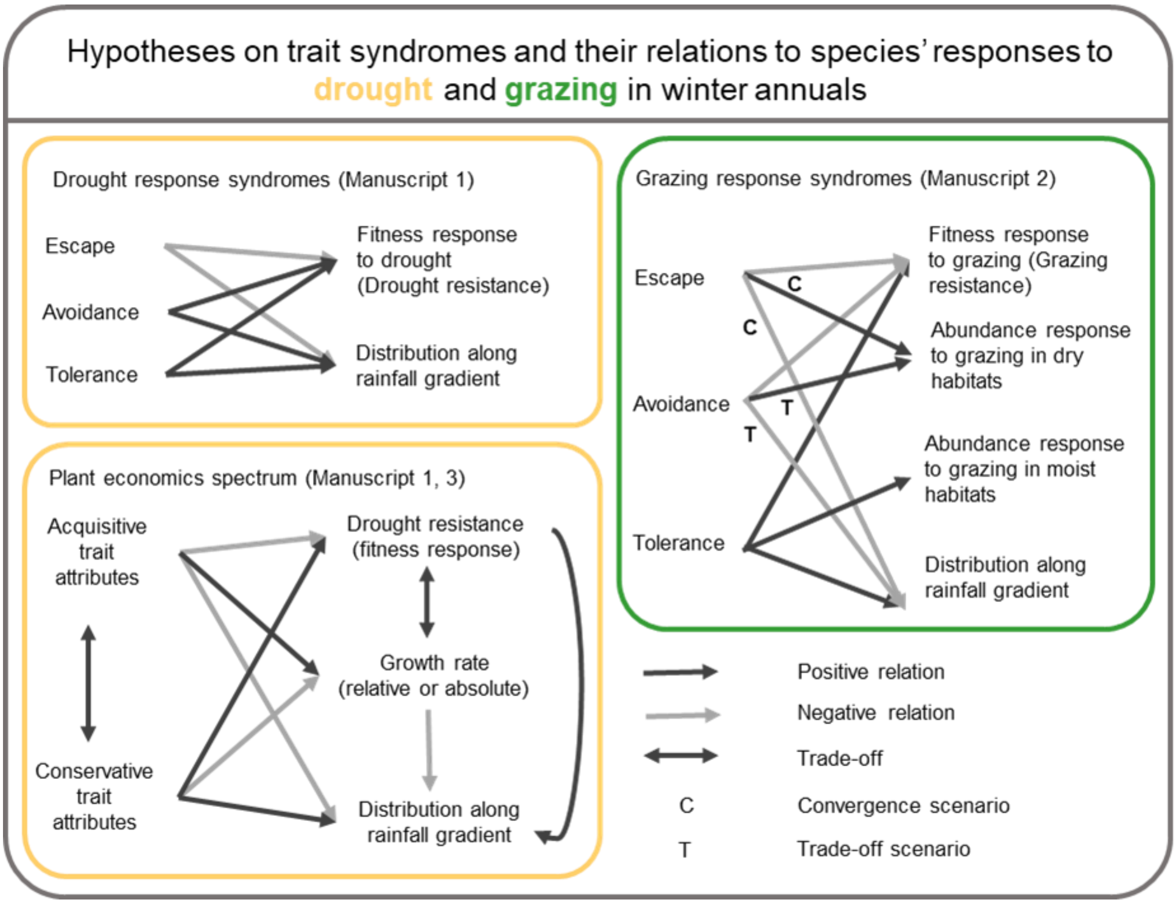

**Figure 5.** Overview of the hypotheses and manuscripts included in this thesis. Positive relations between trait (syndromes) and fitness response or abundance response indicate that species with a pronounced trait syndrome exhibit low fitness or abundance losses, and negative relations indicate high fitness or abundance losses. Positive relations between trait (syndromes) and species' distribution indicate that species with a pronounced trait syndrome are associated with moister conditions, whereas negative relations refer to an association with drier conditions.

# 3 Material and Methods

In this section, I briefly describe the study system, study species, greenhouse and field experiments, and trait measurements. Details are given in the Manuscripts' 1-3.

## 3.1 Study system

The southwestern Levant in the Middle East is characterized by hot, long, rainless summers, wet, mild winters, and mean annual temperatures of 17-20°C (IMS, 2021). In this region, mean annual rainfall varies approximately 40-fold (Figure 6) and aridity index between zero to 0.65 from south to north and from the Dead Sea to east or west (Trabucco & Zomer, 2019; Ziv et al., 2014). The arid areas in the south and in the surroundings of the Dead Sea exhibit low and unpredictable rainfall in a short rainfall season (up to less than 20 mm/year ± 55 %, mean ± coefficient of variation, December/January-March), whereas the moister areas in the north, east, and west are characterized by higher, more predictable rainfall in a longer rainfall season (up to 900 mm/year ± 18 %, October/November-April/May; Tielbörger et al., 2014; Ziv et al., 2014). Dry spells of at least 4-6 days within the rainfall season are common along the whole gradient (Ziv et al., 2014).

The vegetation consists of semi-arid shrublands (including small trees in moister conditions) with winter annuals (summer annuals are not present) dominating the inter-shrub matrix (Figure 6). Winter annuals account for 80-90 % of species diversity and 55-99 % of net primary production. They co-occur in the inter-shrub matrix with a few geophytes, perennial grasses, and perennial forbs. Towards arid conditions, vegetation becomes more open with larger proportion of annuals, lower primary productivity, and lower competition intensity between shrubs and annuals and among annuals (Figure 6; Schiffers & Tielbörger, 2006; Tielbörger et al., 2014).

The Levant is characterized by a long history of grazing. Wild ungulates (e.g. onagers, antelopes, goats) graze the resident plant communities since millennia, while grazing by domesticated ungulates is documented for more than 10,000 years (Noy-Meir & Seligman, 1979).

The high diversity of winter annuals, the steep rainfall gradient, and the long grazing history render the southwestern Levant ideal for investigating interspecific trait differences in winter annuals and their consequences for species' fitness responses to drought and grazing and for their distribution along rainfall gradients.

Species' abundance responses to natural grazing were assessed in a grazing exclosure experiment in semiarid conditions (mean annual rainfall 200-400 mm) in the north of the Dead Sea in Wadi Shuayb in Jordan (Figure 6). The experiment comprised four sites located within 10 km in an intensively grazed area.

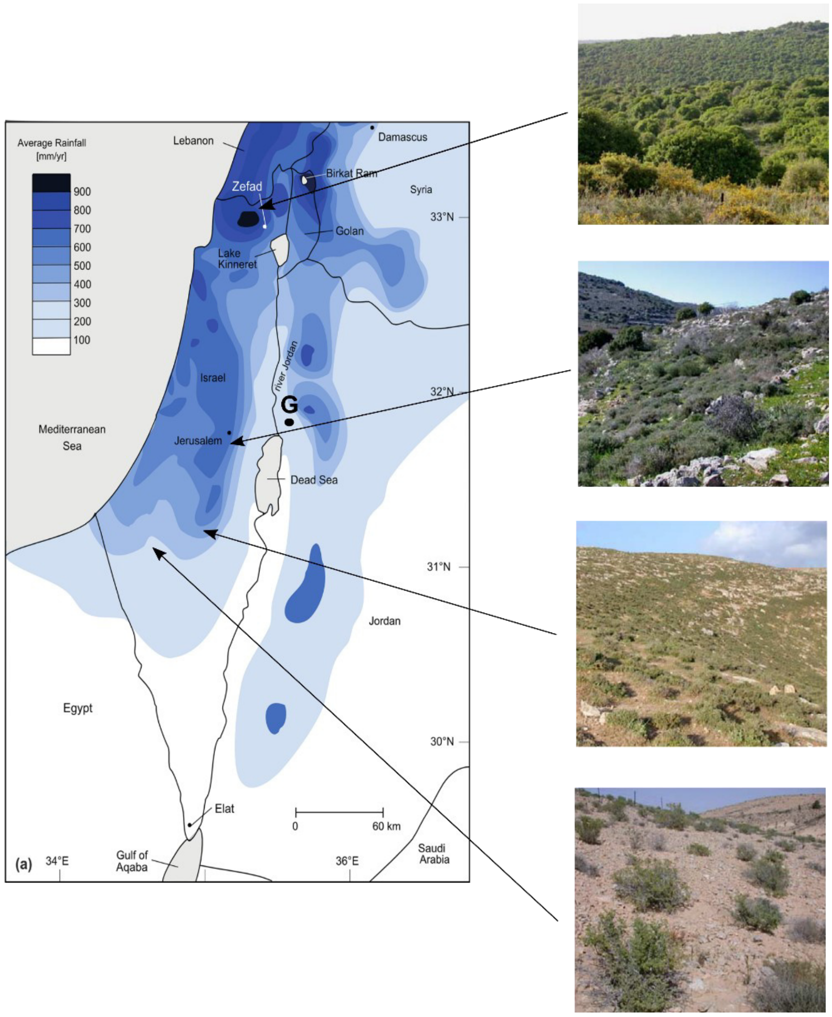

**Figure 6.** Mean annual rainfall and characteristic vegetation in the southwestern Levant. G indicate the location of the grazing exclosure experiment. The map originated from Schiebel & Litt (2018) and the photos from Tielbörger et al. (2014). Schiebel and Litt (2018) (https://doi.org/10.1007/s00334-017-0658-3) and Tielbörger et al. (2014) (https://doi.org/10.1038/ncomms6102) are distributed under the terms of the Creative Commons CC BY 4.0 license. To view a copy of this license, visit http://creativecommons.org/licenses/by/4.0/. The map and the photos were re-arranged and arrows, the point, and 'G' were added.

## 3.2 Study species and plant material

This thesis focused on 30 winter annual species, comprising 22 forbs (including six legumes) and eight grasses. Species selection considered the following criteria: (1) high abundance in the southwestern Levant, (2) inclusion of several plant families, (3) wide differences in their distribution along the rainfall gradient (based on BioGIS, 2018), and (4) seed availability. All species exhibited C3 photosynthesis. Traits (except of growth rates and compensation ability) were measured on 29-30 species. Species' fecundity responses (as proxy for fitness responses) to drought and grazing were assessed in subsets of 18-23 species with high seed availability.

Seeds of the study species were collected from one population per species in the field in Israel. The seeds were grown in a greenhouse under favourable conditions to obtain F1 seeds with homogenized parental effects.

All greenhouse experiments were conducted with the F1 seeds. This approach of growing plants from one population per species with homogenized parental effects (F1 seeds) under common conditions (i.e. in a greenhouse) minimized confounding influences, such as environmental heterogeneity or intraspecific variation. It allowed us to comparatively measure species' traits and fecundity responses to rigorously test the relations between species' traits and their fitness responses (see Langstroff et al., 2022; Shipley et al., 2016). Species' trait attributes measured in the greenhouse should be also relevant for their performance in the field since intraspecific trait variation is commonly smaller than interspecific trait differences (stable species hierarchy hypothesis; Kazakou et al., 2014; Siefert et al., 2015). Higher inter- than intraspecific trait variation has been shown in various species groups, including annuals, and is especially pronounced along steep environmental gradients and in species-rich communities (Albert, Thuiller, Yoccoz, Douzet, et al., 2010; Garnier et al., 2001; Kazakou et al., 2014; Siefert et al., 2015), as investigated here.

## 3.3 Plant cultivation in the greenhouse

Plants were germinated from F1 seeds and individually grown in pots in a greenhouse in Bayreuth. They were grown on a sandy substrate under common favourable conditions with ample water and nutrient supply and temperature and day length adjusted to the natural variation in Israel. At the onset of seed production, plants were wrapped in light transparent fabric (organza) to prevent seed loss. We harvested the plants at the end of their life cycle indicated by the start of leaf senescence.

## 3.4 Trait measurements

In this thesis, 33 morphological, anatomical, physiological, and life-history traits were considered based on their hypothesized or known association with the drought and/or grazing response strategies and/or the plant economics spectrum (see Table 2).

The traits (except seed dormancy[4]) were measured on 5-16[5] individuals per species grown under common, favourable conditions in the greenhouse (see 3.3). We followed standardised protocols for trait measurements when available (e.g. Pérez-Harguindeguy et al., 2013).

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[4] Seed dormancy was assessed with germination trials in a greenhouse in Tübingen.

[5] The number of measured individuals per species was almost similar per trait but differed among traits.

**Table 2.** Traits with their hypothesized or known association with the escape, avoidance, and tolerance strategy in respect to drought or grazing, and resource-use strategy based on the plant economics spectrum (PES) considered in this thesis. In the columns of the drought and grazing response strategies + or - indicate whether a high or low trait value is expected to confer higher drought or grazing resistance in the respective strategy. In the PES column, a and c indicate whether a high trait value is associated with an acquisitive (a) or conservative (c) resource-use strategy. The column 'Method' provides a short description of the trait or its measurement; details and references are given in the Manuscripts' 1-3. Traits are ordered based on their association with the strategies from left to right.

| Trait | Unit | Drought | | | Grazing | | | PES | Method |
|---|---|---|---|---|---|---|---|---|---|
| | | Escape | Avoidance | Tolerance | Escape | Avoidance | Tolerance | | |
| Seed dormancy | - | + | | | + | | | | Proportion of ungerminated seeds in germination trials |
| Reproductive mass fraction | g/g | + | | | + | | | | Total seed weight (seed number * seed mass) per total plant biomass |
| Maximum photosynthetic rate (area- or mass-based) | µmol/ (m$^2$ * s)<br>µmol/ (g * s) | $+^{\#}$ | | | $+^{\#}$ | | | a | Rate of net carbon assimilation per unit leaf area or unit leaf mass, here measured with an infra-red gas analyser. Net carbon assimilation rate reflects the balance between carbon uptake by carboxylation and carbon loss by respiratory processes. |
| Specific leaf area | mm$^2$/mg | + | - | | + | - | + | a | Leaf area per leaf dry mass |
| Leaf mass fraction | g/g | + | - | | + | - | | | Leaf biomass per total plant biomass |
| Age at onset of flowering | days | - | | | - | | | | Plant age at first appearance of reproductive organs |
| Leaf number at flowering | - | - | | | - | | | | Count of leaf number at flowering onset |
| Height at seed set | cm | - | | | - | - | | | Distance between soil surface and highest point of the plant at the end of the life cycle |
| Total biomass | g | - | | | - | | | | Above- and belowground biomass at the end of the life cycle |
| Root mass fraction | g/g | - | + | | - | | + | | Root biomass per total plant biomass |

| Trait | Unit | Drought | | | Grazing | | | PES | Method |
|---|---|---|---|---|---|---|---|---|---|
| | | Escape | Avoidance | Tolerance | Escape | Avoidance | Tolerance | | |
| Instantaneous water-use efficiency | µmol $CO_2$/ mmol $H_2O$ | | + | | | | | | Ratio of net carbon assimilation rate to stomatal conductance of water vapor, here measured with an infra-red gas analyser; describes the water cost of carbon assimilation. |
| Integrated water-use efficiency | ‰ | | + | | | | | | Assessed based on leaf carbon isotope ratio ($\delta^{13}C$) |
| Specific root length | m/g | | + | | | | | a | Root length per root dry weight of fine roots (diameter < 2 mm) |
| Leaf thickness | mm | | + | | | | | c | Lamina thickness without primary veins |
| Leaf water content | - | | + | | | | | | Proportion of water in leaves and roots, respectively, in the middle of plant's life cycle |
| Root water content | - | | + | | | | | | |
| Cuticular conductance | mmol/ ($m^2$ * s) | | - | | | | | | Vapour conductance of leaf epidermis with closed stomata, measured gravimetrically |
| Turgor loss point | MPa | | + | - | | | | | Leaf water potential at which the turgor pressure of the cells is zero, measured with an osmometer |
| Leaf tissue density | g/cm³ | | | + | | | | c | Leaf mass per volume |
| Root tissue density | g/cm³ | | | + | | | | c | Root mass per volume of fine roots (diameter < 2 mm) |
| Leaf area | cm² | | | - | | - | | | One-sided area of a single leaf |
| Leaf xylem vessel diameter | µm | | | - | | | | | Average diameter of the two largest xylem vessels in the leaf midvein |

| Trait | Unit | Drought | | | Grazing | | | PES | Method |
|---|---|---|---|---|---|---|---|---|---|
| | | Escape | Avoidance | Tolerance | Escape | Avoidance | Tolerance | | |
| Leaf dry matter content | mg/g | | | | - | + | - | **c** | Ratio of leaf dry mass to fresh mass |
| C:N ratio | %/% | | | | - | + | - | | Ratio of proportional carbon and nitrogen content (based on leaf dry mass) |
| Compensation ability | - | | | | - | - | + | | Response ratio (i.e. log-scaled difference) of total biomass between clipped and control plants |
| Leaf toughness | N/mm | | | | | + | | | Measured as force to punch in a leaf blade |
| Nitrogen content (area- or mass-based) | $mg/mm^2$<br>mg/g | | | | | | | **a** | Nitrogen content per unit leaf area or unit leaf dry mass |
| Mass-based carbon content | mg/g | | | | | | | **c** | Carbon content per unit leaf dry mass |
| Root diameter | mm | | | | | | | **c** | Average diameter of fine roots (diameter < 2 mm) |
| Absolute growth rate | g/day | + | - | - | + | - | + | **a** | Rate of total biomass increase in vegetative phase |
| Relative growth rate | g/(g * days) | | | | | | | **a** | Amount of new biomass produced by already existing biomass in a certain period; measure of efficiency of biomass production |

[#] Only area-based photosynthetic rate was considered in the assessments of species' drought and grazing response syndromes in Manuscript 1 and 2.

## 3.5 Drought experiment and grazing simulation experiment under common conditions

To comparatively assess species' fitness responses (based on fecundity responses) to a period of low water availability and to grazing in the winter annuals, I conducted a drought and grazing simulation experiment under common conditions in a greenhouse in Bayreuth. Both experiments were independent from each other. In both experiments, half of the individuals (8-16 individuals) per species were exposed to a drought and grazing treatment, respectively, and the other half grew as control under favourable conditions (see 3.3). The species were exposed to the drought or simulated grazing in the middle of their life cycle before successful reproduction, i.e. none of the species escaped the drought or the simulated grazing.

In the drought treatment, watering was reduced for 46 days (approximately 6.5 weeks, Figure 7a). After the drought period, drought-stressed plants were re-watered and received the same amount of water as control plants until the end of their life cycle (i.e. final harvest). During the drought period, all species were dried out at the same rate and then maintained at soil water contents of 3-4 % (for details see Manuscript 1, pp. 79, 104-105). Maintaining similar soil water contents across species avoided that species with higher transpiration rates dried out faster and ensured the comparability of drought effects across species (Gilbert & Medina, 2016; Sack, 2004). The drought treatment simulated a dry spell within the growing season.

In the grazing treatment, I clipped plants once with scissors and removed approximately 75 % of plants' aboveground biomass (including all reproductive biomass) in all species (Figure 7b, for details see Manuscript 2, p. 123). Natural grazing usually also occurs once within the growing season due to the nomadic lifestyle of the herders (pers. observation K. Tielbörger and M. Bilton). The removal of a similar relative amount of biomass in all species did not mimic natural (selective) grazing by ungulates, but it ensured the comparability of grazing effects across species.

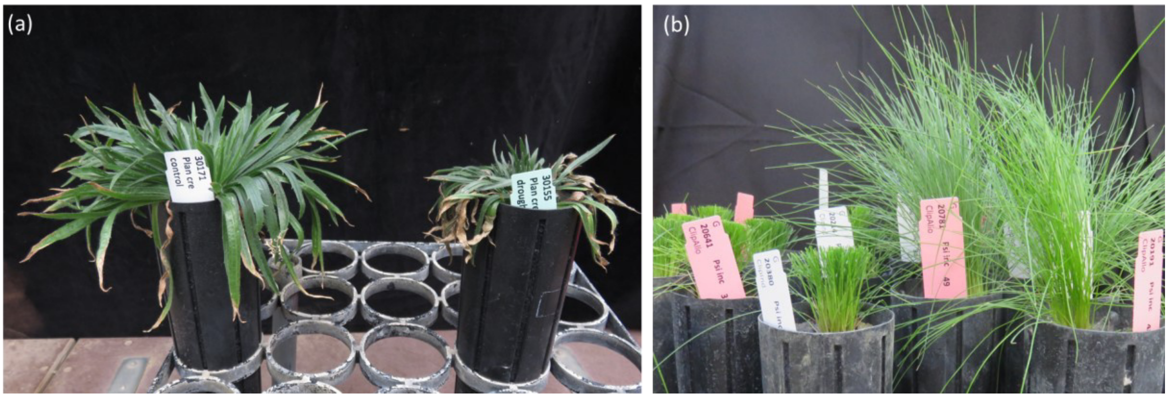

**Figure 7.** (a) Control (left) and drought-stressed plant (right) of *Plantago cretica* in the drought experiment four weeks after the start of the drought; (b) Clipped (left) and control (right) plants of *Psilurus incurvus* in the grazing simulation experiment directly after clipping. © Susanne Kurze

In both experiments, life time fecundity of each plant was assessed as total seed weight (total seed weight = seed number * seed mass) at the end of the life cycle. The fecundity response of each species to drought and grazing was calculated as response ratio (see Hedges et al., 1999) of total seed weight between stressed plants (drought stressed or clipped) and control plants, using separate response ratios for species' fecundity response to drought and grazing (see details in Manuscript 1,

p. 79 and Manuscript 2, p. 123). Species' fecundity response comprised both the number of possible offspring (i.e. seed number) that the individuals produced during their life time and the probability of plant survival that is related to seed mass (Metz et al., 20210). Therefore, it was considered a solid proxy for species' fitness response and (reciprocally) for their drought and grazing resistance, respectively.

## 3.6 Grazing exclosure experiment in the field

The responses of winter annuals to natural grazing in the field (Jordan) were assessed by comparing species' abundances in fenced plots (to exclude sheep and goats) with species' abundances in paired adjacent plots intensively grazed by domesticated ungulates of local herders (Figure 8).

**Figure 8.** Grazing exclosure in Wadi Shuayb (Jordan) on a north-facing slope. © Sara Bangerter The photo was published with Manuscript 2 (Kurze, Bilton et al., 2021; https://doi.org/10.1111/1365-2745.13721), which is distributed under the terms of the Creative Commons CC BY 4.0 license. To view a copy of this license, visit http://creativecommons.org/licenses/by/4.0/).

In each of the four experimental sites, four plot pairs (i.e. an ungrazed and grazed plot) were installed on a south-facing and on a north-facing slope (4 sites * 2 slopes * 4 plot pairs = 32 plot pairs, see details in Manuscript 2, pp. 123-124, 143). Opposite slopes differ in their environmental conditions with a more arid microclimate, lower soil moisture, and lower standing biomass on south-facing slopes compared to north-facing slopes (Kutiel, 1992; Kutiel & Lavee, 1999). Therefore, south-facing slopes were considered as dry habitats and north-facing slopes as moister habitats in the grazing exclosure experiment.

I analysed species' abundances in three consecutive years and considered the 20 annuals that overlapped with the grazing simulation experiment. Abundance responses to grazing were determined for each species in each slope with response ratios of abundances between grazed and ungrazed plots (see details in Manuscript 2, pp. 124).

## 3.7 Species distribution along the rainfall gradient

Species' distribution along the rainfall gradient in the southwestern Levant (see 3.1, Figure 6) was characterized based on their occurrences (presence/absence data) in independent biological records in Israel (BioGIS, 2018). The BioGIS database provides for each species a mean annual rainfall niche, which is the average of mean annual rainfall across all occurrences of a species.

## 3.8 Overview of the main statistical analyses

The main aims of the statistical analyses were (i) to identify the main trait syndromes in each of the three trait sets, i.e. in drought (Manuscript 1), or grazing (Manuscript 2) response-related traits, or in resource-use related traits considered in the plant economics spectrum (Manuscript 3, Table 2) and (ii) to evaluate if species' strengths of these trait syndromes are related to their fecundity or abundance responses to drought or grazing, their growth rates, and/or to their mean annual rainfall niches (i.e. species' distribution along the rainfall gradient).

To determine the main trait syndromes, principal component analyses (PCA) based on each trait set were calculated, i.e. I conducted one PCA for drought response-related traits, one for grazing response-related traits, and one for resource-use related traits. We identified the principal component axes (PC) associated with trait coordinations similar to the expected stress response strategies or the 'fast-slow' plant economics spectrum. Species' positions (scores) along these PCs (in the following referred to trait axes) were used to characterize species' strengths of the respective trait syndrome.

Relations between species' positions along the trait axes (i.e. species' strengths of the trait syndrome), their fecundity response to drought or grazing, their abundance response to grazing, their growth rates, or their mean annual rainfall niches were tested with F-tests on linear models. Each linear model contained species' positions along one or several trait axes of one PCA (based on one trait set, see above) as explanatory variable(s) and fecundity responses, abundance responses, growth rates, or mean annual rainfall niches as response variable.

Pairwise relations between single traits and/or performance parameters were calculated with Spearman rank correlation coefficients and pairwise relations between species' positions along trait axes with Pearson correlation coefficients.

# 4 Results and Discussion

## 4.1 Annuals are a functionally diverse species group

The winter annuals significantly differed in all investigated traits (up to 150-fold variation across species). In several traits, the magnitude of their range (maximum – minimum trait value) corresponded to almost 40-80 % of the globally documented magnitude of the range in plant species from different life forms and ecosystems (see details in Manuscript 3, p. 174). Winter annuals' trait range magnitudes were in several traits also similar to those of similarly sized[6] species sets of perennial herbaceous and woody species from temperate or dryland ecosystems (Blumenthal, Kray et al., 2020; de la Riva et al., 2015; Mudrák et al., 2019; Sun, 2019). Accordingly, interspecific trait differences in winter annuals are similar to those in perennials. Winter annuals' trait values though fell within or exceeded the acquisitive end of the range observed globally or in perennial species (Blumenthal, Kray et al., 2020; de la Riva et al., 2015; Kattge et al., 2020; Mudrák et al., 2019; Sun, 2019). Winter annuals thus exhibit more acquisitive trait values than perennials in line with previous studies (Garnier et al., 1997; Roumet et al., 2006).

## 4.2 Drought and grazing response strategies in winter annuals

### 4.2.1 Drought and grazing response syndromes

In this section, I briefly describe the drought and grazing response syndromes in the studied winter annuals (for details on single traits, see Figure 9, Manuscript 1 and 2) and compare them to findings in perennials (perennial herbaceous and woody species). In addition to the findings presented in Manuscript 1 and 2, I analysed the relations between species' strengths of the drought and grazing response syndromes. These relations point to the relevance of the trait syndromes for annuals' concomitant response to drought and grazing.

#### 4.2.1.1 Four drought response syndromes (Manuscript 1)

Drought response-related traits in the winter annuals were coordinated into four syndromes. Two syndromes were consistent with the expected strategies of dehydration avoidance and tolerance (*sensu* Fang & Xiong, 2015; Levitt, 1980), whereas escape traits were unexpectedly coordinated into two (rather than one) independent syndromes (Figure 9).

The dehydration avoidance syndrome and tolerance syndrome in the winter annuals were consistent with the appropriate strategies in perennials (Figure 9a-b; Bartlett et al., 2012; Comita & Engelbrecht, 2014; Pérez-Ramos et al., 2013; Powers et al., 2020; Sun et al., 2020). Both syndromes were traded-off in the winter annuals, i.e. avoidance and tolerance traits were associated with the opposite sides of one trait axis (in the following called dehydration avoidance-tolerance axis).

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[6] The species sets of perennials encompassed a similar number of species as the present species set of winter annuals (approximately 40-60 species).

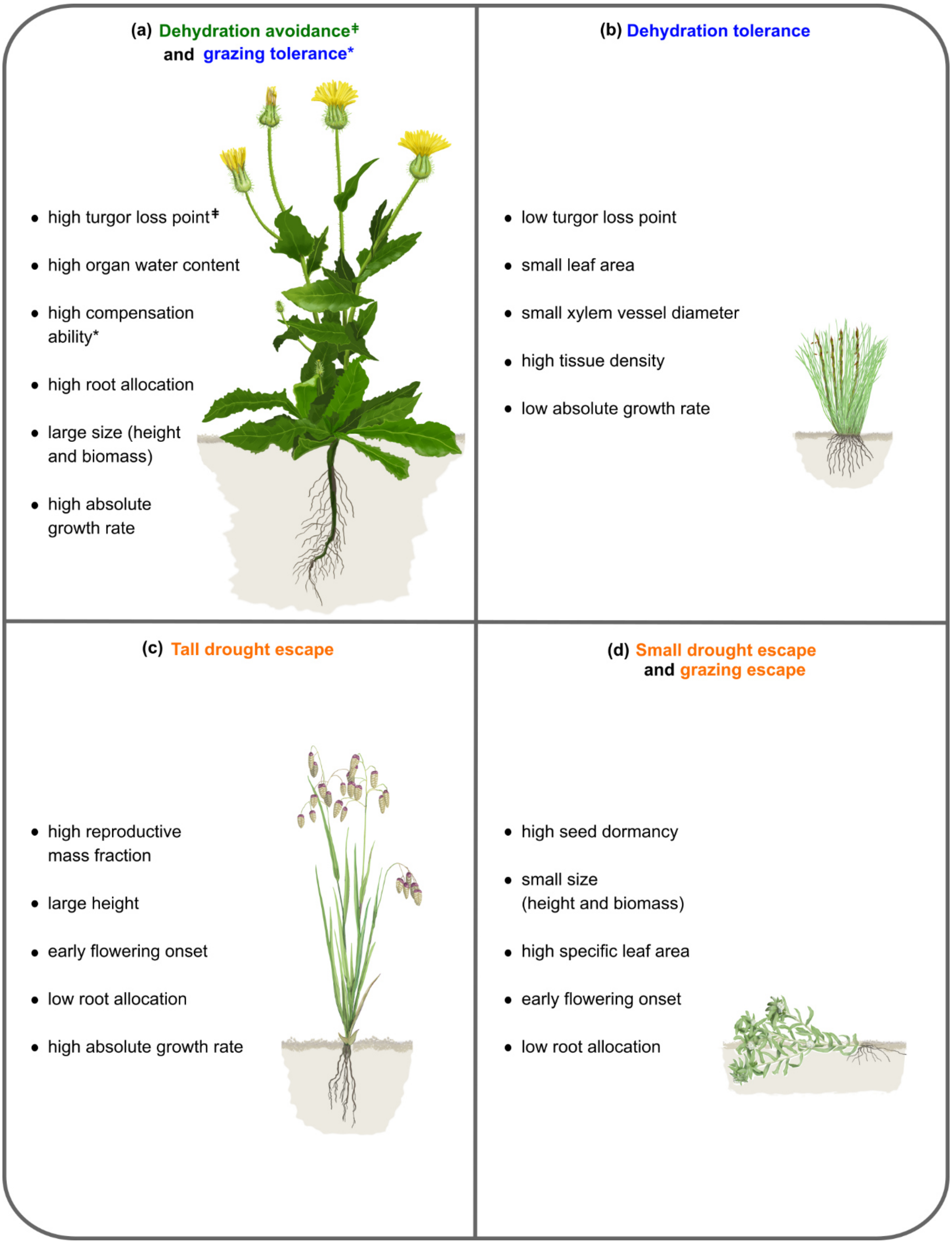

**Figure 9.** The main syndromes of drought and grazing-response related traits in the studied winter annuals with their most important traits and an exemplary, characteristic species. The named traits exhibited the highest loadings on the trait axes and are ordered according to their loading. In (a) * and ǂ indicate traits which were only associated with one of the syndromes (continued on following page).

**Figure 9 continued:** The plant icons are on scale and show the following species: (a) *Urospermum picroides*, (b) *Psilurus incurvus*, (c) *Briza maxima*, (d) *Filago palaestina*. The four trait syndromes are not discrete entities but continuums. Icons were created by © 'DharmaBeren Studio' (www.dharmaberen.com). The figure is distributed under the terms of the Creative Commons CC BY-NC-ND 4.0 license. To view a copy of this license, visit https://creativecommons.org/licenses/by-nc-nd/4.0/. Figure shown with kind permission of 'DharmaBeren Studio'.

The two escape syndromes in the winter annuals indicate that the species differ in their ability to escape drought despite their common life history. Both syndromes were characterized by an early flowering onset and low root allocation, as expected by an escape syndrome (*sensu* Kooyers, 2015), but differed in other traits (Figure 9c-d). One escape syndrome encompassed besides further characteristic escape trait attributes (e.g. high reproductive allocation, high growth rate) also trait attributes opposite to those expected (e.g. low leaf mass fraction, large height, low seed dormancy) and attributes considered to be not relevant for drought escape (e.g. large leaves, large xylem vessel diameter). This syndrome is in the following called *tall (drought) escape syndrome/axis* based on its association with a large height (Figure 9c). The other escape syndrome was almost consistent with the expected escape strategy (*sensu* Kooyers, 2015). This syndrome is in the following called *small (drought) escape syndrome/axis* based on its association with a small size (height and biomass) (Figure 9d). Winter annuals with a pronounced drought escape syndrome can thus differ in their traits.

Both escape axes (syndromes) were independent from the avoidance-tolerance axis, i.e. no trade-off among both escape syndromes and avoidance or tolerance emerged. Instead, the winter annuals exhibited a continuum of trait combinations pertaining to more or less pronounced drought escape (tall or small) and to dehydration avoidance *or* tolerance.

#### 4.2.1.2 Two grazing response syndromes (Manuscript 2)

The grazing response-related traits in the winter annuals were coordinated into syndromes that were almost consistent with the expected grazing escape and tolerance strategy (Figure 9a, d). The tolerance syndrome also corresponded to the appropriate strategy observed in perennials (Adler et al., 2004; Briske, 1996; Strauss & Agrawal, 1999). Avoidance traits, in contrast, were not coordinated in the annuals.

Unexpectedly, the grazing tolerance and to lesser extend the escape syndrome in the annuals encompassed a high compensation ability, i.e. a high ability to regrow after tissue loss. Additionally, the syndromes emerged as independent axes, i.e. they were not traded-off. Consequently, some winter annuals exhibited pronounced attributes of both grazing escape and tolerance.

#### 4.2.1.3 Relations between species' strengths of drought and grazing response syndromes

Species' strengths of the drought and grazing response syndromes in the winter annuals were related to each other (Figure 10).

Annuals with a pronounced dehydration avoidance syndrome also exhibited a pronounced grazing tolerance syndrome (Figure 10a). Accordingly, annuals may concomitantly withstand drought and grazing by minimizing tissue dehydration and compensating tissue loss. The convergence of the dehydration avoidance and grazing tolerance syndrome in the annuals differs from findings in perennials, showing a convergence between dehydration avoidance and grazing avoidance (Quiroga et al., 2010). Perennials thus exhibit a high resistance to grazing and drought by avoiding both factors (generalized grazing model; Adler et al., 2004; Quiroga et al., 2010; Milchunas et al., 1988). The different relations between drought and grazing response syndromes in annuals and perennials should influence their concomitant resistance to drought and grazing under different environmental conditions (see also 4.2.3).

Annuals' strengths of the escape syndromes were also related to each other (Figure 10b-c). The tall drought escape and grazing escape syndrome were traded-off, but annuals with a pronounced small drought escape syndrome also exhibited a pronounced grazing escape syndrome (Figure 10b-c). The convergence of the small drought escape and grazing escape syndrome agrees with our convergence scenario, assuming a convergent filtering of escape traits by drought and grazing. However, the trade-off between the grazing and tall drought escape syndrome indicates that this convergence does not apply to all annuals with a pronounced drought escape syndrome. Annuals with a tall drought escape syndrome should escape drought but not grazing.

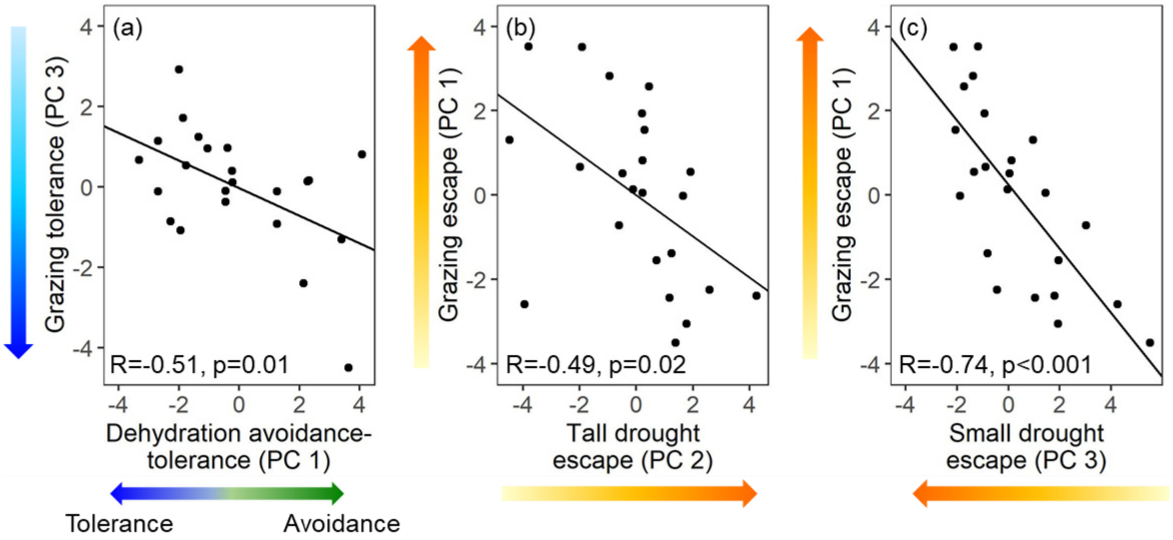

**Figure 10.** Relations between species' strengths of the drought and grazing response syndromes in 23 winter annuals, with species' positions along the (a) grazing tolerance axis and dehydration avoidance-tolerance axis, (b) grazing escape axis and tall drought escape axis, and (c) grazing escape axis and small drought escape axis. PC 1-PC 3 refers to the principal component axes in the respective PCA (see details in Manuscript 1 and 2). Pearson correlation coefficients (R) and significance (p) are given. Other relations between species' strengths of the drought and grazing response syndromes were not significant ($R < |0.35|$, $p \geq 0.09$).

### 4.2.2 Different drought response syndromes confer annuals' similar fecundity responses to drought (Manuscript 1)

All studied annuals reproduced during or after the experimental drought in the growing season, but the species differed in their fecundity responses to the drought. Fecundity responses across the annuals ranged from reductions of fecundity by approximately 50 % in drought-stressed compared to control plants to 30 % higher fecundity in drought-stressed compared to control plants. The fecundity responses resulted from changes in seed number and/or seed mass but not from changes in the proportion of reproductive (i.e. surviving) individuals (see details in Manuscript 1, pp. 83, 112). Also in the field, the studied annuals maintained high survival proportions under an experimental drought with 60 % less rainfall in the growing season than in the moist treatment (Tielbörger et al., unpublished data[7]). In this experiment, species' survival responses ranged from approximately 40 % lower to 30 % higher survival proportions in the dry compared to the moist treatment. These findings indicate wide interspecific differences in winter annuals' drought resistance (based on survival or fecundity), with several annuals exhibiting a high resistance to drought within the growing season.

Species' strengths of the small drought escape but not tall drought escape syndrome were related to their fecundity responses to the experimental drought in the growing season (Figure 11a). Annuals with a pronounced small escape syndrome exhibited high fecundity losses under drought (Figure 11a). This finding agrees with our hypothesis that drought escape reduces species' fecundity under drought in the growing season since the small escape syndrome corresponded to the expected escape strategy (Figure 11a). Accordingly, the present findings solidify the assumption of escape as fitness related strategy in response to drought across annuals. So far, relations between escape traits and performance responses to drought in annuals have been only suggested by a few intraspecific studies based on single traits (Aronson et al., 1992; Tielbörger et al., 2012). Here, we provide empirical support for drought escape as fitness related strategy across annuals in a multi-trait and multi-species experiment with controlled drought conditions (i.e. the effect of drought was separated from other factors). The high fecundity losses in annuals with a pronounced small escape syndrome should result from the association of this syndrome with trait attributes indicating a low capacity of resource storage (carbon and nutrients) and acquisition, such as low root mass fraction and low photosynthetic rate (Craine et al., 2013; Zwicke et al., 2015).

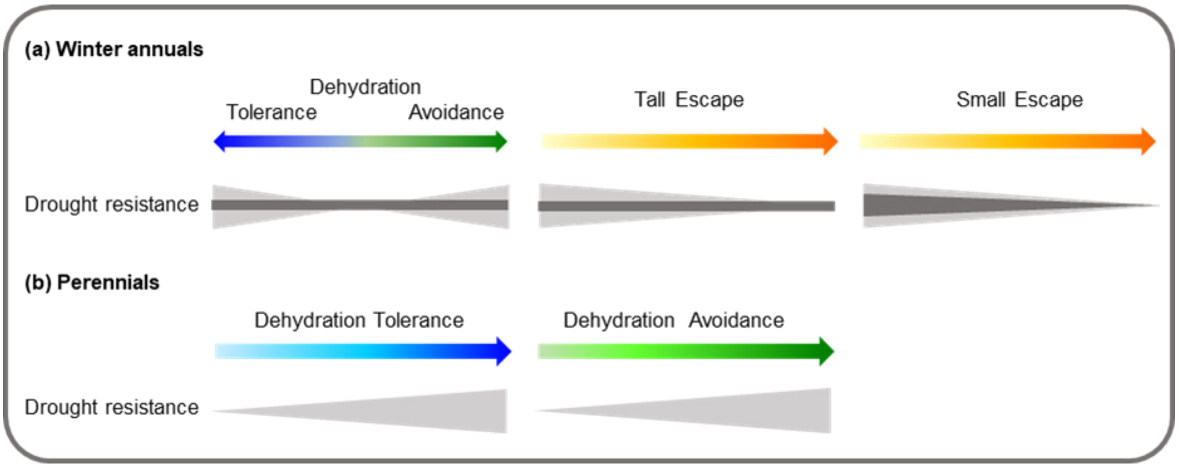

**Figure 11.** Drought response syndromes and their relations to species' drought resistance in (a) the studied winter annuals and (b) perennials. Arrows (triangles) indicate significant relations and lines an independence between species' trait syndrome strengths and drought resistance, light grey symbols indicate hypotheses and dark grey symbols the present findings. In the winter annuals (a) drought resistance was based on fecundity responses. In perennials (b) the hypotheses of the stress response strategy concept are shown (Fang & Xiong, 2015; Levitt 1980), which have been supported by several studies based on survival (see references in the text).

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[7] I analysed these data based on the climate manipulation experiments conducted by Tielbörger et al., (2014). These data/findings have not been explicitly published, yet.

Annuals' strengths of the dehydration avoidance and tolerance syndrome were independent from their fecundity responses to the experimental drought, i.e. species with differing strengths of the avoidance and tolerance syndromes exhibited similar fecundity responses in the studied annuals (Figure 11a). This independence disagrees with our hypothesis that annuals with a pronounced avoidance or tolerance syndrome maintain high fecundity under drought (Figure 11a). Previous studies in annuals also indicate that pronounced avoidance traits confer species higher drought resistance (Harrison & LaForgia, 2019; Huxman et al., 2013), and in perennials, species with pronounced avoidance or tolerance traits maintain high survival under drought (Figure 11b; Álvarez-Cansino et al., 2022; Martínez-Vilalta et al., 2010; Powell et al., 2017; Sun et al., 2020). The different findings in the present and previous studies may result from differences in the drought conditions. Previous studies (see references above) focused on lethal droughts, while we assessed annuals' fecundity responses to a non-lethal drought. Avoidance and tolerance traits may only be associated with species' performance or fitness responses to lethal drought but not non-lethal drought. Species' strengths of the avoidance and tolerance syndrome in the studied annuals were indeed related to their survival responses to an experimental drought in the field (Kurze et al., in prep.[8]). These relations show that both annuals with a pronounced avoidance and tolerance syndrome maintain high survival under drought (Kurze et al., in prep). Accordingly, in winter annuals not only one syndrome, i.e. avoidance *or* tolerance, but both syndromes confer species high drought survival. This finding indicates that winter annuals do not only escape but also withstand drought in the growing season.

The relations between annuals' trait syndrome strengths and their fecundity or survival responses to drought were weak and exhibited a low explanatory power in respect to all trait axes (coefficient of determination, $R^2 \leq 0.16$). The low explanatory power emerged since along each trait axes (including the small drought escape axis) annuals with different trait attribute combinations partly exhibited similar fecundity or survival responses, i.e. the annuals exhibited alternative trait combinations[9]. Alternative trait combinations have been also shown in perennials (Li et al., 2020; Worthy et al., 2020) and predicted by theoretical models (Marks & Lechowicz, 2006). They can be explicitly detected with statistical methods that can assess non-linear relations and/or indirect effects between explanatory (here traits) and response variables (here performance or fitness response), such as Bayesian approaches, adaptive landscapes, or structural equation models (see Laughlin & Messier, 2015; Pistón et al., 2019). These statistical methods require higher species numbers (i.e. higher sample sizes, Pistón et al., 2019) and therefore go beyond the scope and feasibility of this thesis. Future studies should account for alternative trait combinations and their consequences in winter annuals to improve our mechanistic understanding of this species group (see Pistón et al., 2019; Worthy et al., 2020). The present study provides the basis for these investigations by highlighting four drought response syndromes in winter annuals for the first time.

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[8] Kurze et al., in prep refers to a manuscript in preparation, in which species' strengths of the four drought response syndromes in the winter annuals are related to their survival responses (and other parameters) to an experimental drought in the field (based on the climate manipulation experiment by Tielbörger et al., 2014). Preliminary analyses show that annuals with a pronounced dehydration tolerance syndrome and early flowering (based on the tall escape syndrome) as well as late flowering species with a pronounced dehydration avoidance syndrome maintain high survival proportions under drought.

[9] Alternative trait combinations are trait combinations that confer species similar performance or fitness responses to a certain factor, i.e. multiple, non-linear performance or fitness peaks emerge (see Pistón et al., 2019).

### 4.2.3 Grazing escape and tolerance are successful strategies in response to grazing (Manuscript 2)

All studied annuals regrew and reproduced after the simulated grazing, but their fecundity responses to grazing differed across species. Species' fecundity responses ranged from fecundity losses of approximately 50 % in clipped compared to control plants to almost no response, i.e. similar fecundity in clipped and control plants. In the field, natural grazing reduced species' abundances by maximum approximately 50 % in both dry and moister habitats. Both winter annuals with a pronounced escape and tolerance syndrome maintained high fecundity under simulated grazing (Figure 12a). This finding emphasizes the escape and tolerance syndrome as successful fitness related strategies in response to grazing in winter annuals. The high fecundity of annuals with a pronounced escape or tolerance syndrome should result from the high compensation ability associated with both syndromes (see 4.2.1.2). Accordingly, annuals with an escape strategy exhibited high grazing resistance although grazing escape *per se* was experimentally precluded (i.e. tissue was removed before successful reproduction). This finding disagrees with the assumption of our trade-off scenario that annuals with an escape strategy show high fecundity losses under grazing in the growing season due to their low compensation ability (Figure 12a, see 1.5.1.2).

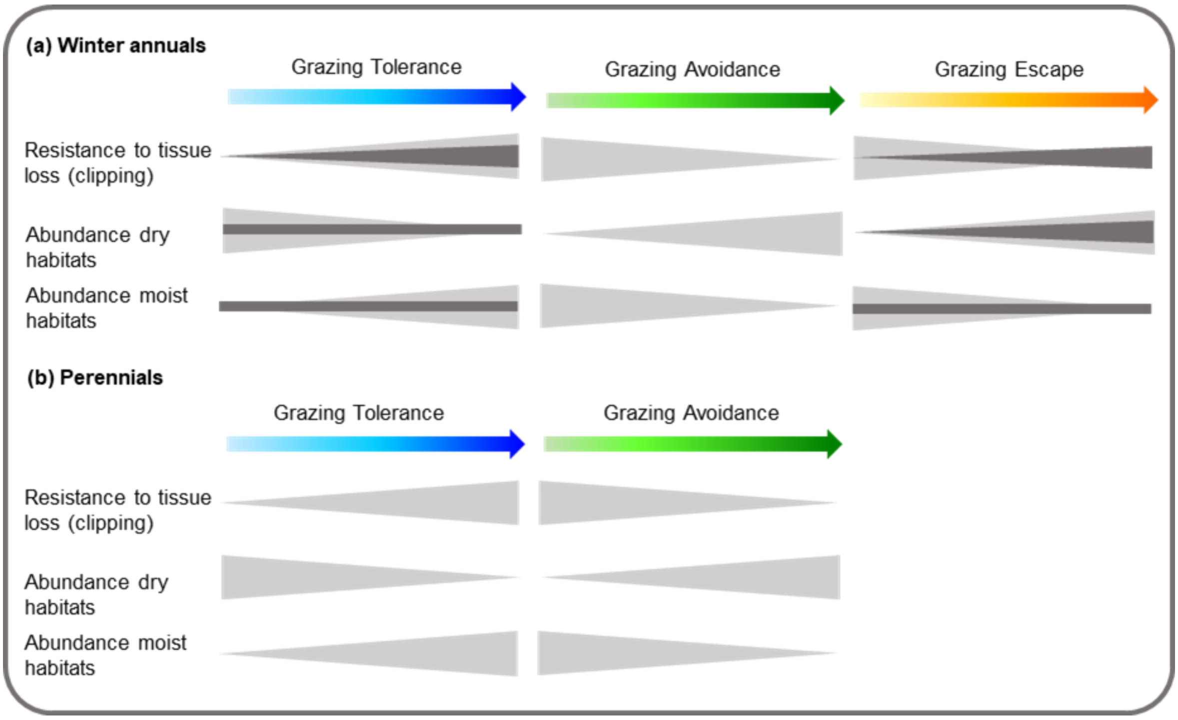

**Figure 12.** Grazing response syndromes and their relations to species' resistance to tissue loss or their abundance under grazing in (a) the studied winter annuals and (b) perennials. Arrows indicate significant relations and lines an independence between species' trait syndrome strengths and their resistance or abundance, light grey symbols indicate hypotheses and dark grey symbols the present findings. In winter annuals (a) the light grey arrows for grazing avoidance refer to the trade-off scenario and for grazing escape to the convergence scenario (see 1.5.1.2). In perennials (b) the hypotheses of the stress response strategy concept and generalized grazing model are shown (Briske, 1996; Levitt, 1980; Milchunas et al., 1988), which have been supported by several studies in respect to abundance (see references in 1.5.1.2).

Annuals with an escape strategy also maintained high abundances under grazing in dry habitats in our field experiment (Figure 12a). The favouring of the grazing escape strategy in drier conditions should result from its convergence with the small drought escape strategy (see 4.2.1.3)[10]. This convergence should enable the winter annuals to successfully cope with both grazing and drought, by withstanding and escaping it, respectively. The present findings thus support our convergence scenario (see 1.5.1.2). However, contrary to the assumptions of the convergence scenario, escape emerged as a successful strategy in sites that are intensively rather than infrequently grazed in the growing season, i.e. annuals with an escape strategy exhibited high abundances under a grazing regime that commonly precludes successful grazing escape. This unexpected finding is likely due to the unexpected high compensation ability of annuals with a grazing escape strategy, which enables them to maintain high fecundity despite tissue loss, as observed in the greenhouse experiment (see above). Furthermore, the high seed dormancy associated with the grazing escape strategy should reduce negative effects of grazing on species' abundances by buffering reproductive failure (see Tielbörger et al., 2012).

The convergent favouring of escape traits by grazing and drought in winter annuals corresponds to the generalized grazing model that states convergent filtering of traits by grazing and drought in perennials but in respect to avoidance (Figure 12; Milchunas et al., 1988). Accordingly, the generalized grazing model can be extended to winter annuals with respect to escape. The difference in the favoured strategies between perennials and annuals (i.e. avoidance *vs*. escape) should influence the functioning and services of their communities under grazing and drought. In both life-history groups, the favoured species are rather small, i.e. produce less biomass and forage. In perennials, the favouring of the avoidance strategy also reduces forage quality since this strategy is associated with conservative trait attributes (e.g. high leaf dry matter content, low nitrogen content; Adler et al., 2004). The escape strategy in annuals encompassed acquisitive trait attributes (e.g. low toughness, high specific leaf area). A favouring of the escape strategy should thus not affect forage quality. However, it likely reduces the period in the growing season in which alive biomass is available since annuals with an escape strategy die off earlier (see Blumenthal, Mueller, et al., 2020). Consequently, the different strategies favoured by drought and grazing in annuals and perennials should be considered in assessments of global change consequences.

Annuals' strengths of the tolerance strategy were unexpectedly independent from their abundance responses to grazing in our field experiment (Figure 12a). This independence can result from confounding factors, such as demographic stochasticity, differences in species' establishment probability, and/or changes in abiotic conditions due to dunging or trampling (Huang et al., 2016; Kohler et al., 2004; Shipley et al., 2012), which may overrule the relation between species' strengths of the tolerance strategy and their fecundity responses to grazing. Additionally, annuals with a pronounced tolerance strategy should experience higher relative tissue loss under natural grazing due to their large sizes and the feeding behaviour of ungulates than smaller annuals. Ungulates feed as much biomass as possible, i.e. they eat off all (palatable) plants to a similar height independently of their former size (Briske, 1996; M. Bilton personal observation). This uneven tissue removal can lead to similar performance responses in annuals with wide differences in grazing tolerance.

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[10] Species' strengths of the small drought escape syndrome were also related to their abundance responses to grazing in dry habitats (LM statistics $F_{1,18} = 5.1$, $p = 0.037$, $R^2 = 0.18$), i.e. annuals with a pronounced small drought escape syndrome maintained high abundances under grazing in dry slopes.

The present finding of two grazing response strategies, escape and tolerance, in winter annuals helps to contextualize previous observations of a few community-based studies, which related single traits to annuals' abundance responses to grazing (Carmona et al., 2015; Díaz et al., 2001; Fernández Alés et al., 1993; Lavorel et al., 1999; Osem et al., 2004; Rota et al., 2017). These studies show that annuals with trait attributes characteristic of our identified escape syndrome, such as high specific leaf area, small size, and low leaf toughness, are favoured under grazing. Tolerance traits remained, to my knowledge, unaddressed. The ecological relevance of the tolerance strategy in winter annuals thus needs further attention, but the community-based observations support the present finding of grazing escape as ecologically highly relevant strategy in winter annuals.

### 4.2.4 Annuals with different drought and grazing response syndromes co-occur along the rainfall gradient (Manuscript 1 and 2)

Species' strengths of the drought and grazing response syndromes in the winter annuals were predominantly[11] independent from their distribution along the rainfall gradient in Israel. Accordingly, annuals with different trait syndromes co-occur across the gradient (Figure 13a). This finding disagrees with our hypothesis of an interspecific shift from drought and grazing escape in arid conditions (allowing to reproduce within the short growing season) to dehydration avoidance, dehydration tolerance, and grazing tolerance in moister conditions (allowing to reach high competitive effect; Figure 13a).

The co-occurrence of annuals with different trait syndromes along the rainfall gradient in Israel indicates that several trait attribute combinations enable them to persist in a wide range from arid to moister conditions. Also in perennials, different trait combinations have been shown to be similarly successful along large-scale moisture gradients (Carvajal et al., 2019; Cernusak et al., 2011; Frenette-Dussault et al., 2013; Sun et al. 2020; Wright et al., 2004) in line with theoretical findings (Marks & Lechowicz, 2006). The studied annuals likely either escape or withstand drought under arid conditions as indicated by the findings from our drought experiments (see 4.2.2). Under moister conditions, the annuals may cope with the higher competition intensity by a high competitive effect or high competitive response[12] (Goldberg & Landa, 1991; Liancourt et al., 2009). Furthermore, annuals with a pronounced escape syndrome may evade competition by larger, late-flowering species in moister conditions and buffer reproductive failure (Venable & Brown, 1988; Verdú & Traveset, 2005). The co-occurrence of winter annuals with different trait syndromes should be additionally facilitated by the high temporal and spatial variability of rainfall and grazing in our study system. In several annual plant communities, inter-annual rainfall variability has been shown to favour each species or syndrome in some years, allowing for the co-occurrence of species with different trait attributes (Angert et al., 2009; Chesson et al., 2004; Kraft et al., 2015).

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[11] Only species' strengths of the dehydration avoidance and tolerance syndrome were weakly ($p = 0.06$) related to their distribution along the rainfall gradient. Possible mechanisms underlying this interspecific shift are discussed in Manuscript 1 (p. 87). They co-occur with the ones, mentioned above, assumed to underlie the independence between species' trait syndrome strengths and their distribution along the rainfall gradient.

[12] Species with high competitive effect exhibit high competitive ability by reducing the fitness of neighbours, and species with high competitive response exhibit high competitive ability by maintaining high fitness despite the presence of strong competitors (see Goldberg & Werner, 1983).

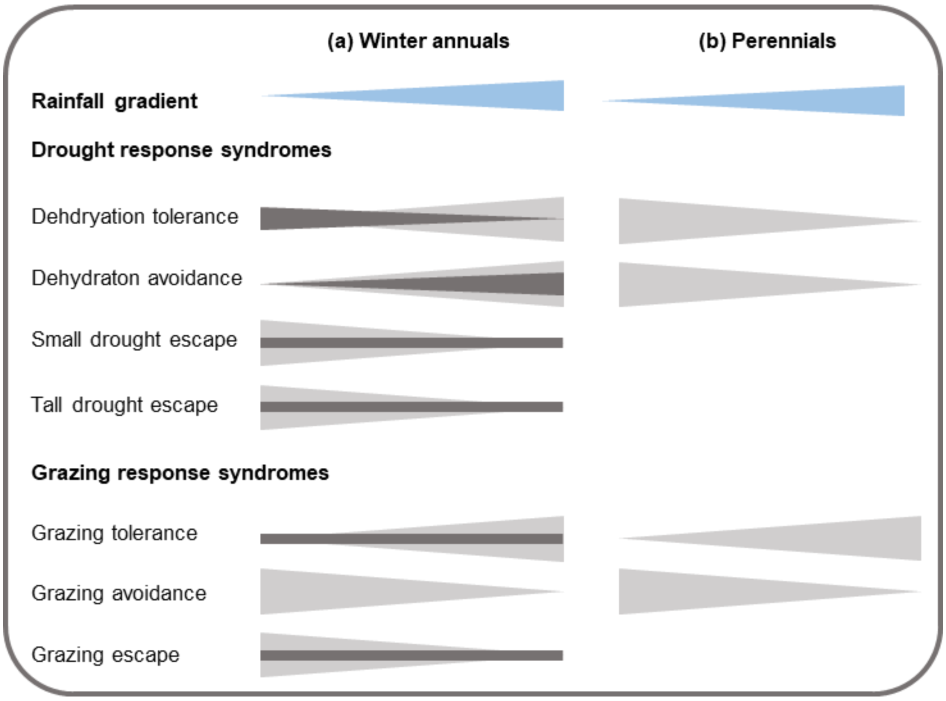

**Figure 13.** Distribution of drought and grazing response syndromes along rainfall or moisture gradients in (a) the studied winter annuals and (b) perennials. Arrows (triangles) indicate significant relations and lines an independence between species' strengths of the trait syndrome and their distribution along the rainfall gradient, light grey symbols indicate hypotheses and dark grey symbols the present findings. In winter annuals (a) the light grey arrows for grazing avoidance refer to the trade-off scenario and for grazing escape to the convergence scenario (see 1.5.1.2). In perennials (b) the hypotheses of the stress response strategy concept and generalized grazing model are shown (see Levitt, 1980; Milchunas et al., 1988), which have been supported by several studies (see references in 1.5.1.2).

The predominant independence between annuals' trait syndrome strengths and their large-scale distribution along the rainfall gradient does not rule out that annuals are filtered at smaller spatial scales, i.e. by local conditions. Large-scale studies, such as the present one, frequently elucidate trait-environment relations (e.g. Griffin-Nolan et al., 2019; Thuiller et al., 2004), but local conditions and species' abundance can be also crucial for detecting species' ecological filtering (Bruelheide et al., 2018). A strong effect of local moisture conditions on annual plant community composition has been observed in our study system (Finkel et al., 2001; Kutiel, 1992). The findings from the grazing exclosure experiment (based on abundances) also indicate that local environmental conditions (i.e. north-facing *vs.* south-facing slopes) influence the ecological filtering of annuals and their strategies (see 4.2.3). Ecological filtering of annuals by local conditions should thus be addressed further. If local moisture conditions emerge as relevant for annuals' ecological filtering, they should be considered in global change assessments (see Bruelheide et al., 2018). Furthermore, our focus on interspecific trait differences did not account for adaptations of populations to local conditions, i.e. intraspecific trait variation. If and to what extent intraspecific trait variation influences annuals' ecological filtering is speculative, since intraspecific variation usually differs among species and traits (Albert, Thuiller, Yoccoz, Soudant, et al., 2010; Tautenhahn et al., 2019; Yang et al., 2021). At large spatial scales and steep environmental gradients, as investigated here, intraspecific trait variation is unlikely to override interspecific relations, since it is commonly much smaller than interspecific trait differences (Cornwell & Ackerly, 2009; Kazakou et al., 2014; Siefert et al., 2015).

### 4.2.5 Applicability of the concept of drought and grazing response strategies to winter annuals

The present findings indicate that the concept of stress response strategies (*sensu* Levitt, 1980) is suitable to identify the mechanisms underlying winter annual species' responses to drought and grazing. Explicitly testing this concept in winter annuals showed that several of the identified trait syndromes and their relations to species' fitness responses, abundance responses, or distribution agree with the hypotheses of this concept, whereas a few hypotheses (e.g. the generalized grazing model, tall drought escape syndrome) need to be adapted to this species group (see details in 4.2-4.5, Figure 11-13). The inconsistencies between the observed and hypothesized syndromes and relations emphasize that explicitly testing the concept of stress response strategies is a precondition for using it to assess or project species' performance, community composition, or ecosystem functioning in a certain species group.

Some trait syndromes and their relations to fitness or abundance responses in the winter annuals also differ from previous findings in perennials (see details in 4.2-4.5, Figure 11-13). The life history and associated trait differences between both groups have thus pervasive consequences for the mechanisms underlying species' performance or fitness responses to drought and grazing. Accordingly, trait syndromes and their relations to species' responses to drought and grazing cannot be thoroughly generalized across both life-history groups (annuals *vs.* perennials). However, the winter annuals exhibited a similar number of drought or grazing response syndromes as perennials. This finding indicates that winter annuals are functional similarly diverse as perennials, undermining the traditional view of annuals as a homogenous functional group (see Grime, 1977; Levitt, 1980).

Whether the present findings on trait syndromes and their relations to species' fitness or abundance responses to drought or grazing or their distribution along large-scale rainfall gradients generally apply to winter annuals remain elusive. Studies on annuals from other drylands, which are comparable to our approach, are, to my knowledge, missing. The trait ranges of our study annuals were similar to annuals from other drylands, such as North America and the Iberian Peninsula (Blumenthal, Kray, et al., 2020; Pérez-Ramos et al., 2019), but trait-trait, trait-performance, and trait-distribution relations also depend on the environmental conditions (Keddy, 1992; Laughlin & Messier, 2015). Considering the wide differences in environmental conditions and grazing histories among drylands (Díaz et al., 2007; Maestre et al., 2021; Safriel & Adeel, 2005), to assess the generality of the present findings would be speculative. Accordingly, further studies on stress response strategies are necessary to evaluate the generality of this concept to (winter) annuals. The present thesis though is the first study highlighting the suitability of this concept for annuals.

## 4.3 Plant economics spectrum in winter annuals

### 4.3.1 Independence of carbon gain traits and structural traits (Manuscript 3)

A key hypothesis of the plant economics spectrum is the interspecific coordination of resource-use related traits along one axis, comprising both structural and carbon gain traits (Reich, 2014). The studied annuals, however, showed a decoupling between structural (e.g. tissue density, leaf thickness, leaf dry matter content, root diameter, specific root length) and carbon gain traits (e.g. photosynthetic rate, nitrogen content, specific leaf area, carbon content), i.e. both trait sets were associated with independent axes. This decoupling emerged since structural leaf trait differences in the annuals, i.e. species' differences in leaf tissue density and thickness, resulted from differences in silicon content, leaf hairiness, and water content, and not from differences in carbon content as assumed by the plant economics spectrum and shown in perennials (de la Riva, Olmo, et al., 2016; Onoda et al., 2017;

Reich, 2014; Roderick et al., 1999; Wright et al., 2004, see details in Manuscript 3, pp. 163-164, 177). In contrast to a high carbon content, pronounced leaf silicon content, leaf hairiness, and leaf water content do not affect mass-based photosynthetic rate since these attributes neither constrain the proportion of mass-based nitrogen content nor the diffusion resistance to carbon dioxide (compare to Grubb, 2016). Therefore, structural traits vary independently from carbon gain traits in winter annuals.

The decoupling of structural and carbon gain traits releases winter annuals from the trade-off between structural investment, leaf lifespan, and mass-based photosynthetic rate assumed by the plant economics spectrum (Wright et al., 2004). In perennials, leaves with a high structural investment (i.e. high thickness or tissue density) need a long life span to balance their initial carbon investment by their low mass-based photosynthetic rate (Reich et al., 1991; Wright et al., 2004). In the winter annuals, leaves with high structural investment can exhibit high mass-based photosynthetic rate, i.e. they do not need a long lifespan to balance their initial investment. Accordingly, winter annuals can exhibit leaves with higher thickness or tissue density than expected by their short leaf lifespan and the relations observed in perennials (Ryser & Urbas, 2000; Sartori et al., 2019; Wright et al., 2004).

High leaf silicon content, leaf hairiness, and/or leaf water content are not only characteristic for winter annuals but also pronounced in other species groups, such as perennial grasses, succulent perennials, or alpine species (see Grubb, 2016). Furthermore, a decoupling of structural and carbon gain traits can result from further traits, such as colourless tissue, spines, or fibres in the lamina, which are pronounced in understory plants of tropical forests, in Bromeliaceae, Orchidaceae, or sedges (Grubb, 2016). A decoupling between structural and carbon gain traits contrary to the hypothesis of the plant economics spectrum may thus not be restricted to winter annuals.

### 4.3.2 Independence of growth rate and drought resistance (Manuscript 1 and 3)

In the following paragraph, I present the relations among species' positions along the carbon gain or structural trait axes, and their growth rates (absolute and relative growth rate), their positions along the axes of drought response trait syndromes, and their drought resistance (i.e. fecundity response to drought). These analyses elucidate whether the hypothesized growth-drought resistance trade-off apply to absolute or relative growth rate in the annuals, and whether species' positions along the axes of resource-use related traits can be used as proxies for their drought response syndrome strengths and/or their drought resistance as suggested by the plant economics spectrum. The presented relations complement the analyses in Manuscript 1 and 3.

According to the hypothesis of the plant economics spectrum, species' positions along the single axis of resource-use related traits influence their growth rate and drought resistance (Reich, 2014). The studied winter annuals did not fulfil an assumption of this hypothesis, since they showed a decoupling between structural and carbon gain traits. Nevertheless, species' positions along the carbon gain trait axis were related to relative growth rates in the annuals. Annuals with pronounced carbon gain trait attributes (e.g. high mass-based photosynthetic rate, high specific leaf area) exhibited higher relative growth rates (Table 3). This relation should emerge since the efficiency of biomass production (i.e. relative growth rate) closely depends on photosynthetic rate (Lambers & Poorter, 1992). Absolute growth rates, in contrast, were independent from species' positions along the carbon gain trait axis (Table 3). This independence agrees with the assumption that annuals' absolute growth rates depend not only on resource acquisition as metabolically active plant but also on seed mass (mass of a single seed; DeMalach et al., 2018; Simpson et al., 2021). Absolute growth rate was positively related to seed mass in the studied annuals (Spearman rank correlation coefficient $\rho = 0.46$, $p = 0.048$). Species' positions along the structural trait axis were independent from both growth rates (Table 3).

Species' positions along the structural or carbon gain trait axes were associated with their strengths of the dehydration avoidance, tolerance, or tall escape syndrome but independent from their strengths of the small escape syndrome - the only syndrome related to species' drought resistance (Table 3). In line with these relations, species' positions along both axes of resource-use related traits were independent from their drought resistance (Table 3). Accordingly, species' positions along the structural or carbon gain trait axes in winter annuals should not be used as proxy for their drought resistance.

**Table 3.** Relations between species' positions along both axes of resource-use related traits, their growth rates, species' positions along the axes of drought response trait syndromes, and drought resistance (i.e. species' fecundity response to drought). Relations between species' positions along the axes of resource-use related traits, growth rate, and drought resistance were tested with F-tests on linear models (F-value and significance are given). Relations between species' positions along different trait axes were tested with Pearson correlation coefficient based on 29 species (Pearson correlation coefficient and significance are given). Significant relations are given in bold. Significance is given with ** $p < 0.001$, * $p \leq 0.05$, ns not significant $p > 0.05$.

| | Structural trait axis | Carbon gain trait axis |
|---|---|---|
| Relative growth rate ($F_{1,17}$) | 0.08 ns | **5.95 *** |
| Absolute growth rate ($F_{1,17}$) | 0.18 ns | 2.33 ns |
| Drought resistance ($F_{1,16}$) | 2.88 ns | 0.43 ns |
| Dehydration avoidance-tolerance axis | **0.79 **** | **0.44 *** |
| Tall drought escape axis | **-0.43 *** | 0.35 ns |
| Small drought escape axis | -0.33 ns | 0.37 ns |

The present findings show that growth rate and drought resistance are differently influenced by resource-use related traits in winter annuals. The assumption of the growth-stress resistance trade-off that both parameters reciprocally depend on the same traits (Reich, 2014) thus does not apply to this species group. In line with this finding, species' drought resistance was independent from both relative and absolute growth rates in the annuals (linear model statistics: $F_{1,16} < 0.77$, $p > 0.39$)[13]. Accordingly, winter annuals do not show a trade-off between growth rates and drought resistance as expected by the plant economics spectrum. An interspecific independence between growth rate and drought resistance has been also observed in a few studies on perennial species (Fernández & Reynolds, 2000; Jung et al., 2020; Russo et al., 2021). These findings in annuals and perennials caution to generalize the growth-drought resistance trade-off both within and across life-history strategies (annuals and perennials).

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[13] In line with this finding, species' survival responses to experimental drought in the field were independent from both growth rates (Spearman rank correlation coefficient $\rho < 0.21$, $p > 0.47$, Kurze et al., in prep).

### 4.3.3 Independence of resource-use related traits and species' distribution along the rainfall gradient (Manuscript 3)

In the winter annuals, species' positions along both axes of resource-use related traits, their growth rates, and drought resistance were independent from their distribution along the rainfall gradient. The annuals thus did not show an interspecific shift from fast (acquisitive) to slow (conservative) trait attributes with decreasing or increasing rainfall as assumed by the plant economics spectrum or our hypotheses, respectively.

The independence between species' positions along both axes of resource-use related traits and their distribution is not surprising considering that annuals' strengths of the drought response trait syndromes were also predominantly independent from their distribution along the rainfall gradient (see 4.2.4). Resource-use related traits influence species' responses to biotic and abiotic factors besides water availability (Holdaway et al., 2011; Reich, 2014). Therefore, they are limited in their ability to capture species' responses to a single abiotic factor, such as water availability in the present study[14] (see Griffin-Nolan et al., 2018; Májeková et al., 2021).

The co-occurrence of annuals with wide differences in growth rate and drought resistance along the rainfall gradient should be a consequence of the independence between both parameters. Also in those perennials, in which growth rate and drought resistance were independent, species with wide differences in both parameters co-occurred along moisture gradients (Jung et al., 2020). The annuals may either withstand or escape drought in arid conditions and successfully cope with the more intense competition in moister conditions by a high competitive effect or high competitive response, with all these abilities differently associated with growth rate and drought resistance (see also 4.2.4).

### 4.3.4 The plant economics spectrum is not applicable to winter annuals

The present findings emphasize that the plant economics spectrum is not applicable to winter annuals. The annuals did not show the interspecific functional constraints (i.e. trait-trait, trait-growth, growth-drought resistance relations) or trait-rainfall relations hypothesized by this concept (Figure 14). Consequently, winter annuals cannot be ranked along a single axis of resource-use related traits from acquisitive (or fast) to conservative (or slow) as proposed by the plant economics spectrum.

The generality of the plant economics spectrum is not only questioned by the present study on winter annuals but has been also undermined by a few studies on woody and perennial herbaceous species from different ecosystems (Baraloto et al., 2010; Carvajal et al., 2019; Fortunel et al., 2012; Sun, 2019). The studies in perennials did not identify the mechanisms underlying the unexpected trait coordinations. This understanding though is necessary to identify the framework conditions in respect to plant traits or the environment under which the hypotheses of the plant economics spectrum apply (or not).

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[14] Due to this different ability to indicate species' drought responses, species' positions along the structural trait axis likely did not mirror the trait-rainfall relation observed based on the dehydration avoidance-tolerance axis in the annuals, although both axes were correlated.

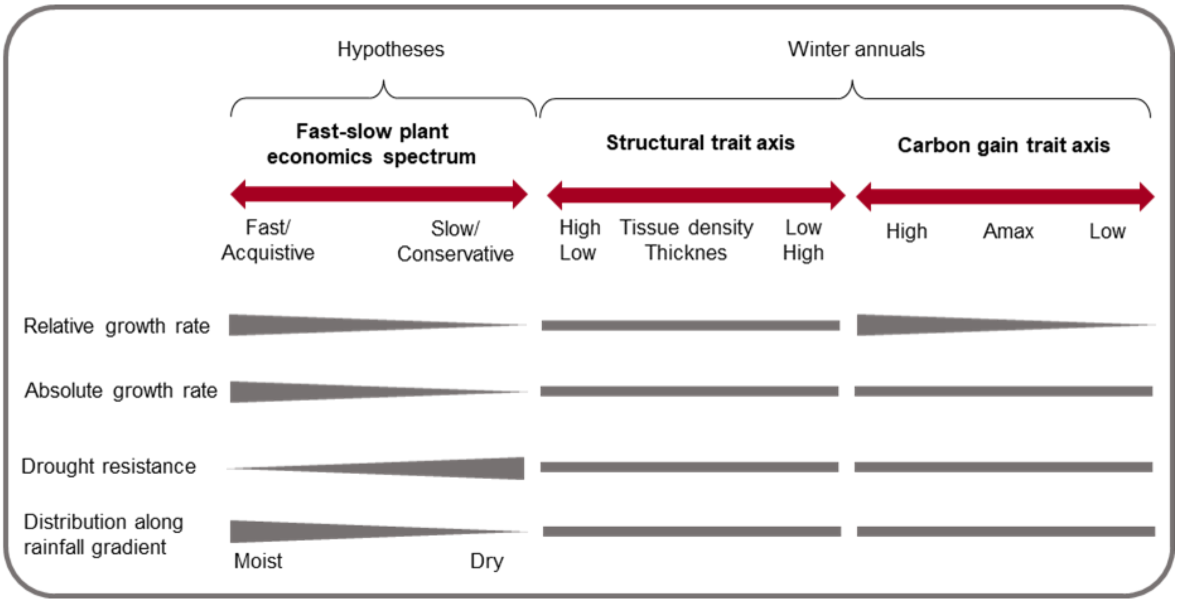

**Figure 14.** Hypotheses of the plant economics spectrum and present findings in winter annuals. Arrows (triangles) indicate significant relations and lines an independence between a parameter (left column) and trait axis. The traits mentioned along the axes in winter annuals are exemplary, for details see Manuscript 3. Thickness refers to leaf thickness, Amax to maximum mass-based photosynthetic rate.

The present findings in the winter annuals also caution to use species' positions along the axes of resource-use related traits as proxy for their drought resistance. Annuals' positions along both axes of resource-use related traits did not mirror the trait-drought resistance or trait-distribution relations identified based on the drought response trait syndromes (see 4.2.2, 4.2.4). The limited ability of resource-use related traits to reflect species' drought resistance and distribution could be a consequence of the missing applicability of the plant economics spectrum to winter annuals. However, some studies in perennials, which predominantly show the trait coordination expected by this concept, also observed weak or even missing relations between resource-use related traits and species' drought resistance or species' association to moisture (Ordoñez et al., 2009; Powers et al., 2020; Sun, 2019). Species' drought resistance in perennials was more strongly associated with hydraulic traits, such as turgor loss point or water potential at a certain percentage of embolisms, which are, if at all, weakly related to resource-use related traits (Kunert et al., 2021; Maréchaux et al., 2015; Powers et al., 2020; Rodríguez et al., 2022). In line with these findings, species' positions along the axes of resource-use related traits and drought response-related traits differ in their relations to species' performance responses to drought or distribution along moisture gradients in herbaceous perennials (Sun, 2019; Sun et al., unpublished data). This finding in herbaceous perennials is similar to the present one in winter annuals (see above). The assumption of the plant economics spectrum to project species' drought resistance or distribution based on easily measurable, resource-use related traits should thus considered with caution in both winter annuals and perennials.

# 5 Conclusion

In the following, I discuss the functionality and predictive ability of traits in winter annuals and assess global change consequences on their communities based on the findings from all three manuscripts'.

## 5.1 Functionality and predictive ability of traits in winter annuals

Relations between traits and species' fitness responses in the studied annuals almost exclusively emerged based on species' trait syndrome strengths, i.e. based on multiple traits. Single traits were predominantly independent from species' fitness responses (see for details Manuscript 1 p. 111 and Manuscript 2, p. 147). Weak or missing relations between species' performance and single traits have been also observed in perennials (Brenes-Arguedas et al., 2013; Poorter et al., 2008; Sun et al., 2020). The limited fitness and performance relevance of single traits likely emerges since species' performance and fitness responses depend on several, often coordinated traits (Laughlin, 2014; Laughlin & Messier, 2015). Furthermore, only large trait sets reveal unexpected trait coordinations that can be crucial for understanding species' performance and fitness responses (see 4.2.2 and 4.2.3, Medeiros et al., 2019; Sun, 2019). Accordingly, considering species' whole phenotype, i.e. comprehensive trait sets, is necessary to understand and assess species' performance and fitness responses to the environment in both annuals and perennials (see Laughlin, 2014; Medeiros et al., 2019; Pistón et al., 2019).

By considering comprehensive trait sets, we identified the small drought escape, grazing escape, and grazing tolerance syndrome as fitness related strategies in winter annuals in the face of drought and grazing, respectively. These findings close a gap on the mechanistic understanding of annuals' drought and grazing responses and their strategy differences from perennials. It emphasizes the functional diversity within winter annuals and its pervasive consequences for species' performance responses to drought and grazing. This knowledge provides a basis for establishing 'trait-based laws' (see Lawton, 1999) in winter annuals, such as the applicability of the generalized grazing model, stress response strategies or plant economics spectrum (see details in 4.2 and 4.3). The explicit links between species' trait syndrome strengths and their fitness responses also reinforce a foundational assumption of trait-based ecology, i.e. the relations between traits and fitness responses across species, in winter annuals (Laughlin et al., 2020; Shipley et al., 2016). Investigating these relations is a prerequisite of trait-based ecology since the direction and strengths of these relations can vary across life-history strategies or biomes (Laughlin et al., 2020; Shipley et al., 2016). Our findings on the relevance of species whole phenotype and alternative trait combinations for assessing species' fitness responses (see above and 4.2.2) indicate that explicitly establishing these relations is far from being trivial. Interspecific relations between traits and fitness response should not be taken for granted but thoroughly tested before using traits to project species' responses in a certain species group or ecosystem. Accordingly, multi-species and multi-trait datasets, such as the present one, are crucial for establishing a trait-basis for understanding and projecting species' responses to the environment (see Laughlin et al., 2020; Shipley et al., 2016).

Based on the premises of the predictive ability and transferability of trait-based relations, the present findings in winter annuals should be suitable for projecting global change consequences (see details in 5.2). The explanatory power of the relations between species' trait syndrome strengths and their fitness responses in the studied annuals ($0.08 \leq R^2 \leq 0.43$) was similar to perennials (e.g. Esquivel-Muelbert et al., 2017; Li et al., 2015; Medeiros et al., 2019; Poorter et al., 2008; Powers et al., 2020; Visser et al., 2016). In perennials, relations with such an explanatory power have been used to provide careful hints on global change consequences on their communities and ecosystems (Esquivel-

Muelbert et al., 2017; Li et al., 2015; Powers et al., 2020). Furthermore, the present trait-based findings in winter annuals can be incorporated in models, which simulate responses of winter annual species or communities to drought and/or grazing. Models simulating the consequences of (increasing) drought and/or grazing on plant communities in drylands are so far scarce (Tietjen & Jeltsch, 2007), although dynamic vegetation models are a powerful tool for assessing long-term global change consequences (McDowell et al., 2013). Most dynamic (global) vegetation models are so far relatively simple formulated in respect to the mechanisms underlying plants' functioning and consider only a few plant functional types (McDowell et al., 2013, Scheiter et al., 2013; Yang et al., 2015). These simplifications can cause uncertainties in model predictions (McDowell et al., 2013; Powell et al., 2017). Therefore, there is a growing consensus and effort to directly incorporate traits (McDowell et al., 2013; Powell et al., 2017, Scheiter et al., 2013; Yang et al., 2015). This requires comprehensive knowledge on trait attributes and relevant mechanisms (McDowell et al., 2013, Scheiter et al., 2013; Yang et al., 2015). This thesis contributes to this knowledge for winter annuals and should stimulate model developments for these communities.

## 5.2 Assessment of global change consequences on winter annual plant communities in the southwestern Levant

The present findings show that winter annuals from the southwestern Levant reproduce despite drought or grazing within the growing season, with several of the annuals exhibiting high drought or grazing resistance. The high resistance of the annuals agrees with the negligible compositional changes in their communities under drought or grazing in some field studies in this region (e.g. Sternberg et al., 2015; Tielbörger et al., 2014). Our findings suggest that these negligible changes result not only from annuals' pronounced seed dormancy but also from their ability to maintain high fecundity under drought and grazing by different trait syndromes. Winter annuals' high drought and grazing resistance has likely evolved due to the high temporal and spatial variability of rainfall and grazing in the southwestern Levant for millennia (Noy-Meir & Seligman, 1979; Tielbörger et al., 2014).

Under global change, the annual plant communities in the southwestern Levant are expected to be permanently exposed to above-average drought and grazing intensity compared to current conditions (Smiatek et al., 2011; Thornton, 2010). Already in the last decades (1975-2010), mean annual rainfall slightly decreased in the southwestern Levant (Ziv et al., 2014). These environmental changes will likely affect annual plant community composition despite species' high resistance to drought and grazing. Indeed, annual plant community composition has been observed to slightly change under extreme drought or grazing or intensified drought in the long-term (Alon & Sternberg, 2019; Bilton et al., 2016; Carmona et al., 2012). The interspecific differences in traits and fecundity responses to drought and grazing in the annuals, presented in this thesis, also indicate that global change will differently affect the species in their performance.

Increasing drought and grazing intensity under global change in the southwestern Levant should favour winter annuals with a pronounced grazing and small drought escape strategy. These species successfully cope with both drought and grazing and can buffer reproductive failure by their pronounced seed dormancy (see 4.2.3). An increasing dominance of annuals with a pronounced escape strategy should influence ecosystem functioning and services. The escape strategy encompasses low total biomass, low root allocation, and a short life cycle (early onset of flowering). These trait attributes should reduce the carrying capacity of annual plant communities for livestock production due to a lower forage quantity and a shorter period in which alive biomass is available. Furthermore, they may affect water and climate regulation due to a lower infiltration rate of water in the soil, higher albedo, and higher surface temperatures (Huang et al., 2017; Safriel & Adeel, 2005). Accordingly, a high dominance of annuals with an escape strategy may increase the likelihood that water evaporates without being used by vegetation, exacerbating the already existing water limitation. An increasing dominance of winter annuals with an escape strategy will thus likely reduce the multifunctionality of drylands in the southwestern Levant.

Under a hypothetical global change scenario that only comprises rainfall decreases but no changes in grazing intensity, annual plant community composition should change less strongly. The present findings on species' fecundity and survival under drought and species' distribution along the rainfall gradient indicate that annuals with different trait syndromes successfully cope with drought (see 4.2.2 and 4.2.4). A co-occurrence of annuals with different trait syndromes should more strongly promote the multifunctionality of drylands than a strong favouring of annuals with an escape strategy, which is expected under the concomitant increasing intensity of drought and grazing (see above). High grazing intensity thus likely exacerbates the (slight) compositional changes in winter annual plant communities under lower water availability. This assessment of grazing intensity as critical factor that influences annual plant community composition under global change based on the present trait-based findings agrees with community-based observations in winter annual plant communities from the Iberian Peninsula (Carmona et al., 2012) and from our study system (Bilton[15] et al., in prep.). These studies show that grazing more strongly reduce taxonomic and functional diversity under dry rather than wet conditions. Consequently, grazing intensity, i.e. the land use by humans, will strongly affect annual plant community composition and ecosystem functioning under lower water availability in the southwestern Levant.

A sustainable land-use management under global change in the southwestern Levant should avoid high grazing intensities especially under arid conditions and in dry years (see Carmona et al., 2012). Complete grazing abandonment is not recommended since it likely reduces species and functional diversity by woody encroachment and a suppression of winter annuals (Montalvo et al., 1993; Peco et al., 2006). Adapting grazing intensity to the average and annual climatic conditions of a region is characteristic for the traditional land use in drylands. Traditional land use was directed to ensure productivity and sustainability in the worst years rather than maximising production in favourable years (Davies et al., 2015). The variable grazing intensities to avoid overexploitation were ensured by mobile herding with different ungulates and a dairy or fibre-based economy (Davies et al., 2012; Safriel & Adeel, 2005). In recent times, this traditional land use has been replaced by sedentary livestock production with single ungulate species and private tenure to maximize meat production in the short-term (Davies et al., 2012). If we want to maintain biodiversity and multifunctionality of drylands, global change might force us to remember traditional land-use strategies that can be improved by nowadays technologies, such as (remote) pasture and rainfall tracking or selling markets for livestock (Davies et al., 2012; Davies et al., 2015). The consequences of present-day and traditional land-use strategies on community composition and ecosystem functioning in drylands can be simulated with the help of trait-based findings (see 5.1). The present findings can thus contribute to a knowledge-based decision making regarding future land-use management in the southwestern Levant.

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[15] Bilton et al., in prep refers to a manuscript in preparation, analysing whole community composition of the grazing exclosure experiment in Jordan (see 3.6).

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# II Manuscripts

## List of included manuscripts and author contributions

### Manuscript 1

Title: Evaluating drought response strategies in winter annuals: Results from a multi-trait, multi-species experiment

Authors: Susanne Kurze, Bettina M. J. Engelbrecht, Katja Tielbörger, Mark C. Bilton, Leonor Álvarez-Cansino

Status: in preparation for submission to Functional Ecology

Contribution: LA, BE, MB, and KT conceived the general ideas for the study. SK, LA, and BE defined the experimental design and hypotheses. SK coordinated and conducted the plant traits measurements and the drought experiment in the greenhouse with help of several student assistants and bachelor students (see acknowledgements), MB conducted the seed dormancy assessments. SK analysed the data, created figures and tables, and wrote the first draft of the manuscript. The manuscript (including tables and figures) was revised by SK, LA, and BE. SK will be the corresponding author.

### Manuscript 2

Title: Evaluating grazing response strategies in winter annuals: a multi-trait approach

Authors: Susanne Kurze, Mark C. Bilton, Leonor Álvarez-Cansino, Sara Bangerter, Rüdiger Prasse, Katja Tielbörger, Bettina M. J. Engelbrecht

Status: Published in Journal of Ecology, 2021

Contribution: LA, BE, MB, and KT conceived the ideas for the study. SK, LA, and BE defined the experimental design and hypotheses. SK coordinated and conducted the plant traits measurements and the grazing simulation experiment in the greenhouse with help of several student assistants and bachelor students (see acknowledgements), MB conducted the seed dormancy assessments. RP, KT, and SB implemented the grazing exclosure experiment in the field. SK analysed the data, wrote the first draft of the manuscript, and created figures and tables with comments from BE. The manuscript was revised by SK and BE, with input from KT, LA, MB, and RP. SK is the corresponding author.

**Manuscript 3**

Title: Rethinking the plant economics spectrum for annuals - a multi-species study

Authors: Susanne Kurze, Bettina M. J. Engelbrecht, Mark C. Bilton, Katja Tielbörger, Leonor Álvarez-Cansino

Status: Published in Frontiers in Plant Science, 2021

Contribution: SK developed the concept and study design with support from BE and LA. SK coordinated and conducted the traits measurements with the help of several student assistants and a bachelor student (see acknowledgements). SK analysed the data, created figures and tables, and wrote the first draft of the manuscript. The manuscript (including tables and figures) was revised by SK, LA, and BE with input from KT and MB. SK is the corresponding author.

# Manuscript 1:

## Evaluating drought response strategies in winter annuals: Results from a multi-trait, multi-species experiment

**Susanne Kurze[1], Bettina Engelbrecht[1, 2], Mark C. Bilton[3, 4], Katja Tielbörger[3], Leonor Álvarez-Cansino[1, 5]**

[1] University of Bayreuth, Functional and Tropical Plant Ecology, Bayreuth Centre of Ecology and Environmental Research (BayCEER), Universitätsstraße 30, 95447 Bayreuth, Germany

[2] Smithsonian Tropical Research Institute, Apartado 0843-03092, Balboa, Ancón, Panama

[3] Namibia University of Science and Technology (NUST), Department of Agriculture and Natural Resources Sciences, 13 Jackson Kaujeua Street, Private Bag 13388, Windhoek, Namibia

[4] University of Tübingen, Plant Ecology Group, Institute of Evolution and Ecology, Auf der Morgenstelle 5, 72076 Tübingen, Germany

[5] University of Seville, Department of Plant Biology and Ecology, Faculty of Biology, Avda. Reina Mercedes s/n, 41012 Seville, Spain

## Keywords

Annual species, Dehydration avoidance, Dehydration tolerance, Drought escape, Drought resistance, Ecological filtering, Growth rate, Species' distribution, Rainfall gradient

Manuscript is in preparation for submission to Functional Ecology. Susanne Kurze is planned to be the corresponding author.

## Abstract

(1) Winter annual species are a dominant life form in drylands. They escape the seasonal drought by their specific life history associated with early flowering and pronounced seed dormancy (drought escape strategy). Whether they also withstand drought within their growing season by reducing tissue dehydration (dehydration avoidance strategy) or maintaining functioning under drought (dehydration tolerance strategy) remains unclear. Understanding the mechanisms underlying species' fitness responses to drought and ecological filtering along rainfall gradients in winter annuals though is critical for assessing global change consequences in drylands.

(2) We measured 22 traits hypothesized to influence drought responses in 29 winter annual species from Israel under common conditions. We examined the coordinations of the traits into syndromes and linked species' trait syndrome strengths to their fecundity responses to an experimental drought in the growing season, maximum growth rates (in 18 species), and distribution along a rainfall gradient.

(3) Winter annuals' traits were coordinated into syndromes consistent with the expected dehydration avoidance and tolerance strategy and unexpectedly into two escape syndromes associated with either tall or small size. Annuals with a pronounced small escape syndrome exhibited high fecundity losses under drought. Species' strengths of the avoidance, tolerance, and tall escape syndrome as well as species' maximum growth rates were independent from their fecundity responses to drought, i.e. no trade-off between species' growth rates and drought resistance emerged. Species' strengths of the avoidance and tolerance syndrome were weakly related to their distribution along the rainfall gradient, with an interspecific shift from tolerance to avoidance with increasing rainfall. Species' strengths of both escape syndromes were unrelated to their distribution along the rainfall gradient.

(4) Our findings highlight that winter annuals, despite their common life history, exhibit four drought response trait syndromes. They do not only escape drought but also withstand it in the growing season, with several trait combinations conferring them similar fecundity responses to drought or distribution along a rainfall gradient. The similar success of several trait combinations in response to drought should minimize compositional changes in annual plant communities under global change.

## Introduction

Winter annual plants are a dominant life form in drylands with substantial contribution to biomass production and ecosystem services (Friedman, 2020). Under global change, winter annuals will likely be increasingly subjected to drought as rainfall is expected to decrease in amount and to increase in interannual variability in drylands (IPCC, 2014; Maestre et al., 2016). An understanding of the mechanisms underlying species' drought responses in winter annuals is critical for assessing global change consequences in drylands.

Winter annuals grow and reproduce in the favourable rainy (winter) season and escape the unfavourable dry (summer) season as desiccation tolerant seeds (Kooyers, 2015; Levitt, 1980). Despite this life history, winter annuals are exposed to drought as metabolically active plants (Harrison & LaForgia, 2019; Tielbörger et al., 2014) since dry spells within the growing season are common in drylands (Noy-Meir, 1973). Accordingly, annuals should withstand dry spells in the growing season, in addition to evading the summer drought as seeds. Winter annuals have been shown to differ in the length of their vegetative and reproductive phase and in several traits related to plant water relations, such as water use-efficiency, morphological root traits, or turgor loss point (Harrison & LaForgia, 2019; Kraft et al., 2015; Kurze, Bilton et al., 2021; Kurze, Engelbrecht, et al., 2021; Pérez-Ramos et al., 2019). These interspecific trait differences indicate that annuals differ in both their ability to escape drought and to withstand drought within the growing season. Considering winter annuals as one homogenous functional group of species escaping drought, as traditionally assumed (see Levitt, 1980), thus might be too simplistic. Yet, how traits assumed to influence species' drought responses are coordinated in winter annuals and how traits and their coordinations influence species' fitness responses to drought and ecological filtering along moisture gradients remained unsolved.

Traits related to plant drought responses are hypothesized to be coordinated into syndromes, i.e. suites of covarying traits (Levitt, 1980; Reich et al., 2003). The syndromes should influence species' performance responses (i.e. growth, survival, reproduction) and fitness responses (i.e. species-averaged number of viable offspring produced during their life time) to drought (Reich et al., 2003; Shipley et al., 2016; Violle et al., 2007). Three syndromes, namely drought escape, dehydration avoidance, and dehydration tolerance, are assumed to constitute successful drought response strategies, i.e. they confer species high drought resistance by minimizing performance and fitness losses in response to periods of low water availability (Gilbert & Medina, 2016; Kooyers, 2015; Levitt, 1980). *Drought escape* reduces the risk to be affected by drought before seed production through early reproduction and high growth rates (Fang & Xiong, 2015; Kooyers, 2015). High reproductive allocation and pronounced between-year seed dormancy, spreading germination across years, should buffer reproductive failure in this strategy (Grime, 1977; Tielbörger et al., 2012). *Dehydration avoidance* allows plants to maintain high water status even under drought by traits optimizing water uptake and water storage capacity, and minimizing transpirational water loss (Fang & Xiong, 2015; Kooyers, 2015). *Dehydration tolerance*, in contrast, enables plants to continue physiological processes under drought by maintaining cell turgor and water transport at low tissue water potentials (Comita & Engelbrecht, 2014; Fang & Xiong, 2015). Both strategies, dehydration avoidance and tolerance, allow plants to withstand drought within the growing season (Fang & Xiong, 2015). The three strategies are not mutually exclusive, but functional linkages, trade-offs, or coordinated selection pressures preclude certain trait combinations (Levitt, 1980).

The assumed relations between traits or their syndromes and species' performance or fitness responses to drought have been rarely explicitly tested across species, although these relations are a fundamental assumption of trait-based ecology and crucial for projecting drought effects (Laughlin et al., 2020; Shipley et al., 2016). Some studies in perennials (herbaceous and woody species) related single drought response-related traits to species' survival or growth under drought. They showed that perennials with pronounced avoidance or tolerance traits maintain higher survival or growth under drought (e.g. Álvarez-Cansino et al., 2022; McGregor et al., 2021; Powers et al., 2020; Sun et al., 2020). Direct relations between traits and fitness responses remain unaddressed, likely since fitness responses are hard to assess in perennials. In annuals, species' fitness responses can be more directly and easily assessed by their life time fecundity (Laughlin et al., 2020). Species' life time fecundity, i.e. the product of seed number and seed mass, considers the number of possible offspring (seed number) and the probability of plant survival that is related to seed mass (Metz et al., 2010). Nevertheless, only a few studies addressed interspecific relations between traits and fitness or performance responses to drought in annuals (Harrison & LaForgia, 2019; Huxman et al., 2013 and references therein). These studies show that annuals with pronounced avoidance traits (higher water-use efficiency, deeper roots) maintain higher survival or fitness under drought. However, in both annuals and perennials most of the observed relations between traits and species' performance or fitness responses were weak, limiting their suitability for projecting drought effects (e.g. Harrison & LaForgia, 2019; Martínez-Vilalta et al., 2010; Sun et al., 2020). The weak relations may emerge since the studies considered only a few traits (usually < 5) and/or the relations were investigated under natural conditions, i.e. the effect of drought on species' performance or fitness responses was not separated from co-occurring factors (e.g. nutrient, light availability, but see Álvarez-Cansino et al., 2022; Harrison & LaForgia, 2019; Sun et al., 2020). Here, we considered a large trait set and related trait syndromes to species' fitness responses to an experimental drought under common conditions in winter annuals to establish a solid basis for projecting drought effects on their communities.

Species' drought resistance should also influence their maximum growth rate and distribution along moisture gradients (Reich, 2014). High stress resistance, including drought resistance, is assumed to be traded-off against maximum growth rates (Reich, 2014). The trade-off emerges since dehydration avoidance and tolerance traits that confers species high resistance to drought in the growing season (e.g. high tissue density, high root allocation) are associated with slow growth rates (Reich, 2014). A growth-drought resistance trade-off should have pervasive consequences for species' ecological filtering along moisture gradients: Species with high drought resistance but slow growth are favoured under drier conditions, whereas species with low drought resistance and high growth rates are favoured under moister conditions. The higher growth rates should enable the species to withstand the more intense competition in moister conditions (Reich, 2014). A growth-drought resistance trade-off and its expected consequences for species' distributions across moisture gradients has been shown in perennial species from several, but not from all, ecosystems (Griffin-Nolan et al., 2019; Fernandez & Reynolds, 2000; Jung et al., 2020; Lopez-Iglesias et al., 2014; Reich, 2014).

The hypothesized growth-drought resistance trade-off should also apply to winter annuals but needs to be explicitly studied in this species group. High growth rates allowing for drought escape should be traded-off (incompatible) with dehydration avoidance or tolerance that increase species' resistance to drought within the growing. Accordingly, annuals with a pronounced escape syndrome should experience high fitness losses when they are affected by dry spells within the growing season. However, the consequences of a growth-drought resistance trade-off for species filtering along rainfall gradients should differ between winter annuals and perennials. Winter annuals with a pronounced escape syndrome (including high growth rates) should be favoured under arid conditions with low, unpredictable rainfall in a short rainfall season since the escape traits enable them to finish reproduction within the short rainfall season and to buffer rainfall unpredictability (Kooyers, 2015; Manzaneda et al., 2015; Tielbörger et al., 2012). Towards moister conditions, rainfall is higher and more predictable, but the longer growing season is still interrupted by occasional dry spells (Noy-Meir, 1973). Under these conditions, annuals with an avoidance or tolerance syndrome (including slow growth rates) should be favoured due to their ability to withstand the occasional dry spells and to utilize the whole length of the growing season. These annuals can thus reach larger sizes, enabling them to successfully cope with higher competition intensity in moister conditions (see Schiffers & Tielbörger, 2006). Contrary to the hypothesis of the growth-drought resistance trade-off, we thus expected an interspecific shift from fast-growing species with an escape syndrome to slow-growing species with an avoidance and/or tolerance syndrome with increasing rainfall in winter annuals.

Here, we investigated traits, their syndromes, and their relations to species' fitness responses (assessed as life time fecundity responses) to drought and ecological filtering along rainfall gradients in 29 winter annuals from semi-arid rangelands in Israel. We comparatively measured 22 traits hypothesized to influence plant drought responses under common conditions and linked species' trait syndrome strengths to their fitness responses to an experimental drought in the growing season, to their maximum growth rates (in a subset of 18 species), and to their distribution along a steep rainfall gradient. We tested the following hypotheses:

(1) Traits relevant for drought responses are coordinated along three major axes, reflecting the syndromes of drought escape, dehydration avoidance, and tolerance.

Species' trait syndrome strengths, i.e. their positions along the axes, influence their fecundity responses to drought in the growing season, their maximum growth rates, and their distribution along rainfall gradients. Specifically:

(2) Species' fecundity losses in response to drought and their maximum growth rates decrease with a pronounced avoidance and/or tolerance syndrome but increase with a pronounced escape syndrome. Consequently, maximum growth rates are traded-off with fecundity responses (growth-drought resistance trade-off).

(3) Along rainfall gradients, winter annuals with a pronounced escape syndrome are associated with arid conditions, whereas species with a pronounced avoidance or tolerance syndrome are associated with moister conditions.

## Material and Methods

### Study species and plant material

The study focused on 29 winter annual species from Israel, including 21 forbs (six families, including six legumes) and eight grasses (see Table S1). Species selection considered the following criteria: (1) high abundance in the region, (2) coverage of different distribution ranges along a rainfall gradient 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 responses to drought (as proxy for fitness responses) and maximum growth rates were assessed in a subset of 18 species with sufficient seeds (Table S1).

Seeds were collected in Israel in two sites, 40 km apart from each other (Lahav 300 mm/year mean annual rainfall, and Matta 540 mm/year, for details see Tielbörger et al., 2014). For trait measurements (except seed dormancy) and the drought experiment, we grew plants from F1 seeds under common favourable conditions in a greenhouse (see details in Method S1). This approach enabled us to comparatively assess trait differences and fecundity responses across species, and to minimize potential bias introduced by uncontrolled intraspecific variation through maternal effects, phenotypic plasticity, or ecotypic differentiation.

## Trait measurements

We measured 22 traits selected based on their known or hypothesized association with the escape, tolerance, and avoidance strategy on 5-16 replicates per species (see details in Table 1, Table S2, and Table S3). We followed standardised protocols for trait measurements, if possible (e.g. Pérez-Harguindeguy et al., 2013; see details in Method S2).

The performance parameter maximum absolute growth rate was measured as biomass increase per day from germination until 16 weeks after sowing on 6-9 replicates per species (see details in Method S2).

**Table 1.** Traits hypothesized to influence drought responses considered in this study with their abbreviation (Abb.) and their expected association with the drought escape (orange), dehydration avoidance (green), and tolerance (blue) strategy. + or - indicate whether a high or low trait value is expected to be associated with higher drought resistance in the respective strategy. Detailed information on the traits and their measurements are given in Table S2 and Method S2.

| Trait | Abb. | Escape | Avoidance | Tolerance |
|---|---|---|---|---|
| Seed dormancy | Sdormancy | + | | |
| Reproductive mass fraction | Rep. MF | + | | |
| Photosynthetic rate | Photo | + | | |
| Leaf mass fraction | Leaf MF | + | - | |
| Specific leaf area | SLA | + | - | |
| Age at flowering onset | Flower Onset | - | | |
| Leaf number at flowering onset | Leaf Number | - | | |
| Height at seed set | Height | - | | |
| Total biomass | Tot. Biomass | - | | |
| Root mass fraction | Root MF | - | + | |
| Instantaneous water-use efficiency | WUEinst | | + | |
| Leaf carbon isotope ratio | WUEint | | + | |
| Specific root length | SRL | | + | |
| Leaf thickness | Lthick | | + | |
| Relative leaf water content | LWC | | + | |
| Relative root water content | RWC | | + | |
| Turgor loss point | TLP | | + | - |
| Cuticular conductance | gmin | | - | |
| Leaf tissue density | LTD | | | + |
| Root tissue density | RTD | | | + |
| Leaf area | LA | | | - |
| Leaf xylem vessel diameter | XVdiam | | | - |

## Drought experiment

To assess and compare species' fecundity responses (as proxy for fitness responses) to a period of low water availability in the growing season, we conducted a drought experiment. Plants were exposed to a drought treatment with reduced watering for 46 days (approximately 6.5 weeks) or were maintained under irrigated control conditions. Each treatment encompassed 8-10 individuals per species. 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). After the drought, plants were re-watered and received the same amount of water as control plants for approximately 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 all species dried out at a similar rate and were then maintained at non-lethal soil water contents (3-4 % compared to 10 % in control group, see details in Method S3 and Figure S1). Our approach avoided that species with higher transpiration rates dried out faster and assured the comparability of fecundity responses to drought across species (Gilbert & Medina, 2016; Sack, 2004).

To assess species' fecundity responses to drought, we measured the total seed weight of each plant (TSW, TSW = seed number * seed mass, see Method S2) at the end of their life cycle. Fecundity response (FR) of each species was calculated as response ratio (see Hedges et al., 1999) of mean total seed weight between drought-stressed and control plants: $FR = \log(\text{meanTSW}_{\text{drought}}/\text{meanTSW}_{\text{control}})$. A more negative value indicates a stronger negative response of species' fecundity to drought and thus lower drought resistance.

## Species' distribution along rainfall gradients in Israel

Israel comprises steep rainfall gradients with a 40-fold increase from low, unpredictable rainfall in a short rainfall season in arid areas in the south and near the Dead Sea (east) (up to less than 20 mm/year ± 55 %, mean ± CV, December/January-March) to higher, more predictable rainfall in a longer rainfall season in moister areas in the north and west (up to 900 mm/year ± 18 %, rainfall season October/November-April/May; Ziv et al., 2014). Dry spells of at least 4-6 days within the rainfall season are common in the whole region (Ziv et al., 2014).

We characterized species' distribution along the rainfall gradients 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 (presence/absence data) of a species based on independent biological records in Israel (BioGIS, 2018).

## Statistical analyses

We identified the main axes of trait variation, i.e. the trait syndromes and evaluated if species' scores along these axes, representing species' strengths 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 maximum 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. Pairwise trait correlations were calculated with Spearman rank correlation coefficients based on species' average trait values.

We assessed the trait coordinations in all species with a principal component analysis (PCA) based on species' average centered and standardized trait values. 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. A PCA with the subset of 18 species with measurements of growth rates and fecundity responses gave similar species' scores along the principal components (PC) as the PCA with the full set of 29 species (Pearson correlation coefficients for PC 1-PC 3 $R \geq |0.87|$). We therefore consistently used species' scores of the PCA with the full species set for all following analyses.

The effect of the experimental drought on fecundity as well as on the proportion of reproducing individuals, seed number, and seed mass was tested with F-tests on LMs (fecundity, seed number, seed mass) or $Chi^2$-tests on generalized linear models (GLM) with binomial error distribution (number of reproducing individuals). 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 assessed 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. their strengths of the trait syndromes) with F-tests on separate LMs. Each LM comprised one response variable (i.e. fecundity response, growth rate, or mean annual rainfall niche) and species' scores along the first three PCs (each explaining > 18 % of variation) as explanatory variables. Interactions between species' scores along the PCs were not significant and excluded from the final models to avoid overfitting. The LMs described above for fecundity responses and growth rates were also calculated with absolute values of the species' scores along PC 1. These LMs tested whether both (and not only one) trait syndromes, associated with the opposite sides of PC 1, were related to species' fecundity responses or maximum growth rates. The results (not shown) were qualitatively similar to the main findings based on the original species' scores. To directly test for a growth-drought resistance trade-off, we assessed the relation between maximum growth rates and fecundity responses with a F-test on a LM. We also tested for relations between mean annual rainfall niches, growth rates, and fecundity responses with F-tests on LMs.

Pairwise correlations between single traits, species' fecundity responses, maximum growth rates, or mean annual rainfall niches were assessed with Spearman rank correlation coefficients.

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

## Results

### Interspecific variation of escape, avoidance and tolerance traits, and their coordinations

All 22 traits hypothesized to influence drought responses and maximum growth rate differed across the winter annuals (all traits $p < 0.001$, up to 52-fold variation, Table S3). Pairwise trait correlations were mostly weak (Table S4).

Dehydration avoidance and tolerance traits were coordinated along PC 1 and associated with the opposite sides of this axis. Winter annuals thus exhibited syndromes of dehydration avoidance and tolerance, which were traded-off against each other (Figure 1a, Figure 2a). Specifically, species with high scores on PC 1 exhibited trait attributes of dehydration avoidance, i.e. thick leaves, high tissue water contents, high turgor loss point, high root mass fraction, and high water-use efficiency, but also large size (height and biomass, Figure 1a, Figure 2a). Species with low (negative) scores on PC 1 exhibited high specific root length and several trait attributes characteristic for dehydration tolerance, such as low turgor loss point, small leaf area, small xylem vessel diameter, and high root tissue density (Figure 1b, Figure 2a). In the following, we refer to PC 1 as avoidance-tolerance axis.

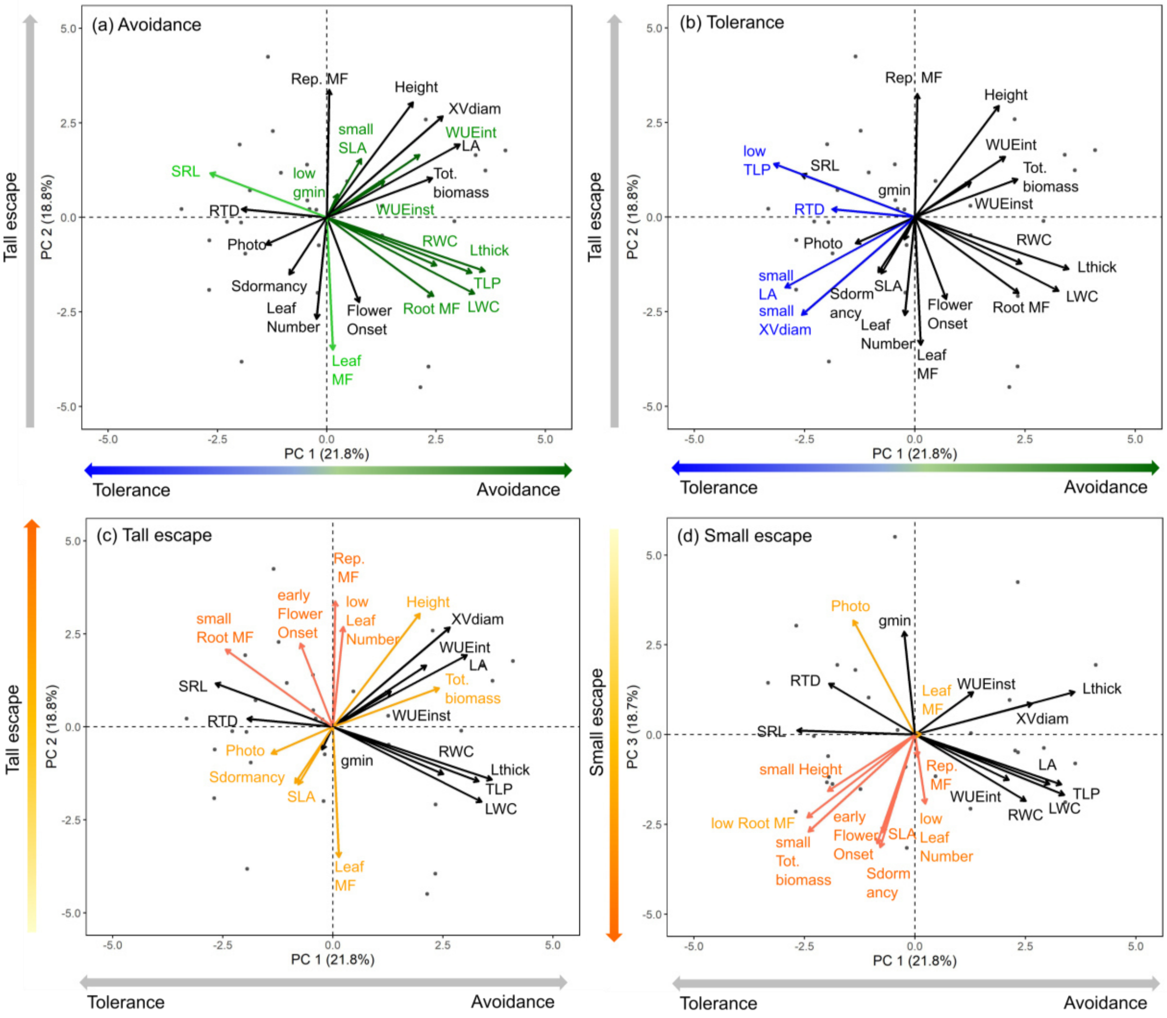

**Figure 1.** Coordination of 21 traits hypothesized to influence drought responses (see Table 1) in 29 winter annuals along the first three axes of a principal component analysis. Panels highlight the coordination of traits hypothesized to be associated with different drought response syndromes: (a, green) dehydration avoidance, (b, blue) dehydration tolerance, and (c, d, orange) drought escape. Trait arrows consistently point to the direction of expected higher drought resistance in the respective syndrome. In a, c, and d traits associated contrary to our expectation are depicted in a lighter shade. Traits not expected to be associated with the respective syndrome are shown in black. Table 1 gives trait abbreviations, Figure 2 trait loadings on the PCs, Figure S2 species identities, and Figure S3 trait coordination along PC 2 and PC 3.

Escape traits were also coordinated, but unexpectedly associated with two PCs (PC 2 and PC 3; Figure 1c-d, Figure 2b-c). The winter annuals thus exhibited two independent escape syndromes. Early flowering onset, low leaf number at flowering, and low root mass fraction characterized species with a pronounced escape syndrome along both axes (i.e. species with high scores on PC 2 and low scores on PC 3, Figure 1c-d, Figure 2b-c). Species with high scores along PC 2 additionally exhibited high reproductive mass fraction, unexpectedly combined with several trait attributes opposite to those expected to confer drought escape (e.g. low leaf mass fraction, large height, low seed dormancy) as well as trait attributes not considered to be relevant for drought escape (e.g. large xylem vessels, large leaves; Figure 1c, Figure 2b). Species with low scores on PC 3 showed several additional trait attributes considered characteristic for drought escape (*sensu* Kooyers, 2015), such as high seed dormancy, high specific leaf area, small size, but unexpectedly also low photosynthetic rate (Figure 1d, Figure 2c). As the two escape syndromes were either associated with being tall (large height) or being small (low biomass and height), we refer to PC 2 and PC 3 as the tall escape and the small escape axis/syndrome, respectively.

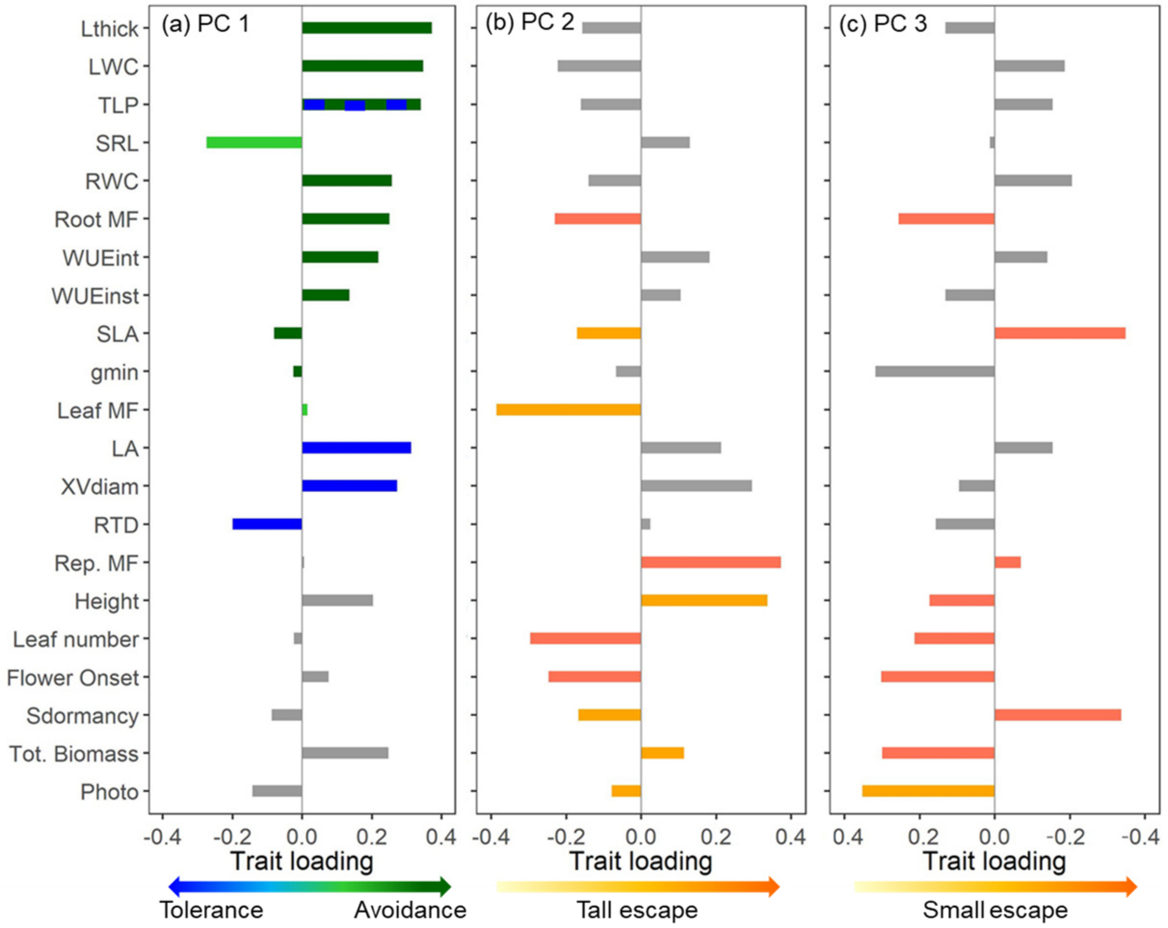

**Figure 2.** Loadings of 21 traits hypothesized to influence drought responses on the first three axes of a principal component analysis (compare Figure 1). PC 1 was associated with dehydration avoidance (green) and tolerance (blue) traits, and PC 2 and PC 3 with escape traits (orange). Traits associated contrary to our expectation are depicted in a lighter shade. Traits not expected to be associated with the respective syndrome are shown in grey. Traits are ordered based on their association with the syndromes and loadings on PC 1. In (c) the x-axis with the trait loadings is flipped (range from 0.4 to -0.4) for easier readability.

### Drought effects on species' fecundity

The experimental drought in the growing season reduced species' fecundity with the response size varying across species (Figure S4, LM statistics: species $F_{17,320} = 98.22$, $p < 0.001$; treatment $F_{1,320} = 8.84$, $p = 0.003$; interaction $F_{17,320} = 1.62$, $p = 0.057$, $R^2 = 0.82$). Species' responses ranged from fecundity reductions by 50 % in drought-stressed compared to control plants to no significant response (almost equal fecundity of drought-stressed and control plants). Fecundity declines resulted from decreases in seed number and/or seed mass but not from changes in the proportion of reproductive individuals (see statistical details in Figure S4).

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

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

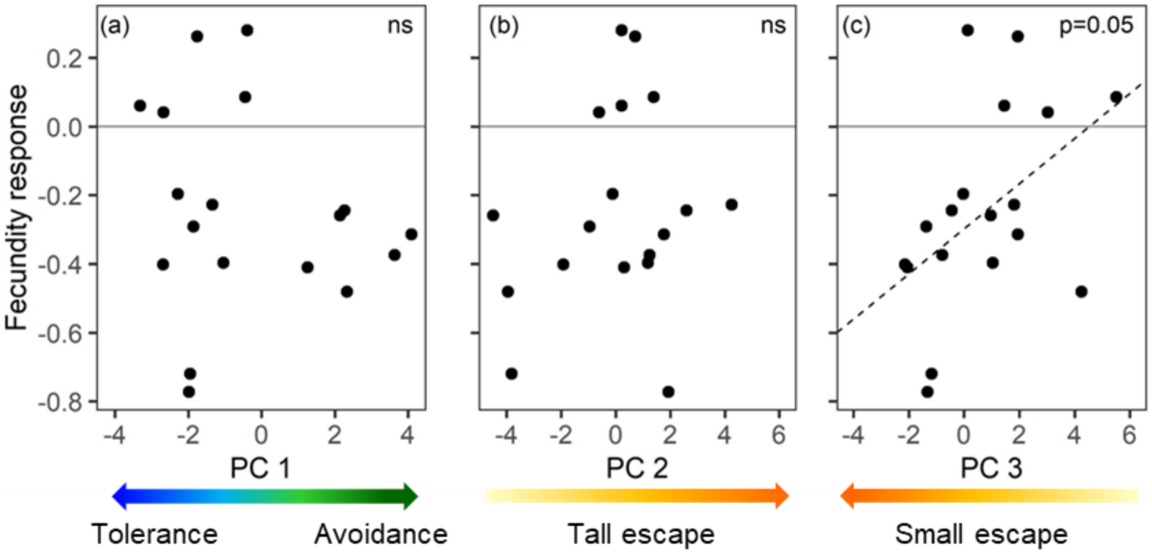

**Figure 3.** Relations between species' fecundity responses to experimental drought in the growing season and their scores along the (a) avoidance-tolerance axis (PC 1), (b) tall escape axis (PC 2), and (c) small escape axis (PC 3) in 18 winter annuals. Significance (ns not significant, dashed line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

Species' scores along both the avoidance-tolerance axis (PC 1) and the tall escape axis (PC 2) were related to their maximum growth rates. Species with a pronounced avoidance or tall escape syndrome showed higher growth rates (Figure 4a-b, Table S5). Species' scores along the small escape axis (PC 3) were independent from growth rates (Figure 4c, Table S5). Species' maximum growth rates were also unrelated to their fecundity responses to drought, i.e. no trade-off emerged (Figure 4d, Table S5). Consistently, growth rate and fecundity response were correlated with different single traits (Table S4).

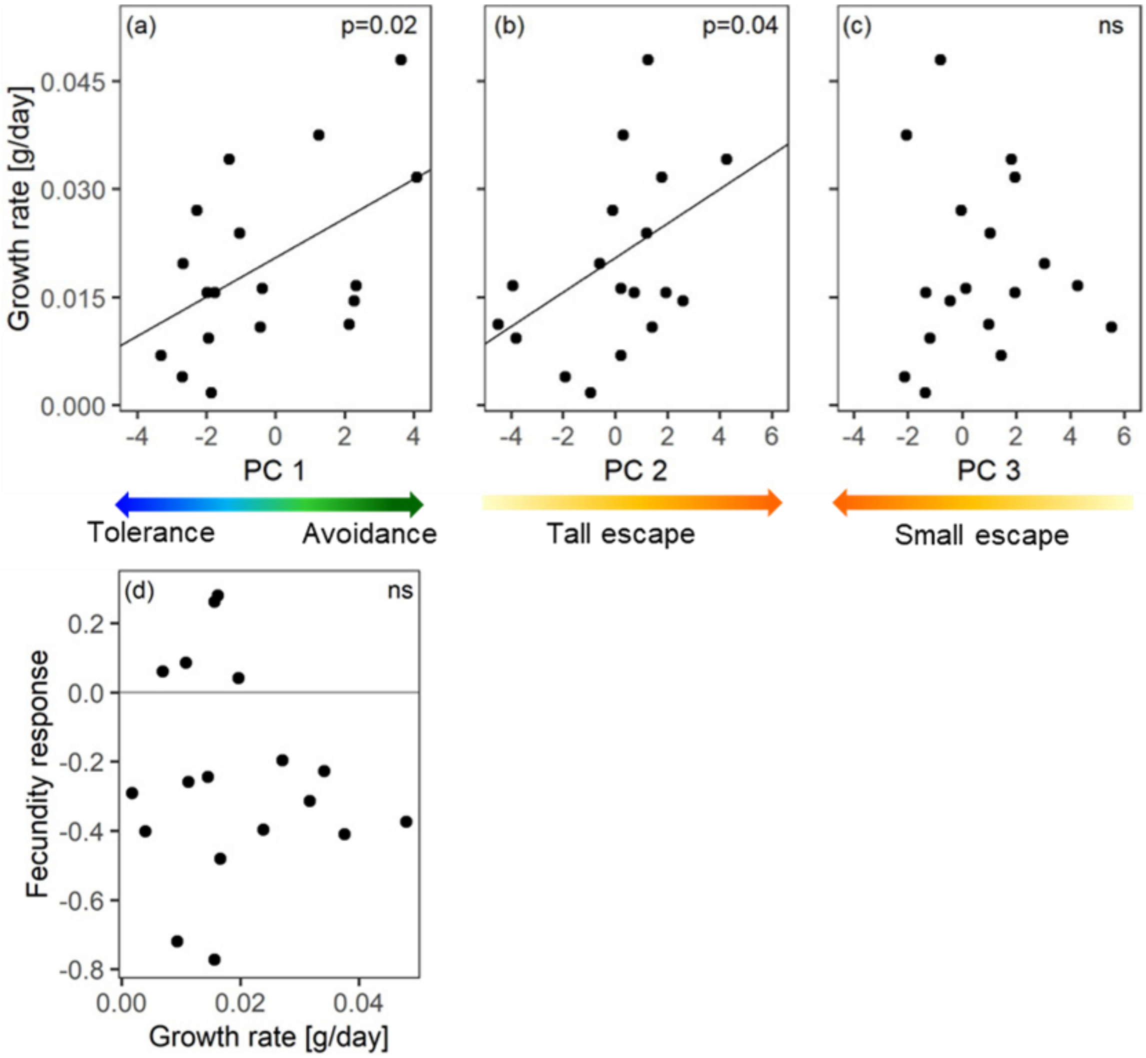

**Figure 4.** Relations between species' maximum growth rates and their scores along the (a) avoidance-tolerance axis (PC 1), (b) tall escape axis (PC 2), and (c) small escape axis (PC 3); and (d) relation between species' fecundity response (proxy for drought resistance) and maximum growth rate in 18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

Species' scores along the avoidance-tolerance axis (PC 1) were marginally significantly associated with their mean annual rainfall niches (p = 0.06). This association indicates an interspecific shift from dehydration tolerance to avoidance with increasing rainfall (Figure 5a, Table S5). Species' scores along both escape axes (PC 2, PC 3), fecundity responses to drought, maximum growth rates, and single traits were independent from mean annual rainfall niches (Figure 5b-c, Table S4, Table S5).

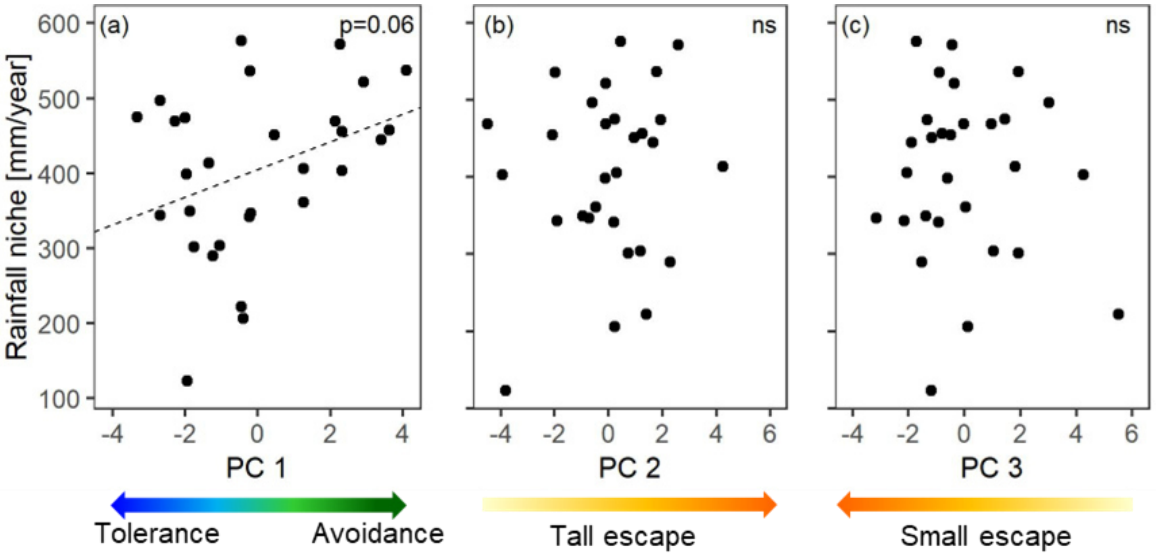

**Figure 5.** Relations between species' mean annual rainfall niches, i.e. species' distribution along the rainfall gradient, and their scores along the (a) avoidance-tolerance axis (PC 1), (b) tall escape axis (PC 2), and (c) small escape axis (PC 3) in 29 winter annuals. Significance is given (ns not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

## Discussion

Drought response-related traits in the winter annuals were coordinated into syndromes consistent with the expected strategies of dehydration avoidance and tolerance and unexpectedly into two escape syndromes. Only species' positions along one trait axes were related to their fecundity response to drought (small escape axis) or their distribution along the rainfall gradient (avoidance-tolerance axis). Species' growth rates were independent from their fecundity responses, i.e. the expected trade-off did not emerge.

### Syndromes of avoidance, tolerance, and escape traits in winter annuals

The dehydration avoidance and tolerance syndrome in the studied winter annuals were consistent with the appropriate strategies in perennial herbaceous and woody species (Comita & Engelbrecht, 2014; Powers et al., 2020; Sun et al., 2020). Also, the attribute range of several avoidance and tolerance traits (e.g. turgor loss point, organ water contents) in the winter annuals was similar to the range observed in perennial herbaceous species from dryland or temperate ecosystems (Blumenthal et al., 2020; Griffin-Nolan et al., 2019; Májeková et al., 2019; Sun et al., 2019).

The coordination of escape traits into two independent syndromes in the winter annuals has two major implications. It (1) indicates that annuals differ in their ability to escape drought despite their common life history and (2) that annuals with a pronounced escape syndrome can differ in their trait attributes.

Both escape axes were independent from the dehydration avoidance-tolerance axis, i.e. the escape syndromes were not traded-off against dehydration avoidance and tolerance (see Huxman et al., 2013). Winter annuals thus exhibited a continuum of trait combinations, ranging from less to more pronounced escape (tall or small) combined with an avoidance *or* tolerance syndrome.

### Relations between species' trait syndrome strengths, their fecundity responses to drought, and maximum growth rates

The trait differences between both escape syndromes had pervasive consequences for species' fecundity responses to our experimental drought in the growing season. Annuals with a pronounced small escape but not tall escape syndrome showed high fecundity losses under drought. This finding of the small escape syndrome as fitness related strategy across annuals agrees with our hypothesis that species with a drought escape strategy (*sensu* Kooyers, 2015) exhibit high fitness losses under drought in the growing season. The high fecundity losses did not result from a trade-off of drought escape against dehydration avoidance or tolerance (see above). Instead, the small escape syndrome comprised traits indicating a low capacity of resource storage (carbon and nutrients) and acquisition (e.g. low root mass fraction and low photosynthetic rate; see Craine et al., 2013; Zwicke et al., 2015). These traits likely limit species' ability to reproduce during or after the drought. The tall escape syndrome, in contrast, was less strongly associated with traits of resource storage or acquisition.

Species' strengths of the dehydration avoidance and tolerance syndrome in the studied annuals were unexpectedly independent from their fecundity responses to drought. This finding differs from our hypothesis and previous studies in perennials and annuals showing that pronounced avoidance or tolerance traits are associated with higher survival or fecundity under drought (e.g. Álvarez-Cansino et al., 2022; Powers et al., 2020; Sun et al., 2020). The discrepancy among the present and previous studies may emerge, since we assessed species' fecundity responses to a non-lethal drought whereas previous studies focused on species' responses to lethal drought. Possibly, interspecific differences in avoidance and tolerance traits are only related to species' performance or fitness responses to lethal but not non-lethal drought. Alternatively, the mechanisms underlying species' performance or fitness responses to drought differ between annuals and perennials. Our findings indicate that different trait attribute combinations along the dehydration avoidance-tolerance axis rather than one syndrome, as observed in perennials (see above), confer species similar fecundity responses to drought. This similar success of several trait combinations in winter annuals is in line with theoretical findings (Marks & Lechowicz, 2006). It is likely only identifiable with large trait sets, and therefore was not observed by previous studies on annuals considering a few traits (Harrison & LaForgia, 2019; Huxman et al., 2013). The similar drought resistance of annuals with different trait combinations, observed in our experiment, also fits to the negligible compositional changes of their communities under intensified drought in field experiments in our study system (Tielbörger et al., 2014).

Contrary to the expected growth-drought resistance trade-off (Reich, 2014), species' maximum growth rates were independent from their drought resistance (i.e. species' fecundity responses to drought) in the studied annuals. This independence relies on the different relations of growth rates and fecundity responses to single traits and species' trait syndrome strengths. Growth rates were associated with species' strengths of the avoidance, tolerance, and tall escape syndrome, i.e. the syndromes that were independent from species' fecundity responses. An independence between growth rate and drought resistance (based on survival) has been also shown in a few studies on perennials (Fernández & Reynolds, 2000; Jung et al., 2020; Russo et al., 2021). Accordingly, the widely assumed growth-drought resistance trade-off should be re-considered for assessing drought effects on species' performance both within and across life-history strategies.

### Relations between species' trait syndrome strengths and their distribution along the rainfall gradient

Annuals' distributions along the rainfall gradient in our study system were weakly, if at all, related to their strengths of the drought response trait syndromes. The weak relations may result from our focus on species' large-scale rainfall niches and interspecific trait differences. This approach does not account for local soil moisture differences or intraspecific variation (i.e. local adaptation), which can both influence species' ecological filtering (Bruelheide et al., 2018; Siefert et al., 2015). However, both factors are particularly relevant at smaller spatial scales (Bruelheide et al., 2018; Siefert et al., 2015). At large spatial scales and across steep gradients, as investigated here, species' ecological filtering based on occurrence data (presence/absence data) and without considering intraspecific variation has been documented in this and other ecosystems (Griffin-Nolan et al., 2019; Kurze, Engelbrecht, et al., 2021; Thuiller et al., 2004). Any potentially overseen strong large-scale shift of drought response syndromes in annuals is thus unlikely.

Species' strengths of the dehydration avoidance and tolerance syndrome in the studied annuals were weakly related to their distribution along the rainfall gradient with an interspecific shift from tolerance to avoidance with increasing rainfall. This finding disagrees with our hypothesis on an interspecific shift from escape in arid conditions (allowing to evade seasonal drought) to dehydration avoidance and tolerance (allowing to withstand higher competition intensity) in moisture conditions. However, only the avoidance syndrome was associated with traits assumed to confer high competitive effect, such as large size (height and biomass) and high maximum growth rates (Liancourt et al., 2009). The favouring of annuals with a pronounced tolerance syndrome under drier conditions agrees with findings in perennials from different ecosystems (Bartlett et al., 2012; Griffin-Nolan et al., 2019). Winter annuals may thus not only escape but also withstand drought in arid conditions, as known from perennials.

Species' strengths of both escape syndromes were independent from their distribution along the rainfall gradient. This independence likely emerged since early reproduction, a characteristic escape trait, allows the annuals not only to evade drought in arid conditions (Kooyers, 2015) but also competition by larger, late flowering species in moister conditions (Verdú & Traveset, 2005). Similarly, pronounced seed dormancy, associated with the small escape syndrome, can buffer reproductive failure caused by drought or competition (Venable & Brown, 1988). The high inter-annual rainfall variability in our study system should additionally facilitates the co-occurrence of annuals with different trait syndromes by favouring each species or syndrome in some years (see Chesson et al., 2004).

### Conclusions

Winter annuals exhibit, despite their common life history, syndromes of dehydration avoidance and tolerance, in addition to two escape syndromes. Our findings indicate that they do not only escape, but also withstand drought in the growing season with several trait attribute combinations conferring them similar fecundity responses to drought or distribution along rainfall gradients.

The similar viability of several trait attribute combinations may have evolved due to the high inter-annual rainfall variability and long history of extreme dry spells in our study system (see Tielbörger et al., 2014). Accordingly, annual plant community composition may weakly change under increasing drought under global change.

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## Author contributions[1]

LA, BE, SK, KT, and MB conceived the ideas and designed the study. SK coordinated plant trait measurements and conducted the drought experiment, MB coordinated the assessment of seed dormancy. SK analysed the data and wrote the manuscript with contributions by LA and BE. All authors commented on the manuscript and gave final approval for publication.

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[1] This is the planned version of the author contribution statement. For the current status please see the 'List of included manuscripts and author contributions' on page 71.

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## Supporting Information

**Table S1.** List of the 29 studied winter annuals from Israel with their abbreviation, family, and mean annual rainfall niche.

**Table S2.** Traits hypothesized to influence drought responses considered in this study and the mechanisms for their expected association with the drought escape, dehydration avoidance, and tolerance strategy.

**Method S1.** Plant cultivation in the greenhouse.

**Method S2.** Trait measurements.

**Method S3.** Drought experiment.

**Figure S1.** Soil water content during the experimental drought.

**Table S3.** Summary statistics for the 22 traits hypothesized to influence drought responses and maximum growth rate in 29 winter annuals.

**Figure S2.** Coordination of 21 traits hypothesized to influence drought responses (see Table 1) in winter annuals along PC 2 and PC 3 of a principal component analysis.

**Figure S3.** Species' position of 29 winter annuals along the first three axes of a principal component analysis and coordination of 21 traits hypothesized to influence drought responses.

**Table S4.** Correlation matrix based on Spearman rank correlation coefficient including the 22 traits hypothesized to influence drought responses, species' fecundity responses to drought, maximum growth rates, and mean annual rainfall niches (species' distribution along the rainfall gradient).

**Figure S4.** Species' fecundity response to drought in 18 winter annuals.

**Table S5.** Results of linear models testing the relations between species' fecundity responses to drought, maximum growth rates, or mean annual rainfall niches (i.e. species' distribution along the rainfall gradient) and species' scores along the three trait axes (PC 1-PC 3), as well as the relations between fecundity responses, maximum growth rates, and mean annual rainfall niches.

**Figure S5.** Relations between species' mean annual rainfall niches (i.e. species' distributions along the rainfall gradient), (a) species' fecundity responses to drought, and (b) maximum growth rates in 18 winter annuals.

**Table S1.** List of the 29 studied winter annuals from Israel with their abbreviation, family, and mean annual rainfall niche according to BioGIS (2018). Asterisks denote the 18 species with measurements of growth rate and fecundity response to experimental drought.

| Species name | Abbreviation | Family | Mean annual rainfall niche [mm/year] |
|---|---|---|---|
| *Atractylis cancellata* | Atrcan | Asteraceae | 361.2 |
| *Biscutella didyma* | Bisdid | Brassicaceae | 450.9 |
| *Brachypodium hybridum s.l** | Brahyb | Poaceae | 413.5 |
| *Briza maxima** | Brimax | Poaceae | 572.0 |
| *Bromus fasciculatus** | Brofas | Poaceae | 303.7 |
| *Carrichtera annua** | Caran | Brassicaceae | 206.0 |
| *Catapodium rigidum** | Catrig | Poaceae | 475.0 |
| *Clypeola jonthlaspi* | Clyjon | Brassicaceae | 398.8 |
| *Crithopsis delileana** | Cridel | Poaceae | 301.5 |
| *Crupina crupinastrum** | Crucru | Asteraceae | 536.7 |
| *Daucus subsessilis* | Dausub | Apiaceae | 290.1 |
| *Filago desertorum** | Fildes | Asteraceae | 122.8 |
| *Filago palaestina** | Filpal | Asteraceae | 343.5 |
| *Geropogon hybridus* | Gerhyb | Asteraceae | 521.7 |
| *Hedypnois rhagadioloides** | Hedrha | Asteraceae | 405.6 |
| *Helianthemum salicifolium** | Helsal | Cistaceae | 349.4 |
| *Hippocrepis unisiliquosa* | Hipuni | Fabaceae | 341.8 |
| *Hymenocarpos circinnatus* | Hymcir | Fabaceae | 444.7 |
| *Ononis reclinata* | Onorec | Fabaceae | 346.9 |
| *Plantago afra** | Planafr | Plantaginaceae | 403.4 |
| *Plantago cretica** | Plancre | Plantaginaceae | 468.9 |
| *Psilurus incurvus** | Psiinc | Poaceae | 496.8 |
| *Rostraria cristata** | Roscri | Poaceae | 468.9 |
| *Scorpiurus muricatus* | Scomur | Fabaceae | 455.2 |
| *Stipa capensis** | Sticap | Poaceae | 221.7 |
| *Torilis tenella** | Torten | Apiaceae | 474.2 |
| *Trifolium pilulare* | Tripil | Fabaceae | 576.1 |
| *Trifolium stellatum* | Tristel | Fabaceae | 535.9 |
| *Urospermum picroides** | Uropic | Asteraceae | 457.0 |

**Table S2.** Traits hypothesized to influence drought responses considered in this study and the mechanisms for their expected association with the drought escape, dehydration avoidance, and tolerance strategy. + or - indicate whether a high or low trait attribute is expected to be associated with higher drought resistance in the respective strategy. Details on the trait measurements are given in Method S2.

| Trait | Escape | Avoidance | Tolerance | Mechanism |
|---|---|---|---|---|
| Seed dormancy | + | | | Pronounced seed dormancy spreads germination across years. It should buffer reproductive failure in annuals with a pronounced escape syndrome and a low ability to withstand drought within the growing season (Philippi & Seger, 1989; Tielbörger et al., 2012). |
| Reproductive mass fraction | + | | | High reproductive mass fraction contributes to the buffering of reproductive failure (see seed dormancy; Grime, 1977). |
| Photosynthetic rate | + | | | High photosynthetic rate increases growth rate (Poorter & Garnier, 2007), enabling annuals with a pronounced escape syndrome to rapidly complete their life cycle before drought affects them (Grime, 1977; Kooyers, 2015). |
| Specific leaf area | + | - | | High specific leaf area facilitates high photosynthetic rate (see above; Poorter & Garnier, 2007).<br>Low specific leaf area should reduce transpirational water loss by low transpiration area per unit leaf mass (Poorter et al., 2009). |
| Leaf mass fraction | + | - | | High leaf mass fraction increases growth rate (see photosynthetic rate; Lambers & Poorter, 1992).<br>Low leaf mass fraction should enhance high water status under drought due to high water uptake capacity relative to transpiration area (Comas et al., 2013). |

| Trait | Escape | Avoidance | Tolerance | Mechanism |
|---|---|---|---|---|
| Age at flowering onset | - | | | Early onset of reproduction at an early developmental age facilitates rapid completion of the life cycle and minimizes the risk to be affected by drought before reproduction (Kooyers, 2015). |
| Leaf number at flowering onset | - | | | |
| Height at seed set | - | | | Small size facilitates rapid completion of the life cycle (see age at flowering onset; Grime, 1977). |
| Total biomass | - | | | |
| Root mass fraction | - | + | | Low root mass fraction increases growth rate due to lower investment in non-photosynthetic active tissue (see photosynthetic rate; Lambers & Poorter, 1992).<br>High root mass fraction should support high water status under drought since it increases water uptake capacity relative to transpiration area (see leaf mass fraction, Comas et al., 2013). |
| Instantaneous water-use efficiency | | + | | High water use efficiency (i.e. high instantaneous water-use efficiency or high leaf carbon isotope ratio) indicates low transpirational water loss per carbon uptake and should support high water status under drought (Farquhar et al., 1989). |
| Leaf carbon isotope ratio | | + | | |
| Specific root length | | + | | High specific root length should increases water uptake capacity since roots with a high specific root length explore a larger soil volume per unit invested carbon (Comas et al., 2013). |

| Trait | Escape | Avoidance | Tolerance | Mechanism |
|---|---|---|---|---|
| Leaf thickness | | + | | High leaf thickness indicates high leaf water storage capacity (see relative leaf water content; Eggli & Nyffeler, 2009). |
| Relative leaf water content | | + | | High water content indicates water storage, which can delay tissue dehydration and mortality (Blackman et al., 2016; Zwicke et al., 2015). |
| Relative root water content | | + | | |
| Turgor loss point | | + | - | High turgor loss point is associated with early stomatal closure under drought, facilitating dehydration avoidance by reducing transpirational water loss (Bartlett et al., 2012; Bartlett et al., 2016; Sun et al., 2020; see also Method S2).<br>Low turgor loss point allows plants to maintain functioning under drought, enabling drought tolerance (Bartlett et al., 2012). |
| Cuticular conductance | | - | | Low cuticular conductance supports high water status under drought since it reduces water loss through cuticle (Kerstiens, 1996). |
| Leaf tissue density | | | + | High tissue density is assumed to increase tissue stability and to minimize cavitation risk under low tissue water potentials (Markesteijn et al., 2011). |
| Root tissue density | | | + | |
| Leaf area | | | - | Smaller leaves are assumed to be more resistant to embolism due to their smaller xylem vessel diameters and higher vein length per unit area (Sack & Scoffoni, 2013). |
| Leaf xylem vessel diameter | | | - | Small xylem vessel diameter reduces the risk of cavitation under low water potentials (Pockman & Sperry, 2000; Scoffoni et al., 2017). |

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### Method S1. Plant cultivation in the greenhouse

Seeds were collected in two sites (Lahav 300 mm/year mean annual rainfall, and Matta 540 mm/year, for details see Tielbörger et al., 2014) in the field from at least 50 plants per species in an area of 1.0-1.5 km$^2$ in April 2012. Plants from the field-collected seeds were grown under common, favourable conditions in a greenhouse in Tübingen (Germany) to homogenise maternal effects. The F1 seeds were used to grow plants for the trait measurements (except seed dormancy) and the drought experiment after over-summering them for two months in a greenhouse in Bayreuth (Germany) to break dormancy (see Tielbörger et al., 2012).

Plants were germinated and individually grown in cylindrical pots (1 l volume, 36 cm depth, Deepot Cells, Stuewe & Sons, Oregon, US) in a greenhouse in Bayreuth from October to May in 2017/18 (for trait measurements) and 2018/19 (for maximum growth rate and the drought experiment). Soil consisted of a 1:1 mixture of nutrient-poor sand and compost (2017/18) or sandy clay (2018/19) supplemented with 5 g of amorphous silicon (Aerosil 300, Evonik Industries AG, Essen, Germany). Plants were regularly watered and fertilized to preclude resource limitation. Temperature in the greenhouse was set to 20-23°C in winter and 20-26°C in spring. Daytime photosynthetic active radiation ranged between 150-800 µmol photon/(s * m²) and day length was set to the natural variation in Israel for unbiased phenology. Pots were randomly distributed in the greenhouse and rearranged every second week.

Plants were wrapped in light transparent fabric (organza) at the onset of seed production to prevent seed loss. Plants were grown until the end of their life cycle indicated by leaf senescence (approximately 30-36 weeks after sowing).

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### Method S2. Trait measurements

*Leaf area* (LA) was measured with an Area-meter (Model LI 3100, Li-Cor Bioscience, Lincoln, NE, USA). For *specific leaf area* (SLA = LA/DW) we determined the dry weight of the leaf (DW) after 48 h in a drying oven at 70°C. *Leaf thickness* (Lthick) was measured three times in the middle of the leaf blade avoiding the midrib and primary veins with a micrometer (M110-25, Mitutoyo, Neuss, Germany, graduation 0.01 mm) and averaged. *Leaf tissue density* (LTD) was calculated by dividing DW by leaf volume (LA * Lthick). All leaf traits were measured on one, randomly selected, mature, healthy leaf per individual 8 to 12 weeks after sowing.

*Maximum photosynthetic rate at an area basis* (Photo) and stomatal conductance (gs) were measured with an infra-red gas analyser (Li-Cor 6400, Li-Cor, Lincoln, NE, USA) on randomly selected, mature, healthy leaves. Measurements were taken between 8.30 a.m. and 11.00 a.m. at a light intensity of 2000 µmol photons/($m^2$* s) (based on light response curves for a species subset), a block temperature of 25°C, and 400 ppm $CO_2$. Usually one leaf per individual was measured, but in species with very small or thin leaves (e.g. a few grasses, *Filago*, *Helianthemum*) several leaves were jointly arranged in the chamber. If the leaves did not fill the measurement chamber, photosynthetic rate was re-calculated based on leaf area measurements with an Area Meter (see above). *Instantaneous water-use efficiency* (WUEinst) was calculated as ratio between photosynthetic rate and stomatal conductance: WUEinst = Photo/gs (Pérez-Harguindeguy et al., 2013). Measurements were conducted 8-12 weeks after sowing.

The leaves used for photosynthesis measurements (few exceptions in *Psilurus incurvus*, *Rostraria cristata*) were collected after the measurements, oven-dried (68°C, 48 hours), and ground to analyse the carbon isotope ratio with an EA-IRMS coupling (Elemental Analyzer NA 1108, CE Instruments, Milan, Italy; Interface ConFlo III, Finnigan MAT, Bremen, Germany; Isotope ratio mass spectrometer: delta S, Finnigan MAT, Bremen, Germany) as proxy of *integrated water-use efficiency* (WUEint; Farquhar et al., 1989). The carbon isotope ratio is annotated as delta value calculated as: $\delta\ ^{13}C = (Rsample/Rstandard - 1) \times 1000$ (‰), with the ratio (R) of the heavy to the light isotope of the sample and standard (Vienna Pee Dee Belemite, V-PDB), respectively. A higher (less negative) carbon isotope ratio indicates higher integrated water-use efficiency (Farquhar et al., 1989).

*Leaf xylem vessel diameter* (XVdiam) was determined on transverse sections of the midvein in the first third (close to the petiole) of the leaf blade. The transverse sections were manually cut with razor blades. To identify the xylem vessels, the transverse sections were stained with 0.5 % (w/v) phloroglucin and rinsed in 32 % hydrochloric acid following Kadam et al. (2015). The transverse sections were photographed (camera AM7025X, Dinolite, Naarden, Netherlands) under a microscope (Dialux 22 EB, Leitz, Wetzlar, Germany, 20-40 fold magnification). The diameter of the two largest xylem vessels was determined with DinoCapture 2.0 (Dinolite, Naarden, Netherlands) and averaged. The leaves (one randomly selected, mature, healthy leaf per individual) for the measurements were sampled 10-15 weeks after sowing and stored in 20 % ethanol.

*Minimum cuticular conductance* (gmin) was determined on one (or 2-3 in very small leaves), randomly selected, mature, healthy, fully hydrated leaf per individual with drying curves under standardized conditions following Sack & Scoffoni (2001). The leaf was dried for 75 minutes to ensure stomata closure and then weighed every 20 minutes to determine the slope of the water loss (ΔWL) over 200 minutes (10 measurements). Minimum cuticular conductance was calculated as: $gmin = -\Delta WL/mfVPD/18/(LA * 2)$ (Sack & Scoffoni, 2001). Leaf area (LA) was measured with an Area-meter (see above) at the beginning and end of the drying curve and averaged to account for leaf shrinkage. Mole fraction vapour pressure deficit (mfVPD) was calculated according to the Arden Buck equation. Leaves were sampled 8-12 weeks after sowing.

*Turgor loss point* (TLP) was calculated based on osmotic potential at full turgor determined with an osmometer (Vapor Model 5600, Wescor, Logan, Utah, USA) following Bartlett et al. (2012) and Sun et al. (2020). We measured osmotic potential at full turgor (p0) on leaf discs (one disc per individual) from fully hydrated plants 8-12 weeks after sowing. Turgor loss point was calculated as: $TLP = 0.807 * p0 - 0.680$ (Sun et al., 2020). This equation has been determined in species from different life forms and ecosystems (e.g. Bartlett et al., 2012; Májeková et al., 2019; Sun et al., 2020). Turgor loss point was related to water potential at stomata closure under drought in the investigated annuals (Pearson correlation coefficient, $R = 0.58$, $p = 0.005$, Álvarez-Cansino et al., unpublished data), as shown in herbaceous perennial and woody species (Bartlett et al., 2016; Farell et al., 2017). We used turgor loss point as proxy of stomatal sensitivity under drought.

To assess *maximum relative water content of leaves* (LWC) and *roots* (RWC) fully hydrated plants were harvested in the middle of their life-cycle (14-20 weeks after sowing) and separated into leaves, stems, reproductive biomass, and roots. Roots were washed and cleaned from soil particles and carefully dried before weighing. The saturated fresh weight of leaves and roots was immediately determined after the harvest and the dry weight after five days at 50°C. Maximum water content (WC) of both organs was separately calculated as: WC = (saturated fresh weight - dry weight)/saturated fresh weight.

*Specific root length* and *root tissue density* were determined on three subsamples of fine roots (diameter < 2 mm) from the upper, middle, and lower part of the root (except whole roots in *Filago* and *Helianthemum salicifolium*). The subsamples were stained with toulidine blue (0.2 g/L) and scanned (Scanner Epson Perfection V800/V850 photo scanner, 600 dpi). Images were analysed with WinRHIZO © Reg 2017 (Regent Instruments Inc., Quebec, Canada) to determine the volume and length of the scanned root sample. Scanned root samples were oven-dried to calculate specific root length (SRL = root length/root dry weight) and root tissue density (RTD = root dry weight/root volume). Calculations of SRL and RTD considered diameter heterogeneity by adding total root length or volume from 40 diameter classes (see Rose, 2017). Roots were harvested 14-20 weeks after sowing and stored in 35 % ethanol.

*Seed dormancy* (Sdormancy) was determined for field-collected seeds (over-summered in screenhouses in Israel) in a greenhouse in Tübingen during winter 2013/2014 following an established protocol (Tielbörger et al., 2012). Germination trials were conducted on moistened filter paper in Petri dishes with 14-18 seeds per species (except of *Plantago cretica* with 32 seeds) replicated 12-15 times. The proportion of germinated seeds was determined after two weeks. Germination tests (including a treatment with gibberellic acid) in the following year (M. C. Bilton, unpublished data), as well as previous experiments on our study species (Lampei et al., 2017; Tielbörger et al., 2012) indicated that ungerminated seeds were dormant instead of inviable. Seed dormancy was defined as the proportion of ungerminated seeds.

*Age at flowering onset* (Flower Onset) was calculated as the number of days between germination and the first appearance of reproductive organs (checked daily and every second day, respectively). We non-destructively assessed developmental age *at flowering onset by the number of leaves* (Leaf Number; Sachs, 1992).

For measuring *total plant biomass* (Tot. biomass) and its allocation, plants were harvested at the end of their life cycle, roots washed, and the aboveground biomass separated into leaves, stems, fruits, and further reproductive biomass (e.g. flowering stems, remaining parts of the inflorescence, etc., plants were wrapped in organza to avoid loss of reproductive biomass). All plant organs were oven-dried (five days, 50°C) except fruits, which were air-dried for two weeks (25-30°C) to avoid seed damage. Biomass allocation (*leaf, root,* and *reproductive mass fraction*, Leaf MF, Root MF, Rep. MF) was calculated as the proportion of the respective plant organ weight on total biomass. Total seed weight (see below) was used for reproductive mass fraction.

*Plant height* (Height) was measured at the end of the life cycle (start of leaf senescence) as the distance between soil surface and the highest point of the plant.

*Maximum absolute growth rate* was measured in 18 species (see Table S1) from germination (controlled daily) until 16 weeks after sowing, i.e. before the peak of flowering and when all species still exhibited substantial vegetative growth. Absolute growth rate was calculated as biomass increase per day, i.e. total harvested above- and belowground biomass divided by the number of days between germination and harvest.

*Total seed weight* (TSW, i.e. *fecundity*) was determined for each individual as the product of seed (or fruit) number and seed (or fruit) mass, depending on morphology and family. It was assessed as total seed weight in Cistaceae, and Plantaginaceae, as total fruit weight in legumes, Apiaceae, Asteraceae, and Brassicaceae, and as spikelet weight in grasses, if they were dense and hardly contained any further biomass except of seeds, glumes, and awns. In four grasses (*Briza maxima*, *Crithopsis delileana*, *Psilurus incurvus*, *Stipa capensis*) seeds with their glumes and awns were removed from the infructescence to determine total seed weight. Total seed weight was used for calculating species' fecundity responses to the experimental drought (see Drought experiment).

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### Method S3. Drought experiment

In the drought experiment, plants were exposed to a control and drought treatment.

In the drought treatment, the rate of soil drying was homogenised across species to ensure the comparability of drought effects among species (see Gilbert & Medina, 2016; Sack, 2004). Soil water content of each species was measured daily by weighing the pots of three individuals per species, calculating their gravimetric soil water content (SWC = (soil fresh weight - soil dry weight)/soil dry weight)), and averaging it. Soil water content of all species was adapted to the species with the highest soil water content (i.e. the slowest drying species) by water addition with hand-operated dispensers in the first three weeks of the experimental drought (Figure S1). Afterwards soil water content of 3-4 % was maintained until the end of the drought period (Figure S1). At these soil water contents, predawn water potentials of several species were below levels inducing stomatal closure (Alvarez-Cansino et al., and Satzger et al., unpublished data), indicating severe drought stress.

In the control treatment, soil water content was measured three times per week in three individuals (pots) per species to control that soil water content stays close to saturation (Figure S1).

The difference of the soil water content between the control and drought treatment was tested with a linear mixed model (LMM, package lme4, Bates et al., 2015), considering only the days on which soil water content was measured in both treatments. The LMM included treatment (control *vs*. drought) as fixed explanatory variable and species nested within day of the drought period (as categorical variable) as random factors. We also tested the effect of species identity on soil water content in the drought treatment with a LMM, comprising species as fixed factor and day of the drought period (as categorical variable) as random factor. In this LMM, species identity was expected to be non-significant since our drought treatment was designed to ensure similar soil water content across species. In both LMMs, the significance of the fixed factor was determined with a Wald F-test, the calculation of degrees of freedom and p-values followed the Kenward-Roger approximation (packages lmerTest, Kuznetsova et al., 2017), and the proportion of variance explained by the fixed factor (marginal $R^2$, $R^2m$) was calculated according to Nakagawa et al. (2017) (package MuMIn, Barton, 2020).

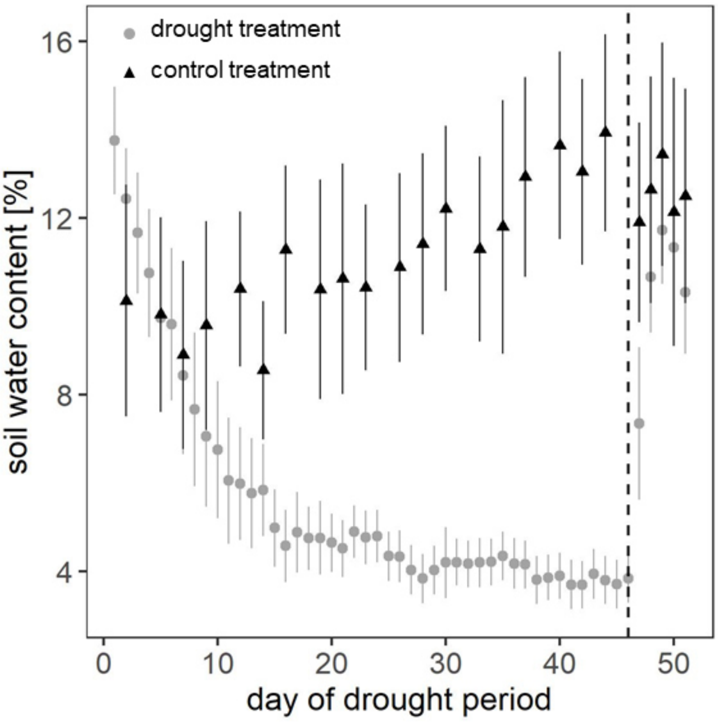

**Figure S1.** Soil water content (mean ± standard deviation) during the experimental drought in the drought and control treatment. Values are averaged across species. The dashed vertical line indicates the end of the drought period (46 days) when water addition to full soil water capacity was resumed. Soil water content differed between treatments during the drought (linear mixed model: $F_{1,2043} = 2413.1$, $p < 0.001$, $R^2m = 0.41$) but was independent from species identity in the drought treatment (linear mixed model $F_{17,1316} = 0.74$, $p = 0.77$).

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**Table S3.** Summary statistics for the 22 traits hypothesized to influence drought responses (Table 1) and maximum growth rate in 29 winter annuals. Given are the unit, number of replicates measured in each species (N), mean ± standard deviation (Std), minimum (Min) and maximum (Max) species' mean, and x-fold variation (Var = Max/Min) across species for each trait as well as results of linear models testing for species differences in each trait (denominator degrees of freedom den. d.f., F-value, p-value, $R^2$, numerator degrees of freedom were 28 for all traits). Species' differences in seed dormancy were tested with a generalised linear model with binomial error distribution, i.e. the F-value corresponds to a Chi$^2$-value (in italics). All traits were natural log-transformed (instantaneous water-use efficiency was multiplied with -1 before transformation) to improve normality and homoscedasticity, except of turgor loss point, leaf water content, total biomass, reproductive mass fraction, and root water content (root water content was arcsin transformed). Species' differences in all traits remained significant under Bonferroni correction of significance level to $p < 0.0022$ for 23 separate tests (traits).

| Trait | Unit | Mean ± Std | Min | Max | Var | N | den. d.f. | F | p | $R^2$ |
|---|---|---|---|---|---|---|---|---|---|---|
| Seed dormancy | - | 0.68 ± 0.27 | 0.07 | 0.98 | 14 | 12-15[a] | - | *2286* | < 0.001 | 0.81 |
| Reproductive mass fraction | g/g | 0.29 ± 0.15 | 0.02 | 0.56 | 22 | 8-11 | 245 | 18.51 | < 0.001 | 0.64 |
| Photosynthetic rate | $\mu$mol/(m$^2$ * s) | 14.43 ± 4.49 | 6.51 | 25.64 | 4 | 7-14 | 286 | 7.49 | < 0.001 | 0.37 |
| Leaf mass fraction | g/g | 0.26 ± 0.10 | 0.10 | 0.62 | 6 | 8-11 | 248 | 13.81 | < 0.001 | 0.57 |
| Specific leaf area | mm$^2$/mg | 33.08 ± 9.21 | 20.65 | 57.56 | 3 | 7-14 | 313 | 12.06 | < 0.001 | 0.48 |
| Age at flowering onset | days | 104.43 ± 33.7 | 47.67 | 165.2 | 3 | 8-11 | 250 | 24.82 | < 0.001 | 0.71 |
| Leaf number at flowering | count | 66.91 ±79.7 | 12.40 | 418.30 | 34 | 8-11 | 250 | 20.05 | < 0.001 | 0.66 |
| Total biomass | g | 11.61 ± 8.29 | 1.22 | 31.26 | 26 | 8-11 | 248 | 29.73 | < 0.001 | 0.74 |
| Height | cm | 51.6 ± 29.1 | 12.7 | 120.7 | 10 | 8-11 | 250 | 30.70 | < 0.001 | 0.75 |
| Root mass fraction | g/g | 0.06 ± 0.03 | 0.02 | 0.14 | 6 | 8-11 | 248 | 5.34 | < 0.001 | 0.31 |
| Instantaneous water-use efficiency | $\mu$mol $CO_2$ / mmol $H_2O$ | 0.03 ± 0.007 | 0.021 | 0.051 | 2 | 7-14 | 286 | 3.09 | < 0.001 | 0.16 |
| Integrated water-use efficiency | ‰ | -32.87 ± 0.89 | -34.38 | -30.61 | 1 | 5-9 | 167 | 5.22 | < 0.001 | 0.38 |

| Trait | Unit | Mean ± Std | Min | Max | Var | N | den. d.f. | F | p | R$^2$ |
|---|---|---|---|---|---|---|---|---|---|---|
| Specific root length | m/g | 577.9 ± 235.7 | 211.5 | 1105.2 | 5 | 8-9 | 201 | 32.46 | < 0.001 | 0.79 |
| Leaf thickness | mm | 0.23 ± 0.09 | 0.12 | 0.47 | 4 | 7-14 | 313 | 44.40 | < 0.001 | 0.78 |
| Root water content | - | 0.91 ± 0.04 | 0.85 | 0.96 | 1 | 8-9 | 201 | 32.07 | < 0.001 | 0.79 |
| Leaf water content | - | 0.86 ± 0.05 | 0.75 | 0.92 | 1 | 6-11 | 267 | 69.55 | < 0.001 | 0.87 |
| Turgor loss point | MPa | -1.49 ± 0.21 | -1.97 | -1.22 | 1 | 8-11 | 274 | 69.46 | < 0.001 | 0.86 |
| Cuticular conductance | mmol/(m$^2$ * s) | 8.14 ± 4.36 | 2.41 | 23.80 | 10 | 8-11 | 273 | 24.71 | < 0.001 | 0.69 |
| Leaf tissue density | g/cm$^3$ | 0.17 ± 0.07 | 0.08 | 0.30 | 4 | 7-14 | 313 | 17.55 | < 0.001 | 0.58 |
| Root tissue density | g/cm$^3$ | 0.07 ± 0.02 | 0.04 | 0.13 | 3 | 8-9 | 201 | 28.93 | < 0.001 | 0.77 |
| Leaf area | cm$^2$ | 4.95 ± 3.83 | 0.30 | 15.82 | 52 | 7-14 | 313 | 72.33 | < 0.001 | 0.85 |
| Xylem vessel diameter | µm | 19.71 ±6.53 | 8.56 | 32.77 | 4 | 7-9 | 223 | 54.99 | < 0.001 | 0.86 |
| Maximum growth rate [b] | g/day | 0.019 ± 0.012 | 0.002 | 0.048 | 28 | 6-9 | 141 | 24.80 | < 0.001 | 0.72 |

*Daucus subsessilis* was only considered with 4-6 individuals in most traits. [a] Germination trials for each species included 12-15 Petri dishes, each with 14-18 seeds (*Plantago cretica* with 32 seeds). [b] measured in 18 species, numerator degrees of freedom = 16

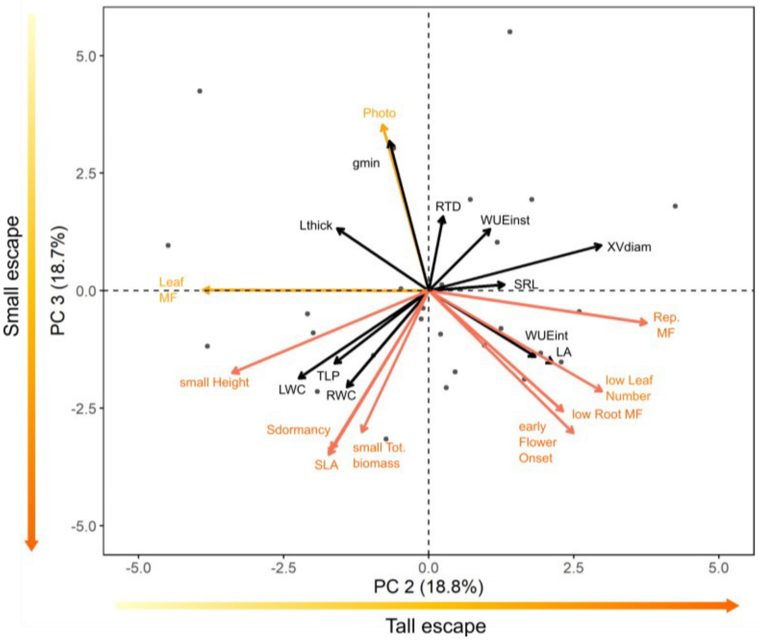


**Figure S2.** Coordination of 21 traits hypothesized to influence drought responses (see Table 1) in winter annuals along PC 2 and PC 3 of a principal component analysis. Expected characteristic traits of the escape syndromes are shown in dark orange, while escape traits associated contrary to our expectation are depicted in lighter orange, traits not expected to be associated with the escape syndromes are shown in black, see details in Figure 1.

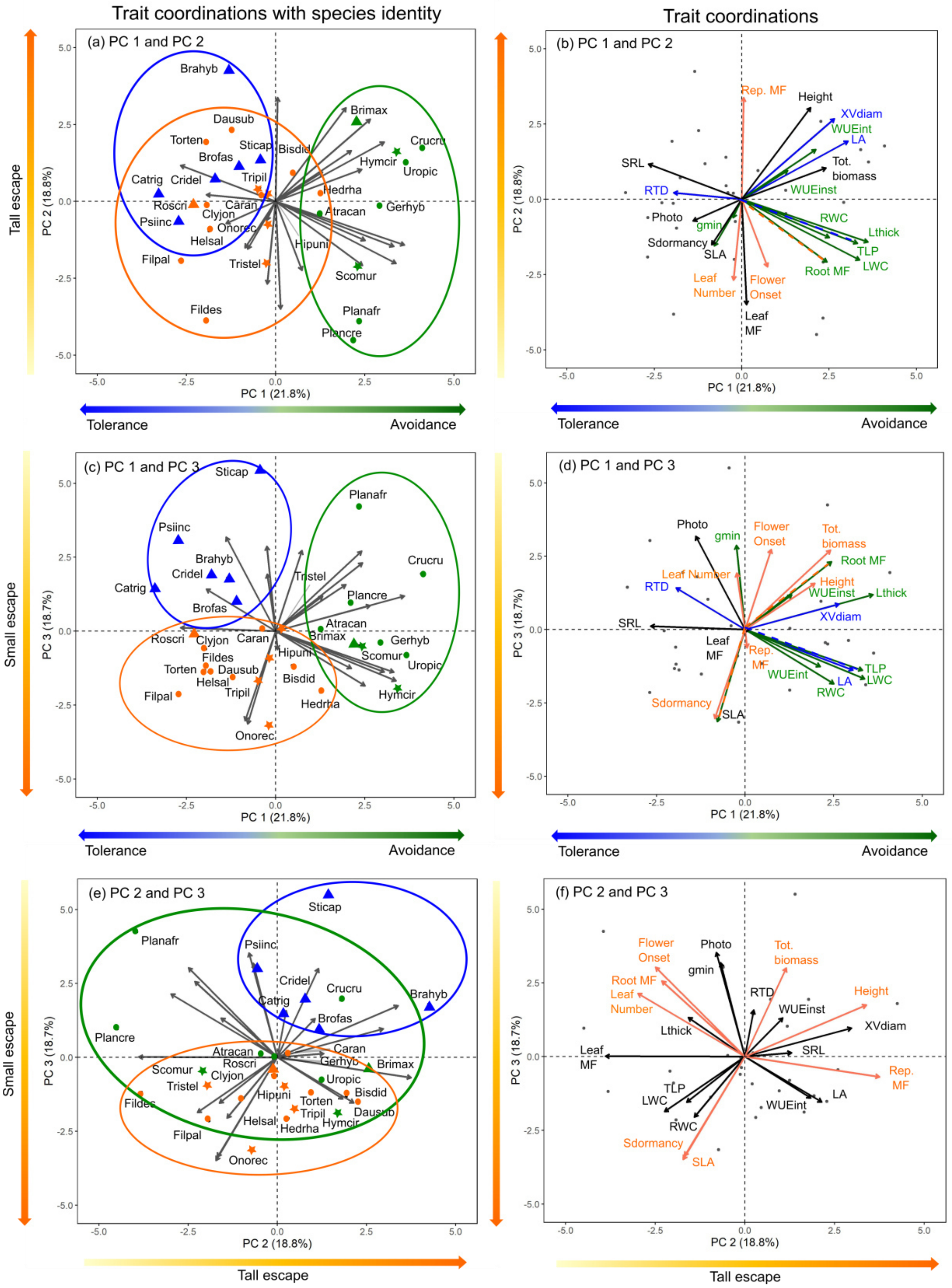
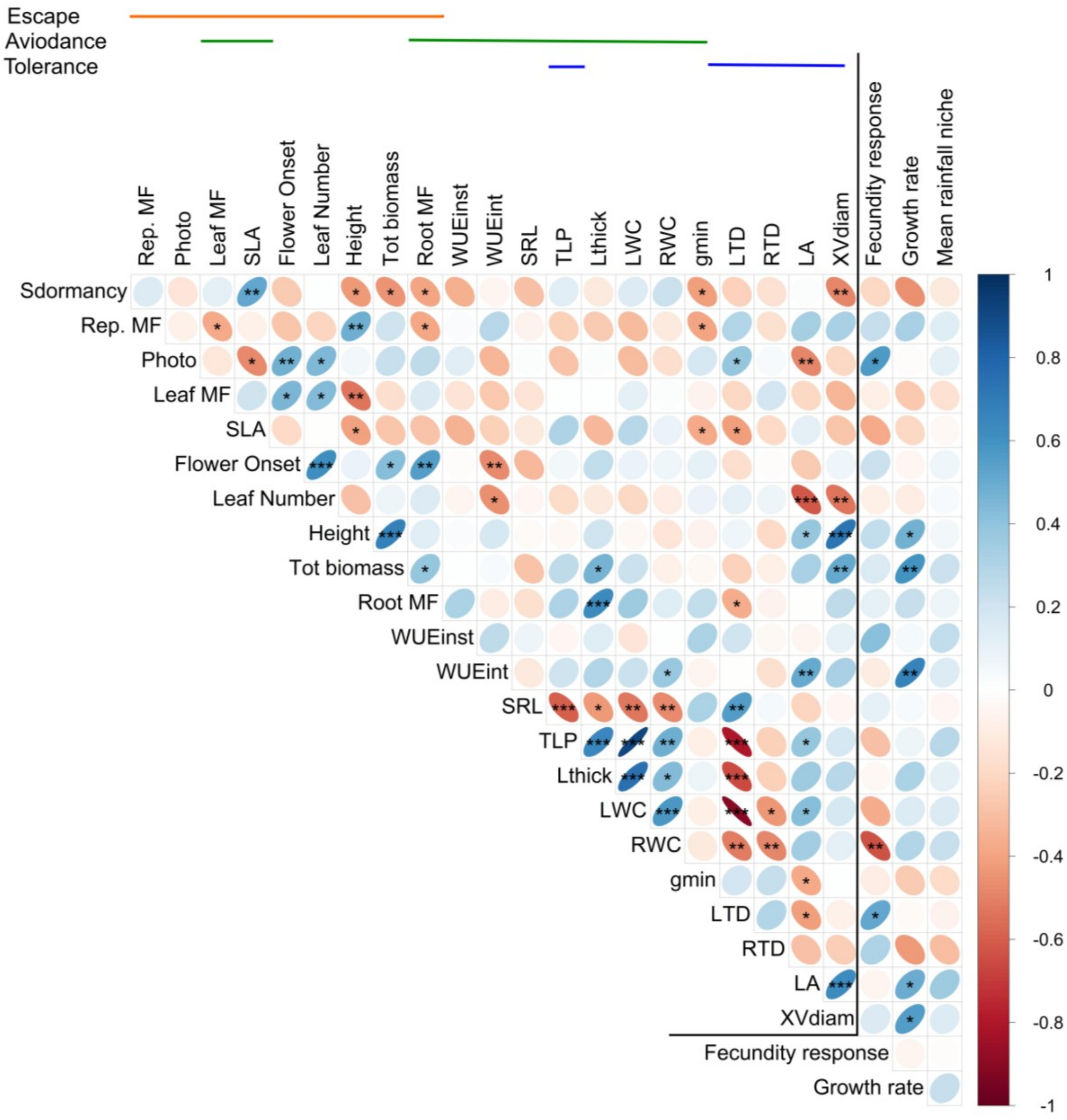


**Figure S3.** Species' positions (a, c, e) of 29 winter annuals and (b, d, f) coordination of 21 traits hypothesized to influence drought responses along the first three axes of a principal component analysis (compare Figure 1 and S2).

**Figure S3 continued:**

In (a), (c), and (e) symbol colour indicate the most pronounced trait syndrome (green avoidance, blue tolerance, orange escape) in each species, and circles functional species groups based on a k-means cluster analysis. Symbol shape indicate life form: triangles for grasses, points for non-legume forbs, asterisks for legumes. Grasses, forbs, and legumes did not differ in their scores along PC 1 and PC 2 (LM statistics: PC 1: $F_{2,26} = 2.43$, $p = 0.11$; PC 2: $F_{2,26} = 2.20$, $p = 0.13$), but along PC 3 ($F_{2,26} = 7.76$, $p = 0.002$, $R^2 = 0.33$) with grasses exhibiting higher scores on PC 3 than forbs and legumes. In (b), (d), and (f) traits characteristic for the dehydration avoidance, tolerance, and drought escape syndrome are shown in green, blue and orange, respectively. Traits coordinated contrary to our expectation or traits expected to be independent from the syndromes shown in the respective subpanel are given in black. Table 1 contains trait abbreviations.

**Table S4.** Correlation matrix based on Spearman rank correlation coefficient including the 22 traits hypothesized to influence drought responses, species' fecundity response to drought, maximum growth rate, and mean annual rainfall niche (i.e. species' distribution along the rainfall gradient). Significance levels, i.e. $p < 0.05$ (*), $p < 0.01$ (**) and $p < 0.001$ (***), are indicated as asterisks within cells. 29 annual species were considered in the trait measurements and in mean annual rainfall niche, and in 18 of them fecundity response and maximum growth rate were measured. For trait abbreviations see Table 1.



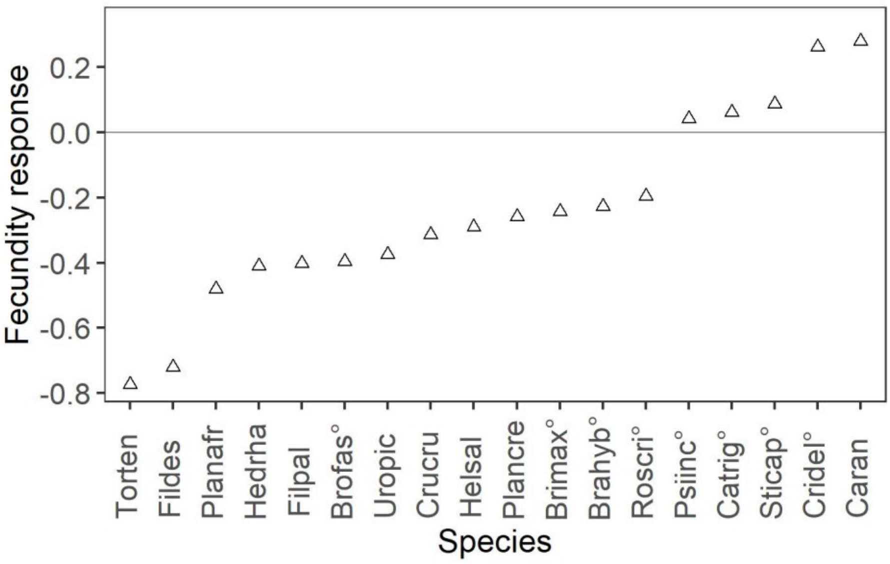


**Figure S4.** Fecundity responses of 18 winter annuals to experimental drought in the growing season. Species' fecundity responses are based on average total seed weight (seed number * seed weight) under drought and control conditions. Species (for species abbreviations see Table S1) were ordered according to their fecundity response. Species' fecundity responses were related to species identity, treatment (both $p < 0.05$), and marginally to their interaction ($p = 0.057$). Forbs exhibited higher fecundity losses in response to drought than grasses (indicated by °) (LM statistics: $F_{1,16} = 5.80$, $p = 0.028$, $R^2 = 0.22$). Fecundity declines resulted from decreases in seed number (average reduction across species 20 %, LM statistics: species $F_{17,320} = 83.25$, $p < 0.001$; treatment $F_{1,320} = 17.97$, $p < 0.001$; interaction $F_{17,320} = 2.02$, $p = 0.010$, $R^2 = 0.80$) and/or seed mass (average reduction almost zero, LM statistics: species $F_{17,298} = 1923.2$, $p < 0.001$; treatment $F_{1,298} = 4.96$, $p = 0.027$; interaction $F_{17,298} = 1.22$, $p = 0.250$, $R^2 = 0.99$), but not from differences in the proportion of reproducing individuals (GLM statistics: species: $\chi^2 = 70.38$, $p < 0.001$, treatment: $\chi^2 = 0.26$, $p = 0.61$, interaction: $\chi^2 = 6.25$, $p = 0.99$, pseudo$R^2 = 0.47$).

**Table S5.** Results of linear models testing the relations between species' fecundity responses to drought, maximum growth rates, or mean annual rainfall niches (i.e. species' distribution along the rainfall gradient) and species' scores along the three trait axes (PC 1-PC 3), as well as the relations between fecundity responses, maximum growth rates, and mean annual rainfall niches. Each model included one response variable (first column) and one or several explanatory variables (given in italics). Trait syndromes and mean annual rainfall niche were investigated in 29 species, fecundity responses and growth rates in 18 species. (Marginal) significant relations ($p < 0.065$) are highlighted in bold.

| Response variable | F | p | F | p | F | p | R² |
|---|---|---|---|---|---|---|---|
| | *PC 1 (avoidance-tolerance axis)* | | *PC 2 (tall escape axis)* | | *PC 3 (small escape axis)* | | |
| Fecundity response ($F_{3,14}$) | 0.61 | 0.448 | 0.97 | 0.342 | **4.54** | **0.051** | 0.16 |
| Growth rate ($F_{3,14}$) | **6.95** | **0.020** | **5.27** | **0.038** | 0.31 | 0.585 | 0.36 |
| Mean rainfall niche ($F_{3,25}$) | **3.77** | **0.063** | 0.67 | 0.422 | 0.20 | 0.663 | 0.06 |
| | *Growth rate* | | | | | | |
| Fecundity response ($F_{1,16}$) | 0.20 | 0.659 | | | | | -0.05 |
| Mean rainfall niche ($F_{1,16}$) | 1.80 | 0.198 | | | | | 0.05 |
| | *Fecundity response* | | | | | | |
| Mean rainfall niche ($F_{1,16}$) | 0.14 | 0.712 | | | | | -0.05 |

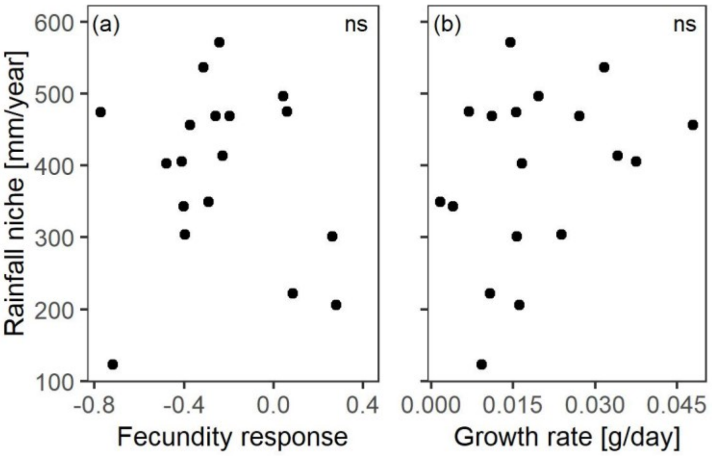


**Figure S5.** Relations between species' mean annual rainfall niches (i.e. species' distribution along the rainfall gradient), (a) species' fecundity responses to drought, and (b) maximum growth rates in 18 winter annuals. Relations were not significant (ns), for statistical details see Table S5.

## Manuscript 2:

# Evaluating grazing response strategies in winter annuals: a multi-trait approach

**Susanne Kurze[1*], Mark C. Bilton[2,3], Leonor Álvarez-Cansino[1], Sara Bangerter[4], Rüdiger Prasse[4], Katja Tielbörger[3], Bettina M. J. Engelbrecht[1,5]**

[1] University of Bayreuth, Functional and Tropical Plant Ecology, Bayreuth Centre of Ecology and Environmental Research (BayCEER), Universitätsstraße 30, 95447 Bayreuth, Germany

[2] Namibia University of Science and Technology (NUST), Department of Agriculture and Natural Resources Sciences, 13 Jackson Kaujeua Street, Private Bag 13388, Windhoek, Namibia

[3] University of Tübingen, Plant Ecology Group, Institute of Evolution and Ecology, Auf der Morgenstelle 5, 72076 Tübingen, Germany

[4] Leibniz University Hannover, Institute of Environmental Planning, Herrenhäuser Str. 2, 30419 Hannover, Germany

[5] Smithsonian Tropical Research Institute, Apartado 0843-03092, Balboa, Ancón, Panama

* Corresponding author

Susanne.Kurze@uni-bayreuth.de

## Keywords

Annual species, Avoidance, Ecological filtering, Escape, Plant-herbivore interaction, Rainfall gradient, Tolerance, Semi-arid rangelands, Trait coordination

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# Abstract

(1) Plants minimize fitness losses through grazing by three fundamental strategies: tolerance, avoidance and escape. Annual species have been traditionally assumed to escape grazing through their short life cycle and seed dormancy, however, their grazing response strategies remain almost unexplored. How traits and their coordination affect species' grazing responses, and whether the generalized grazing model, which posits convergent filtering by grazing and drought, is applicable to this ecologically and economically important species group thus remain unclear.

(2) We used a trait-based approach to evaluate grazing response strategies of winter annuals from the Middle East. Across 23 species we examined the coordination of 16 traits hypothesized to be relevant for grazing responses, and linked them to species' fecundity responses, as proxy for fitness responses, to simulated grazing in controlled conditions, to species' abundance responses to grazing in the field, and to species' distribution along a large-scale rainfall gradient.

(3) Winter annuals exhibited both grazing escape and to a lesser extent tolerance indicated by (i) independent coordination of escape and tolerance traits, and (ii) maintenance of higher fecundity in species with more pronounced escape or tolerance traits under simulated grazing. In the natural habitat, species with a more pronounced escape but not tolerance strategy maintained higher abundance under grazing in dry habitats, indicating convergent favouring of escape by both grazing and drought. However, this finding at the local scale was not mirrored by a strategy shift along a large-scale rainfall gradient.

(4) *Synthesis*. The convergent favouring of escape traits by grazing and drought in annuals is consistent with the generalized grazing model. This model, which has been developed for perennials based on the avoidance strategy, can thus be extended to annuals based on escape, a finding that should facilitate projecting consequences of global change in drylands dominated by annuals.

# Introduction

Grazing by ungulates influences plant performance, species' abundance and distribution, as well as community composition (Díaz et al., 2007; Milchunas et al., 1988). Species vary in their grazing responses, ranging from fitness losses to overcompensation (Agrawal, 2000). The traits and strategies, underlying these interspecific differences, and how they affect ecological filtering along environmental gradients have been mainly investigated in perennial species (e.g. Adler et al., 2004; Quiroga et al., 2010). However, in annual species, which exhibit a different life history and outlast unfavourable conditions as seeds (Levitt, 1980), grazing response strategies remain poorly understood despite the major ecological and economic relevance of annual grasses and forbs in semi-arid rangelands (Noy-Meir, 1973; Ruppert et al., 2015; Sternberg et al., 2015). Under global change, ecosystem services of annual-dominated systems are expected to deteriorate through intensification of land use and decreasing water availability (Maestre et al., 2016; Sala et al., 2000). Elucidating annuals' grazing response strategies and their ecological filtering is thus of increasing significance. It closes a conceptual gap of understanding strategies in species with different life histories (annuals *vs*. perennials), as well as provides crucial information for projecting and mitigating consequences of global change.

Grazing resistance in plants, i.e. the ability to minimize fitness losses under grazing, can be mediated by three fundamental strategies, namely tolerance, avoidance, and escape (Agrawal, 2000; Coley et al., 1985). Plant strategies (or syndromes) are characterized by suites of coordinated (i.e. correlated) traits (Reich et al., 2003), which together influence performance responses (i.e. growth, survival, reproduction, fitness) or abundance responses to different environmental conditions (Shipley et al., 2016). Different strategies form a continuum and are not mutually exclusive, but functional linkages or trade-offs in the underlying traits as well as coordinated selection pressures favour some trait combinations and preclude others (Levitt, 1980).

*Grazing tolerators* are characterised by a high ability to compensate tissue loss through regrowth. A high compensation ability can result from high photosynthetic rates of leaves with high nitrogen contents (low C:N ratio) and high specific leaf area, but also from high biomass allocation to roots for carbon storage (Poorter et al., 2009; Strauss & Agrawal, 1999). *Grazing avoiders* reduce the accessibility of the plant tissue for herbivores. Morphological avoidance traits are a low stature, small leaf area, and tough leaves with high leaf dry matter content (or low specific leaf area) (Díaz et al., 2001; Díaz et al., 2007; Hanley et al., 2007; Poorter et al., 2009). Chemical defenses, such as high C:N ratios or secondary compounds, can also decrease herbivory (Herms & Mattson, 1992). *Escapers* exhibit a short life cycle, which increases the probability of reproduction before grazing or other adverse conditions, such as drought, occur (Kooyers, 2015). The strategy encompasses an early start of reproduction, small plant size, and high biomass allocation to reproduction as well as traits that confer high growth and photosynthetic rates, such as nitrogen-rich leaves with a high specific leaf area and a high biomass allocation to leaves rather than to roots or carbon storage (Grime, 1977; Kooyers, 2015). Seed dormancy, which spreads germination between years, buffers escapers against reproductive failure and acts as a bet-hedging mechanism (Philippi & Seger, 1989; Tielbörger et al., 2012).

Grazing tolerance or avoidance have been shown in perennials, with each strategy favoured under different environmental conditions (Adler et al., 2004; Díaz et al., 2001; Quiroga et al., 2010). Grazing tolerant species have been hypothesized to dominate in resource-rich habitats, because this strategy requires high resource consumption, but also allows for high growth and high competitive effect (Briske, 1996; Coley et al., 1985; Herms & Mattson, 1992). Conversely, in resource-poor habitats tissue replacement is costly, favouring species with grazing avoidance (Coley et al., 1985;

Herms & Mattson, 1992). Grazing response strategies should therefore shift from tolerance to avoidance with decreasing resource availability. This shift should be especially pronounced along rainfall gradients, because several trait attributes concomitantly confer avoidance of grazing and desiccation (e.g. small stature and small, tough leaves) (Milchunas et al., 1988). Ecological filtering under grazing and drought should thus be convergent (generalised grazing model, Milchunas et al., 1988). Accordingly, both communities under arid conditions and grazed communities should be highly resistant to increasing drought or grazing under global change, since their dominant species avoid both grazing and desiccation (Milchunas et al., 1988; Quiroga et al., 2010). The expected interspecific shift from grazing tolerance to avoidance with decreasing rainfall has been shown in several perennial-dominated communities (Adler et al., 2004; Díaz et al., 2007; Quiroga et al., 2010).

Annuals, in contrast to perennials, are traditionally assumed not to withstand unfavourable environmental conditions, such as grazing or drought, in the vegetative and reproductive stage, but endure them as dormant seeds forming a seed bank (Grime, 1977; Levitt, 1980). They are thus commonly considered to exhibit an escape strategy (Kooyers, 2015; Levitt, 1980). However, pooling annuals in a single homogenous functional strategy might be too simple. The high diversity and abundance of annual species in an enormous range of environmental conditions (e.g. Guo et al., 2002; Tielbörger et al., 2014) suggest that they exhibit a wide variation of trait attributes (see Li & Shipley, 2017). Additionally, annuals are an important source of forage (Noy-Meir, 1973; Sternberg et al., 2015), indicating that they are exposed to grazing by livestock in their vegetative and reproductive phase, and do not (only) escape, but also tolerate it.

Winter annuals in Mediterranean and subtropical desert climates grow and reproduce in the rainy, mild season (winter) and survive the dry and hot season (summer) as seeds, i.e. they restrict growth and reproduction to the favourable period and evade (= escape) the unfavourable dry season. Additionally, they buffer unpredictable catastrophic events by between-year seed dormancy (Tielbörger et al., 2012). Due to this specific life history, rainfall patterns should act as strong ecological filter, favouring annual species with a more pronounced escape strategy (faster life cycle and associated traits, including between-year seed dormancy) in areas with a longer dry season and less predictable rainfall (arid areas). Intraspecific studies on annuals indeed show an increasing expression of escape traits towards arid conditions (Aronson et al., 1993; Kurze et al., 2017; Tielbörger et al., 2012). However, across species it has not yet been evaluated whether ecological filtering favours species with a more pronounced escape strategy towards arid areas. How drought and grazing interact and modulate interspecific changes of grazing response strategies (and underlying traits) along moisture gradients in annuals, and whether the generalized grazing model is applicable to this species group thus remain unclear.

We suggest that there may be two possible scenarios. In the first scenario, a short life cycle associated with drought escape also minimizes the probability of tissue loss through grazing before reproduction. In this scenario, grazing and drought act as convergent ecological filters in annuals, similar to perennials (see above), but favour the escape instead of the avoidance strategy towards arid conditions. In the following, we refer to this as the convergence scenario. It might be most likely under grazing regimes where early reproduction allows to successfully escape grazers.

In the second scenario, a pronounced drought escape strategy is traded-off with grazing avoidance or tolerance. Species with a pronounced drought escape strategy should be vulnerable to grazing in the vegetative or reproductive phase (i.e. if escape is not successful), since several escape traits, including high growth rate, low biomass allocation to roots and low carbon storage, are incompatible with grazing avoidance or tolerance. In this scenario, grazing and drought thus do not act as convergent ecological filters in winter annuals under arid conditions, but the long dry season and unpredictability favour escape, while grazing favours avoidance under low resource availability, as in perennials (see above). However, unlike in perennials, grazing avoidance does not concurrently lead to increased drought avoidance in annuals. Instead, the slow-growth traits associated with grazing avoidance should increase the probability to be negatively affected by drought before reproduction under unpredictable, arid conditions (see Carvajal et al., 2019 for shrubs), and thus decrease drought resistance in annuals. In the following, we refer to this as the trade-off scenario. This scenario is consistent with the few relevant data from annual dominated communities, which indicate lower (rather than higher) grazing resistance of annual plant communities in arid areas (Osem et al., 2002; M. C. Bilton, P. Liancourt, S. Bangerter, R. Prasse, & K. Tielbörger, unpublished data). It might be most likely when high grazing intensity precludes successful escape of grazers.

In both scenarios, annuals with a grazing tolerance strategy should be favoured in moister conditions, since this strategy should confer annuals a high competitive effect in more dense vegetation (Liancourt & Tielbörger, 2009).

The two scenarios have different implications for the vulnerability of annual-dominated communities to global change. In the convergence scenario, annuals favoured under drought or grazing should be preadapted to an increasing intensity of both factors, as perennials (see above). In the trade-off scenario, annuals are either adapted to drought (escapers) or grazing (avoiders or tolerators), but not both. Species should thus be more vulnerable to the respective other factor.

Here, we examine grazing response strategies in winter annuals from the Middle East. This region is ideal for our study, since winter annuals comprise the majority of plant species, the long grazing history by domesticated ungulates spans more than ten thousand years, and the area exhibits pronounced large-scale rainfall gradients for assessing species' ecological filtering (Noy-Meir & Seligman, 1979; Tielbörger et al., 2014). We used a trait-based approach to identify the grazing response strategies. Across 23 annuals a comprehensive set of 16 traits hypothesized to be associated with the three grazing response strategies (escape, avoidance, tolerance) was measured under common, controlled conditions. We tested the following hypotheses:

(1) Traits relevant for grazing responses are coordinated along three major axes in annual species, reflecting the three grazing response strategies: escape, tolerance and avoidance.

Species' positions along the trait axes, i.e. the strengths of their trait-based escape, tolerance and avoidance strategy, explain interspecific differences in fitness responses and abundance responses to grazing, and are related to their distribution across rainfall gradients. Specifically:

(2) Under simulated grazing, species with more pronounced trait-based grazing tolerance show lower fitness losses.

(3) In the field, either (a) species with more pronounced escape (convergence scenario), or (b) species with more pronounced avoidance (trade-off scenario) show lower abundance declines in response to grazing in drier habitats. In both scenarios, species with more pronounced tolerance exhibit lower abundance declines in moister habitats.

(4) Along large-scale rainfall gradients a strategy shift occurs: either grazing escape (convergence scenario) or grazing avoidance (trade-off scenario) is more pronounced in species associated with arid conditions, whereas grazing tolerance is more pronounced in species associated with moist conditions.

# Material and Methods

## Study system

The Levant region in the Middle East comprises steep large-scale rainfall gradients, which allow us to test for species' ecological filtering. They range from north to south (across approximately 350 km) and from west to east (approximately 50 km) with higher and more predictable mean annual rainfall (MAR) in mesic-Mediterranean areas in the north (up to 800 mm/year ± 18 %, mean ± CV) and less, very unpredictable rainfall in the desert in the south (20 mm/year ± 55 %) or towards the Dead Sea. The length of the rainfall season, which corresponds to the main growing season, as well as primary productivity and competition intensity decrease towards the arid end of the rainfall gradients (Liancourt & Tielbörger, 2009). The region is characterised by shrubs (desert to semi-arid) to small trees (Mediterranean), with winter annual species dominating the inter-shrub matrix.

A grazing exclosure experiment (see details below) was conducted in a semi-arid region in Jordan (MAR 200-400 mm/year) in Wadi Shuayb (32° 01' 10.34"N, 35° 43' 36.69"E).

## Study species and plant material

The study focused on 23 winter annual species, including 15 forbs (four legumes) and eight grasses (Table S1). Species were selected based on: (1) coverage of different distribution ranges along the large-scale rainfall gradients based on BioGIS (2018), (2) a large taxonomic range (i.e. seven plant families), (3) high abundance in the region, and (4) seed availability. The species belonged to 20 genera, and all had the C3 photosynthesis pathway. Seeds for the experiments were collected in the mid-range of the rainfall gradient in two sites in Israel, approx. 40 km apart (Lahav MAR 300 mm/year and Matta MAR 540 mm/year, for details see Tielbörger et al., 2014). They were collected from a minimum of 50 maternal sibships per species within an area of 1.0-1.5 km$^2$ in April 2012.

Seeds were grown under common, favourable conditions in a greenhouse during winter 2013/2014 to obtain a F1 generation with minimized maternal effects. The F1 seeds were over-summered for two months to break summer dormancy (compare Tielbörger et al., 2012). For the trait measurements (except seed dormancy) and the grazing simulation experiment we grew plants from the F1 seeds under common favourable conditions (i.e. high water and nutrients, without biotic interactions, see details below) in the greenhouse. This approach enabled us to comparatively assess trait differences and fecundity responses (as proxy for fitness responses) across species, and to minimize bias introduced by intraspecific variation due to maternal effects, phenotypic plasticity or ecotypic differentiation. Our comparative measurements of species' traits under favourable conditions should be relevant for the field, since species' trait rankings commonly hold under different environments (stable species hierarchy hypothesis, Kazakou et al., 2014).

## Plant cultivation in the greenhouse

Plants were germinated and grown in a greenhouse in cylindrical pots (1 l volume, 36 cm depth, Deepot Cells, Stuewe & Sons, Oregon, US) with a 1:1 mixture of nutrient-poor sand and compost supplemented with 5 g of amorphous silicon (Aerosil 300, Evonik Industries AG, Essen, Germany). Temperature in the greenhouse was set to 20-23°C in winter and 20-26°C in spring, and daytime photosynthetic active radiation ranged between 150 and 800 µmol photons/(m$^2$ * s). Day length was adjusted to the natural variation in Israel for unbiased phenology. Pots were randomly distributed in the greenhouse and rearranged every second week.

All individuals received ample water and nutrient supply to avoid any resource limitation. They were wrapped in light transparent fabric (organza) when they started to produce seeds to prevent seed loss. Plants were grown until the end of their life cycle after seed ripening when leaves senesced (30-36 weeks after sowing).

## Trait measurements

Sixteen morphological, anatomical, physiological, and life-history traits that are hypothesized to be associated with the three grazing response strategies (i.e. escape, tolerance, avoidance, see Table 1) were measured on unclipped plants or on seeds under favourable conditions (see above). We measured 5-16 replicates per species and trait and followed standardized protocols for trait measurements where available (for details see Table 1 and Method S1). Different sets of plants were measured for leaf traits, whole plant traits, seed dormancy, and growth rate (for details see Table 1). Compensation ability was calculated based on total biomass of clipped and control plants (see below and Method S1).

**Table 1.** Traits hypothesized to influence grazing responses considered in this study, their expected association with the three grazing response strategies, escape, tolerance and avoidance, their abbreviation, unit, and the number of measured individuals (replicates) in each species (N). + or - indicate whether a high or low trait value is expected to be associated with higher grazing resistance in the respective strategy. The column 'Method' gives a brief overview of the definition of the traits, the measurement, or the reference. Detailed information is provided in Method S1. Superscript letters at the trait name indicate plant sets for the trait measurements.

| Trait | Abbreviation | Unit | Escape | Tolerance | Avoidance | N | Method |
|---|---|---|---|---|---|---|---|
| Seed dormancy[a] | Dormancy | - | + | | | 13-15[a] | Proportion of ungerminated seeds in germination trials (Tielbörger et al., 2012) |
| Flowering time[b] | Flowering | day | - | | | 8-11 | Visual checking for first reproductive organs |
| Leaves at flowering[b] | Leaves flower | count | - | | | 8-11 | Count of leaf number at onset of flowering |
| Leaf area[c] | LA | cm² | | | - | 8-15 | Area of individual leaf, Pérez-Harguindeguy et al., (2013) |
| Specific leaf area[c] | SLA | mm²/mg | + | + | - | 8-15 | Pérez-Harguindeguy et al., (2013) |
| Leaf dry matter content[c] | LDMC | mg/g | - | - | + | 9-15 | Pérez-Harguindeguy et al., (2013) |
| Leaf toughness[c] | Toughness | N/mm | | | + | 7-15 | Measured as force to punch, Pérez-Harguindeguy et al., (2013) |
| Photosynthetic rate[d] | $A_{max}$ | µmol/ ($m^2$ * s) | + | + | | 9-14 | Pérez-Harguindeguy et al., (2013) |
| C:N ratio[d] | C:N | %/% | - | - | + | 5-9 | Pérez-Harguindeguy et al., (2013) |
| Height at seed set[c] | Height | cm | - | | - | 12-16 | Distance between soil surface and highest point of the plant |

| Trait | Abbreviation | Unit | Escape | Tolerance | Avoidance | N | Method |
|---|---|---|---|---|---|---|---|
| Total biomass[c] | Tot. biomass | g | - | | | 12-16 | Above- and belowground biomass at the end of the life cycle |
| Leaf mass fraction[c] | Leaf MF | g/g | + | | - | 12-16 | Leaf biomass per total plant biomass |
| Root mass fraction[c] | Root MF | g/g | - | + | | 12-16 | Root biomass per total plant biomass |
| Reproductive mass fraction[c] | Rep. MF | g/g | + | | | 10-16 | Total seed weight per total plant biomass |
| Absolute growth rate[e] | AGR | g/day | + | + | - | 6-9 | Rate of total biomass increase in vegetative phase |
| Compensation ability[f] | | unitless | - | + | - | 1[b] | Difference between total biomass of clipped and control plants |

[a] 13-15 Petri dishes each with 14-18 seeds for each species (*Plantago cretica* with 32 seeds), [b] Compensation ability was based on clipped and control plants, 10-16 individuals each

## Grazing simulation experiment in the greenhouse

To assess and compare species' fecundity responses (as proxy for fitness responses) to grazing and their ability to compensate tissue loss, we conducted a grazing simulation experiment under controlled conditions (see above). In this experiment, plants were either clipped or served as controls. Each treatment comprised 10-16 individuals per species. We clipped plants once 15 weeks after sowing, which corresponds to peak grazing season in the field. Singular grazing events (rather than chronic grazing) are the typical grazing regime in our study system. At clipping, several species had started flowering, but none had ripe fruits or started senescence (i.e. escaped the simulated grazing). All species were thus potentially able to re-grow, but differed in their current investment in reproduction.

We clipped with scissors and removed about 75 % of the aboveground biomass in all species based on visual estimation and previous species-specific assessments of aboveground biomass. Within each species, all individuals were clipped to the same size to ensure that they had similar resources for regrowth. Clipping encompassed mainly distal leaves and stems, but also the removal of any already existing reproductive biomass (only in *Filago palaestina* some reproductive biomass remained). Our approach ensured a similar loss of relative biomass in all species independent of size or growth form, and thus allowed us to compare fecundity responses and compensation abilities across species without risking plant death. It did not aim to mimic selective grazing by ungulates in the field.

We harvested plants in random order when most species started to show senescence. Both clipped and unclipped individuals had enough time to go through their life cycle (i.e. within species, the number of individuals that produced ripe seeds did not differ between clipped and unclipped plants). Fecundity responses were assessed based on the weight of all seeds per individual (total seed weight, TSW = seed number * individual seed mass), and compensation ability based on total biomass per individual (see Method S1).

We calculated fecundity response as the standardized difference between total seed weight of clipped and control plants in each species:

fecundity response = mean $(\log(TSW_{\text{clipped}} + 1)) - \text{mean}(\log(TSW_{\text{control}} + 1))$.

This response parameter is equivalent to the widely used response ratio (Hedges et al., 1999; $RR = \log(a/b) = \log(a) - \log(b)$), except we natural log-transformed TSW before calculating the mean for each treatment (clipped *vs.* control), since data were not normally distributed. One was added before log transformation due to zero values. As in response ratios, negative or positive values refer to a negative or positive species' fecundity response to clipping, respectively.

Fecundity responses based on the total seed weight that the individuals produced during their lifetime considered both the number of possible offspring (i.e. seed number), and the probability of plant survival that is related to seed mass (Metz et al., 2010). We consider this a solid proxy for fitness responses.

## Grazing exclosure experiment in the field

The response of annuals to grazing in the field (Jordan) was assessed by comparing species' abundances in fenced plots to exclude sheep and goats with paired adjacent intensively grazed plots (plot size 1200 m² each). Plot pairs (grazed and ungrazed) were installed on a south-facing and a north-facing slope (4 pairs on each slope) in each of four sites located within 10 km (2 slopes * 4 plot pairs * 4 sites = 32 plot pairs; 64 plots, Figure S1). Each plot contained six randomly chosen permanent quadrats (20 x 20 cm), in which the abundance of each species (i.e. number of individuals) was determined at the peak of the vegetation development in each spring (for further details see M. C. Bilton, P. Liancourt, S. Bangerter, R. Prasse, & K. Tielbörger, unpublished data). The experiment ran from November 2005 until spring 2009. We analysed the abundance responses to grazing in the 20 species that overlapped with the greenhouse experiment (see Table S1) for the years 2007 to 2009, when seed input already originated from manipulated (ungrazed *vs*. grazed) parental generations.

Opposite slopes differ in their environmental conditions with a more arid microclimate, lower soil moisture, and lower standing biomass on south-facing slopes compared with more humid conditions on north-facing slopes, and corresponding differences in species composition (Kutiel, 1992; Kutiel & Lavee, 1999; M. C. Bilton, P. Liancourt, S. Bangerter, R. Prasse, & K. Tielbörger, unpublished data). These exposure differences are independent of inter- and intra-annual rainfall variability and site characteristics, and thus represent consistent soil moisture differences. We thus consider south-facing slopes as dry habitats and north-facing slopes as moist habitats in the grazing exclosure experiment and quantified species' responses to grazing separately for each slope.

For each species, we calculated standardized abundance differences for each plot pair (grazed *vs*. ungrazed) in each year (response ratio; Hedges et al., 1999), and then averaged them across each slope:

Abundance response = mean (log ((abundance$_{\text{grazed}}$ + 1)/(abundance$_{\text{ungrazed}}$ + 1))).

Averaging species' abundance responses in each slope across sites and years focused the analyses on the moisture difference between drier and moister slopes. Including site as additional factor turned out impossible because the low abundances of several species caused zero-inflation and heteroscedasticity. The low species' abundances also prevented us from analysing species' abundances across sites independently of the grazing effects.

## Species distribution across the large-scale rainfall gradient

Species' distribution along the large-scale rainfall gradients in the Levant region was characterized based on their occurrences (presence/absence data) in independent biological records in Israel (BioGIS, 2018). The BioGIS database provides the mean annual rainfall niche of each species (at 100 m resolution), which is modelled as the average of local mean annual rainfall across all occurrence sites of a respective species.

## Statistical analyses

The main aims of the statistical analyses were (1) to determine the main axes of variation of grazing-relevant traits in annuals, and (2) to evaluate if species' positions along these axes are related to their grazing responses in different environments (controlled conditions or field), and to their distribution along the rainfall gradient.

We initially tested species differences in each of the 16 traits (natural log transformed to improve normality and homoscedasticity, except seed dormancy and reproductive mass fraction) with F-tests on linear models. Pairwise trait correlations were assessed with Spearman rank correlation coefficients based on species' average trait values.

The coordinations of the 16 traits were assessed with a principal component analysis. We identified those principal component axes (PCA axes), which reflected trait coordinations consistent with the hypothesized grazing response strategies. Species' positions (i.e. scores) on these PCA axes were used to characterize how strongly a species exhibited the respective trait-based strategy. To ensure that larger values consistently correlate with (hypothesized) higher grazing resistance, species' scores were multiplied with -1, if necessary (in the following referred to as inverse axis).

The effect of simulated grazing on fecundity was tested with F-Tests on a linear model including total seed weight (natural log-transformed after adding 1) as response variable, and species, treatment (clipped *vs*. control) and interaction term as explanatory variables. The significance of fecundity differences between clipped and control plants within each species were assessed with separate t-tests, and the significance level adjusted according to Holm-Bonferroni sequential correction (Gaetano, 2013).

We tested if species differ in their abundance responses to grazing in each slope (dry *vs*. moist slope) with separate linear mixed models (package lme4, Bates et al., 2014). These linear mixed models included species as fixed explanatory variable, and site and year as random factors (see details in Method S2).

We assessed if species' fecundity responses to simulated grazing or their abundance responses to grazing in the field were determined by their scores along the PCA axes (i.e. the strength of their trait-based strategy) with F-tests on separate linear models. Each linear model contained species' scores on one PCA axis as explanatory variable and either their fecundity responses or their abundance responses in one of the slopes as response variable. To improve normality, abundance responses in each slope were natural log-transformed (after adding the lowest value to attain positive values) in the linear models with species' scores along PCA axis 1 as explanatory variable. We similarly tested if species' mean annual rainfall niches are related to their scores along the PCA axes or their fecundity responses with F-tests on separate linear models. Each linear model contained species' scores on one PCA axis or species' fecundity responses as explanatory variable. We also considered species' minimum and maximum rainfall niche (BioGIS, 2018), but results did not change qualitatively (Figure S4). In all linear models described above heterogenous species' distribution along PCA axis 3 could not be resolved by transformation.

We calculated pairwise correlations of individual traits with species' fecundity responses to simulated grazing, abundance responses to grazing in each slope, and mean annual rainfall niche using Spearman rank correlation coefficients. The importance of single traits for species' abundance responses to grazing in each slope was additionally assessed with a random forest algorithm (see Method S3). This algorithm accounts for non-linear relations or interactions among traits (Breimann, 2001). Variables with an importance value greater than the largest negative value (corresponding to the maximum random noise in the dataset) were considered important (alike significant, see Holmes et al., 2015).

All analyses were conducted with R 3.3.3 (R Core Team, 2017).

## Results

All species re-grew and reproduced after simulated grazing. All 16 traits hypothesized to be associated with the grazing response strategies (Table 1) varied across the 23 species (all $p < 0.001$, 2 to 150-fold variation of trait values, Table S2). Pairwise correlations between single traits were predominantly weak (Table S3).

Trait coordinations associated with PCA axis 1 (explaining 28 % of variation, in the following referred to as axis 1) and PCA axis 3 (14 %, axis 3) corresponded to two of the hypothesized grazing response strategies, namely the escape (axis 1) and tolerance strategy (axis 3), and formed independent axes (Figure 1, Table 2). Species with a positive score on axis 1 were characterized by high seed dormancy, early flowering, small height, low total biomass, low root mass fraction, high leaf mass fraction, high specific leaf area, and low toughness (Figure 1, Table 2). These traits are consistent with the hypothesized escape strategy (Table 1). Unexpectedly, axis 1 was also associated with low (rather than high) growth rate and to a lesser extent with high (rather than low) compensation ability (Figure 1, Table 2). Species with a negative score on axis 3 exhibited high compensation ability, high root mass fraction, high growth rate, late flowering and large, nitrogen-rich leaves (low C:N ratio) with low leaf dry matter content (Figure 1, Table 2). These traits refer to the hypothesized grazing tolerance strategy (Table 1). None of the PCA axes reflected the expected grazing avoidance strategy. Instead, the avoidance traits (small, tough leaves with high leaf dry matter content, small height) were differently associated with several PCA axes (Figure 1, Table 2). PCA axis 2 (explaining 20 % of variation) and PCA axis 4 (11 %) did not reflect any hypothesized grazing response strategy (Table 2).

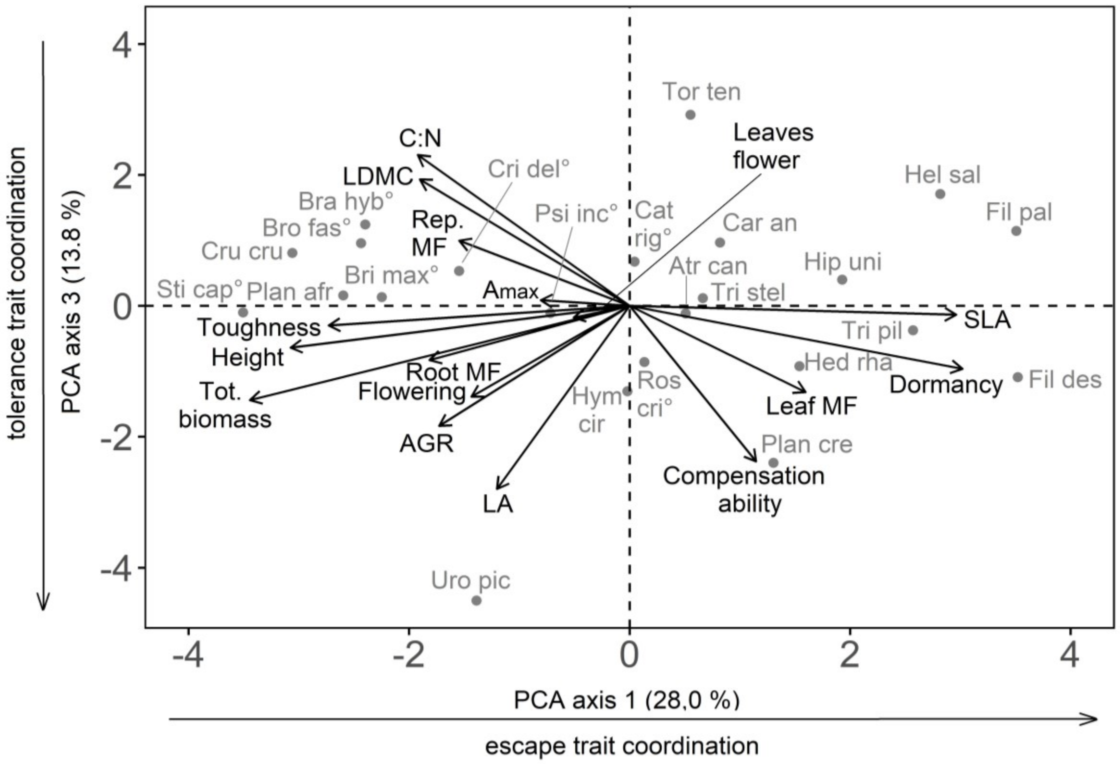

**Figure 1.** Coordination of 16 traits hypothesized to influence grazing responses (see Table 1) in 23 winter annual species (° indicates grasses). PCA axis 1 and 3 of a principal component analysis are shown, which summarized trait coordinations corresponding to the hypothesized grazing escape and tolerance strategy (see Table 2 for trait loadings on PCA axes 1-4). See Tables 1 and S1 for trait and species abbreviations, respectively.

**Table 2.** Loadings of the 16 traits hypothesized to influence grazing responses (see Table 1) on the first four axes of the principal component analysis with 23 annual species (see Figure 1). Traits were ordered according to their |loading| on PCA axis 1. Traits hypothesized to be associated with an escape strategy exhibit high loadings on PCA axis 1, whereas traits hypothesized to be associated with a tolerance strategy exhibit low (negative) loadings on PCA axis 3. Characteristic traits for both strategies (see Table 1) are highlighted in bold. PCA axis 2 and 4 did not reflect any hypothesized grazing response strategy.

| | Axis 1 | Axis 2 | Axis 3 | Axis 4 |
|---|---|---|---|---|
| Eigenvalue | 4.49 | 3.17 | 2.20 | 1.73 |
| Explained variance [%] | 28.0 | 19.8 | 13.8 | 10.8 |
| Tot. biomass | **-0.41** | 0.00 | -0.24 | 0.01 |
| Height | **-0.37** | -0.22 | -0.11 | 0.11 |
| Dormancy | **0.36** | 0.00 | -0.16 | 0.23 |
| SLA | **0.35** | -0.13 | -0.02 | -0.07 |
| Toughness | -0.32 | 0.23 | -0.05 | 0.09 |
| LDMC | -0.23 | 0.07 | **0.33** | 0.38 |
| C:N | -0.23 | -0.14 | **0.39** | -0.37 |
| Root MF | **-0.22** | 0.15 | -0.14 | -0.49 |
| Growth rate | -0.21 | -0.30 | **-0.31** | -0.03 |
| Leaf MF | **0.19** | 0.30 | -0.22 | -0.23 |
| Rep. MF | -0.18 | -0.28 | 0.17 | 0.28 |
| Flowering | **-0.17** | 0.46 | -0.24 | 0.06 |
| LA | -0.14 | -0.26 | -0.47 | -0.04 |
| Compensation ability | 0.14 | -0.13 | **-0.40** | 0.28 |
| $A_{max}$ | -0.10 | 0.37 | 0.01 | 0.43 |
| Leaves flower | -0.06 | 0.37 | -0.03 | -0.08 |

Simulated grazing decreased fecundity (i.e. the total weight of produced seeds per individual) in all species (no overcompensation occurred). On average, fecundity was reduced by 30 % in clipped compared to control plants (Figure 2, linear model statistics: treatment $F_{1,615} = 66.74$, $p \leq 0.001$). The fecundity responses significantly differed across species (Figure 2, linear model statistics: species $F_{22,615} = 93.45$, $p \leq 0.001$, interaction $F_{22,615} = 2.03$, $p = 0.003$, $R^2 = 0.76$). Species' fecundity responses were positively related to their scores along the escape axis (axis 1) and to a lesser extent ($p = 0.08$) to their scores along the tolerance axis (inverse axis 3, Figure 3, Table 3). Thus, species with pronounced escape or tolerance traits maintained higher fecundity under simulated grazing. Correlations of single traits with species' fecundity responses were overall weak ($R < 0.6$), except for positive relations with compensation ability and specific leaf area (Table S3).

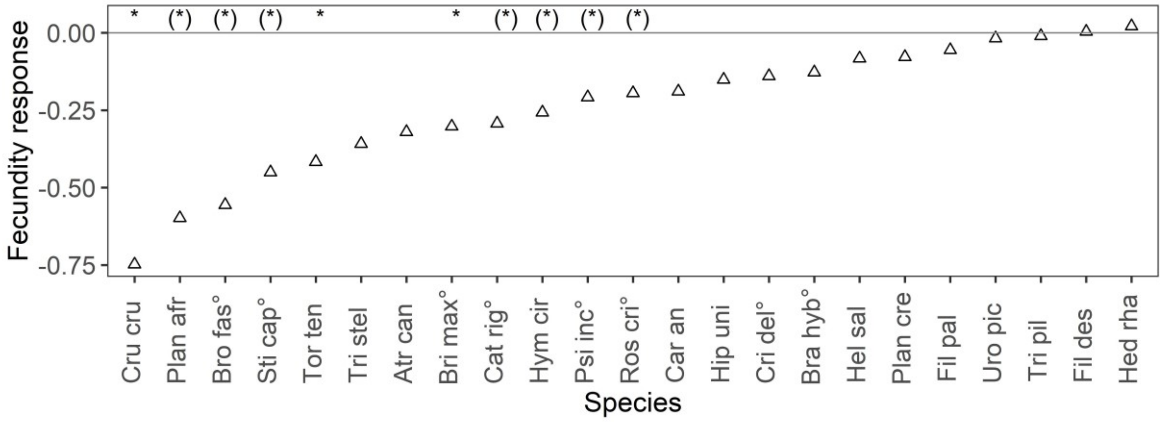

**Figure 2.** Fecundity responses to simulated grazing (clipping) of 23 winter annual species. Asterisks indicate significant differences between clipped and control plants within a species based on single t-tests; * remained significant after Holm-Bonferroni correction. Species' fecundity responses did not differ between grasses and forbs (Kruskal-Wallis-test: $Chi^2 = 1.4$, $p = 0.25$; ° indicates grasses). Species were ordered according to their fecundity response, see Table S1 for species abbreviations.

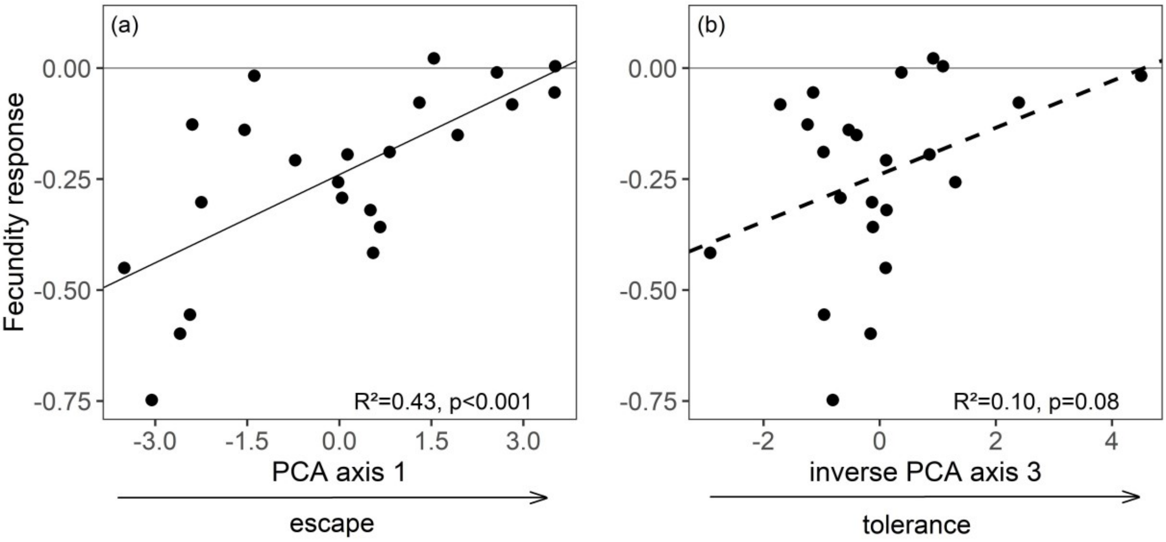

**Figure 3.** Relation between fecundity responses to simulated grazing and species' positions along the (a) escape axis (PCA axis 1) and (b) tolerance axis (inverse PCA axis 3). Significance (p-value) and R² values are given, see Table 3 for full statistical analyses.

Grazing in the field decreased the abundance of most of the species in both dry and moist slopes with an average reduction of species abundance by 30 % in grazed compared to ungrazed plots. Abundance responses varied significantly across species (Figure S2). Species' abundance responses in dry slopes were positively related to their scores along the escape axis (axis 1), i.e. species with pronounced escape traits exhibited lower abundance decreases in response to grazing (Figure 4, Table 3). In moist slopes, abundance responses were independent from species' scores along the escape (axis 1) or tolerance (inverse axis 3) axis (Figure 4, Table 3).

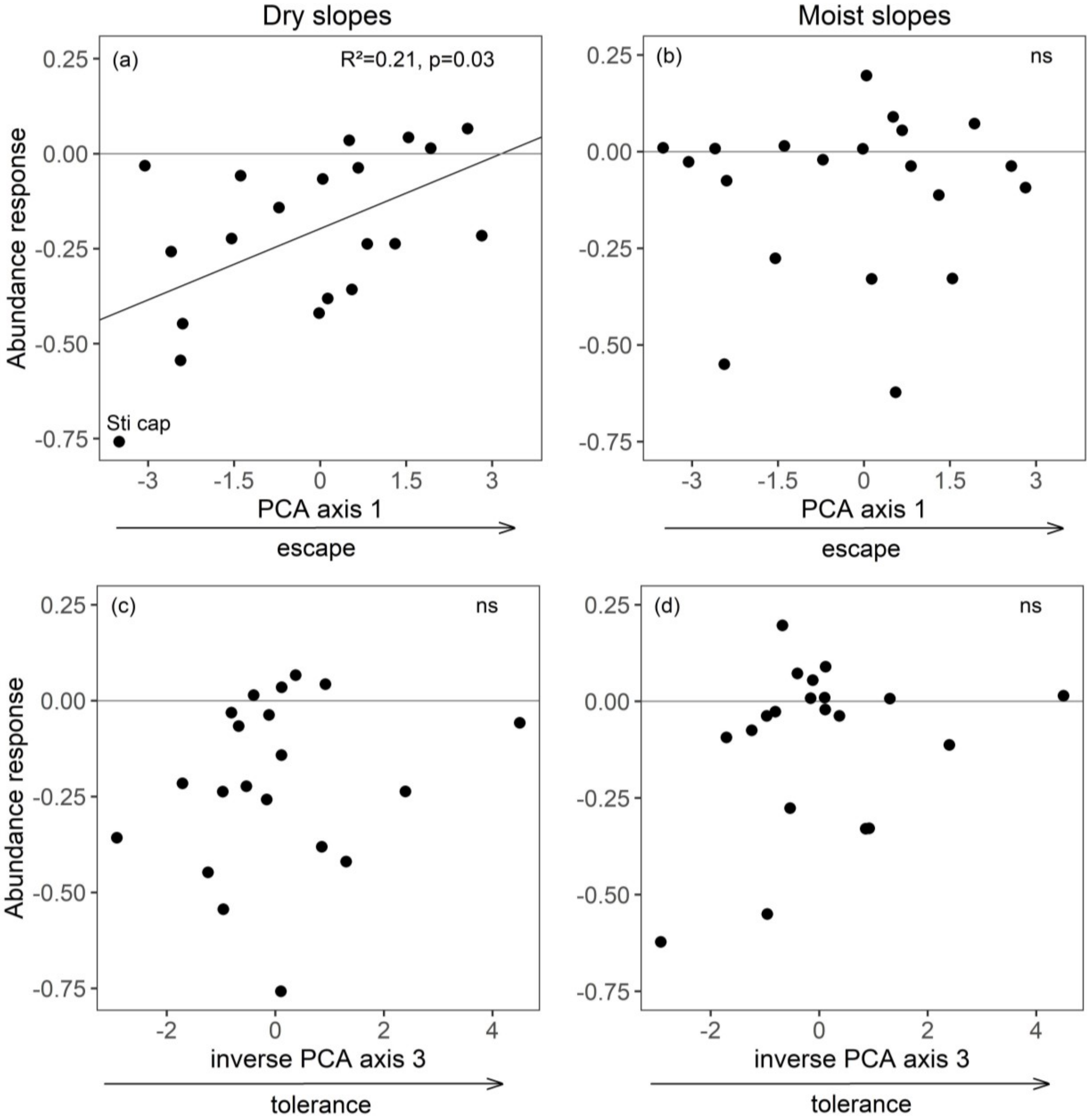

**Figure 4.** Relation between species' abundance responses to grazing in an exclosure experiment in the field and their positions along the escape axis (PCA axis 1) or tolerance axis (inverse PCA axis 3) (a, c) in dry (south-facing) slopes and (b, d) moist (north-facing) slopes. Significance (ns not significant) and R² values are given, see Table 3 for full statistical analyses. In (a) and (b) abundance responses were natural log-transformed for analyses, but not in the figure. In (a) the relation remained marginally significant without the extreme species, *Stipa capensis* (Sti cap) (see Table 3).

Different single traits were important (based on random forest) for the abundance responses to grazing in each slope (Figure S3). In dry slopes, reproductive mass fraction, height, total biomass, leaf dry matter content, toughness, and specific leaf area were assessed as important (Figure S3). Several of these traits were consistent with the escape strategy identified along axis 1. In moist slopes, only C:N ratio emerged as important (Figure S3). Correlations between abundance responses and single traits were not significant, except of a weak one with toughness (Table S3).

Neither species' scores along the escape axis (axis 1), tolerance axis (inverse axis 3), nor any of the 16 single traits were related to species' mean annual rainfall niche (Figure 5, Table 3, Table S3, Figure S4). Consistently, species' fecundity responses to simulated grazing were independent from their mean annual rainfall niche (Figure 5, Table 3, Figure S4).

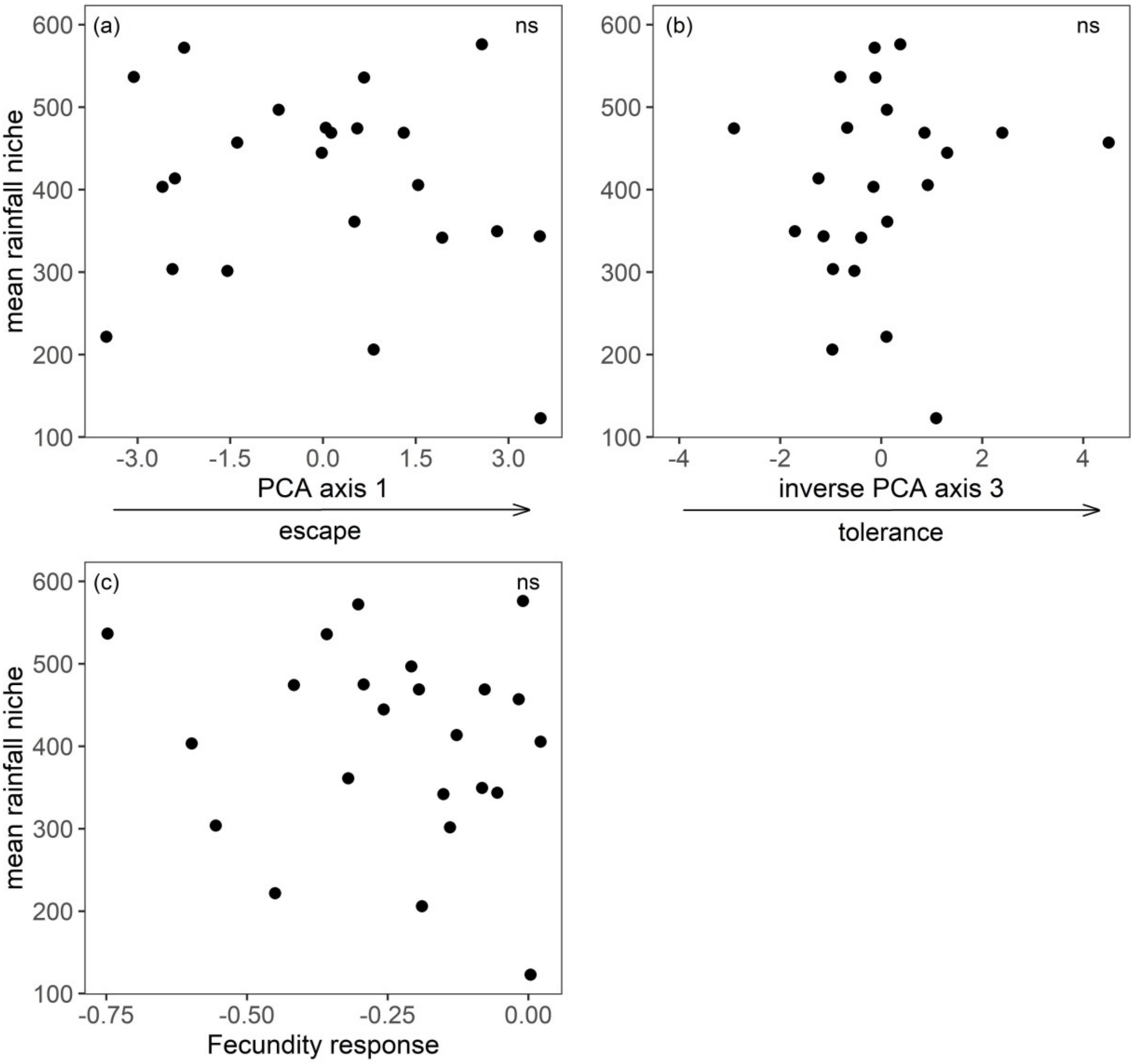

**Figure 5.** Relation between species' mean annual rainfall niche (i.e. species' distribution along the large-scale rainfall gradient) and their positions along the (a) escape axis (PCA axis 1), (b) tolerance axis (inverse PCA axis 3), or (c) their fecundity responses to (simulated) grazing. See Table 3 for full statistical analyses (ns not significant) and Figure S4 for species' entire distribution ranges along the rainfall gradient.

Species' scores along PCA axis 2 and PCA axis 4, which did not reflect the hypothesized grazing response strategies (see above), were unrelated with species' fecundity responses, abundance responses, or mean annual rainfall niche (Table 3). Thus, there is no indication that they represent previously unrecognized ecologically relevant strategies.

**Table 3.** Results of linear models separately testing the effect of species' positions along the trait axes (escape: PCA axis 1; tolerance: inverse PCA axis 3) on their fecundity responses to simulated grazing, their abundance responses to grazing in the field in dry and in moist slopes (south- and north-facing slopes, respectively), or on their mean annual rainfall niche (i.e. species' distribution along the rainfall gradient); and testing the relation between species' fecundity response and mean annual rainfall niche. In the linear models with species' scores along PCA axis 1 as explanatory variable, abundance responses in both slopes were natural log-transformed. 23 annual species were considered in the grazing simulation experiment ($F_{1,21}$) and 20 of these species were included in the grazing exclosure experiment ($F_{1,18}$). Responses significantly related to one of the trait axes are highlighted in bold. Species' positions along PCA axis 2 and 4 were not related to fecundity responses, abundance responses, or mean annual rainfall niche (all $p > 0.18$).

| Trait | F | p | $R^2$ |
|---|---|---|---|
| PCA axis 1 (escape axis) | | | |
| **Fecundity response** | 17.84 | < 0.001 | 0.43 |
| **Abundance response dry slopes**[a] | 5.94 | 0.025 | 0.21 |
| Abundance response moist slopes | 0.00 | 0.998 | -0.06 |
| Mean annual rainfall niche | 0.57 | 0.459 | -0.02 |
| inverse PCA axis 3 (tolerance axis) | | | |
| **Fecundity response** | 3.52 | 0.075 | 0.10 |
| Abundance response dry slopes | 0.70 | 0.413 | -0.02 |
| Abundance response moist slopes | 1.75 | 0.202 | 0.04 |
| Mean annual rainfall niche | 0.19 | 0.664 | -0.04 |
| Fecundity response | | | |
| Mean annual rainfall niche | 0.49 | 0.491 | -0.02 |

[a] Relation remained marginally significant ($F_{1,17} = 3.50$, $p = 0.079$, $R^2 = 0.12$) without species *Stipa capensis* (see Figure 4) with most negative abundance response.

## Discussion

Winter annuals exhibited two grazing response strategies, escape and to a lesser extent tolerance, reflected in lower fecundity declines of species with pronounced escape or tolerance traits under simulated grazing. In the field, only the escape but not the tolerance strategy was related with species' abundance responses. Lower abundance declines in species with pronounced escape traits in dry slopes indicate convergent small-scale favouring of escape traits by grazing and drought. However, grazing response strategies did not shift along large-scale rainfall gradients.

The identified escape strategy was overall consistent with the traits generally hypothesized to characterize annual species, including high seed dormancy, early flowering, small size (biomass and height), low root allocation, and high specific leaf area (see Grime, 1977; Levitt, 1980). However, independently of the escape strategy, several annuals exhibited a trait coordination characteristic for the tolerance strategy known from perennials (see Strauss & Agrawal, 1999), i.e. these annuals showed high compensation ability, high root allocation, high growth rate, low C:N ratio, and low leaf dry matter content. As expected, some of these traits are consistent with both grazing tolerance and escape, but the high compensation ability combined with high root allocation, and the lack of further characteristic escape traits (e.g. seed dormancy, early flowering, small size, see also Table 1) underline that this trait coordination reflects grazing tolerance. Interestingly, none of the trait coordinations along any PCA axes were consistent with the expected avoidance strategy despite substantial interspecific differences in avoidance traits (e.g. low height, high leaf dry matter content and toughness). However, we did not consider chemical defence traits, which might contribute to an avoidance strategy in annuals (Herms & Mattson, 1992). Nevertheless, the two identified strategies of grazing tolerance and escape challenge the classical view that annuals form a single, homogenous group of species escaping stress or disturbance (Grime, 1977; Kooyers, 2015).

Grazing escape and tolerance emerged as independent axes of trait coordinations and did not form the expected trade-off, i.e. they were not associated with the opposite sides of one axis. This implies that both strategies are not mutually exclusive (see Levitt, 1980). Instead, species ranged along a continuum from less to more pronounced escape and/or tolerance traits and can exhibit trait combinations pertaining to both strategies. Interestingly, both the tolerance and (to a lesser extent) the escape strategy encompassed high compensation ability, i.e. even species with pronounced escape traits, re-grew and reproduced after simulated grazing in the greenhouse. The unexpectedly high compensation ability of escapers despite their low root allocation (indicative of low resource storage) may be due to their low growth rates, which decrease the resources necessary to compensate tissue losses compared to fast-growing species (Hilbert et al., 1981). The association between escape traits and high compensation ability undermined our assumption of the hypothesized trade-off scenario, i.e. that species with a grazing escape strategy exhibit low compensation ability and thus experience high fitness losses when exposed to grazing.

Both pronounced escape and (although less strongly) tolerance traits minimized negative fitness responses to tissue loss through grazing, as shown by the positive relationship between species' positions along both trait axes and their fecundity responses to simulated grazing. Surprisingly, escape traits emerged as the dominant fitness-relevant strategy even when escape per se was experimentally precluded (i.e. tissue was removed before successful reproduction). High compensation ability, which was associated with both strategies (see above), and also positively correlated with fecundity responses as a single trait, likely mediated this relation. The relationship between species' trait combinations along the escape and tolerance axis and their fecundity responses indicate that both trait coordinations can influence fitness responses in annuals. Explicitly establishing this link is a prerequisite of trait-based ecology, since the direction and strength of interspecific trait-fitness response relations can vary across life-history strategies or biomes (Shipley et al., 2016). From an evolutionary point of view, it is clear that traits influence fitness differences of individuals within populations, but trait-based studies hardly addressed consequences of interspecific trait variation for differences in fitness responses across species (Shipley et al., 2016). Here, we closed this gap for trait combinations hypothesized to be mechanistically relevant for species' grazing responses in annuals. Working with annuals facilitated establishing this link, because it enabled us to assess fitness responses based on direct measurements of lifetime seed number and seed mass, a parameter hard to assess or even elusive in perennial species.

In the field, species' positions along the escape axis but not along the tolerance axis were related with their abundance responses to grazing. This finding indicates that traits can influence differences in species' abundance despite the multitude of factors and processes that influence species' regeneration and abundance in the field (e.g. microsite heterogeneity, biotic interactions, Boeken, 2018) and that may weaken trait-abundance relations. In dry slopes, species with pronounced escape traits exhibited lower abundance declines in response to grazing. This finding is consistent with the hypothesized convergence scenario that similar trait attributes enable both grazing and drought escape in annuals. Indeed, the grazing escape traits identified in our study (in combination with high reproductive allocation) have previously been shown to confer drought escape (e.g. Aronson et al., 1992; Aronson et al., 1993; Kurze et al., 2017; Tielbörger et al., 2012). We had presumed that the convergence scenario, i.e. the convergent filtering of escape traits by grazing and drought, might be most likely to emerge under grazing regimes where an escape strategy is viable, i.e. infrequent or late grazing. In contrast, we identified grazing escape as a successful strategy even in sites that are intensively grazed at the peak of the growing season (i.e. precluding successful escape). This discrepancy likely again relied on the unexpected high compensation ability of escapers (see above), enabling them to minimize fitness losses under intense grazing. This result from the field is also consistent with our finding in the greenhouse that escapers successfully withstand tissue loss. Additionally, pronounced seed dormancy of escapers should reduce negative impacts of grazing on species' abundance. The observed favouring of escape traits by grazing and drought in winter annuals corresponds to the generalised grazing model, which states convergent filtering by grazing and drought in perennials with respect to avoidance (Milchunas et al., 1988). Our results thus indicate that the generalised grazing model can be extended to annuals, but with respect to escape, which has pervasive implications for projecting consequences of global change in drylands.

The convergent favouring of escape traits by grazing and drought that emerged at the local scale was expected to be mirrored by a strategy shift along the large-scale rainfall gradients, i.e. grazing escapers should be associated with arid conditions, corresponding to the large-scale strategy shift expected by the generalized grazing model and observed in perennials (Adler et al., 2004; Díaz et al., 2007; Milchunas et al., 1988). However, the hypothesized filtering of strategies by grazing and drought was not reflected in species' large-scale distribution. Also, single grazing response traits were not related to species' distribution along the rainfall gradients. Instead, species with the whole range of weak to pronounced grazing escape and tolerance strategies occurred along the entire gradient, implying that alternative trait combinations are similarly successful under a wide range of rainfall conditions. This may be explained by the high temporal and spatial variability of grazing and rainfall in our study system (Sternberg et al., 2015; Tielbörger et al., 2014). Indeed, high inter-annual rainfall variability has been shown to facilitate the coexistence of species or strategies within plant communities, since each has an advantage (or disadvantage) in some years (Chesson et al., 2004). This effect might be increased by inter-annual variability of grazing. Filtering of strategies may also not have emerged along the large-scale rainfall gradients, since species' occurrences in our study system are strongly determined by small-scale hydrological differences, which are not captured by rainfall data (e.g. Kutiel, 1992), e.g. locally favourable conditions in riverbeds can enable drought-sensitive species to occur in arid areas. The restriction to presence/absence data at the large-scale may have additionally obscured changes in species abundance. However, ecological filtering of traits has been documented along large-scale rainfall gradients based on occurrences in this and other ecosystems (Griffin-Nolan et al., 2019; Kurze, Engelbrecht et al., 2021; Thuiller et al., 2004). Any potentially overseen large-scale shift of grazing response strategies in annuals should thus be weak.

Our study explicitly focused on interspecific trait coordinations and their relevance for species' differential fitness and abundance responses, and ecological filtering. If and to what extent trait expression of individuals in the natural habitat may weaken or strengthen such interspecific relations remains an important aspect for further studies (Yang et al., 2021). However, intraspecific variation is unlikely to override the observed (or missing) interspecific relations, since it is usually lower than interspecific variation (Kazakou et al., 2014; Siefert et al., 2015). This especially applies to steep environmental gradients and species-rich communities (Siefert et al., 2015), as we investigated here, and it has also been shown in our study species (L. Álvarez-Cansino et al. unpublished data).

The co-occurrence of annuals with a wide range of grazing escape and tolerance traits along the large-scale rainfall gradient and their overall high grazing resistance are likely due to the long grazing history combined with the high temporal and spatial variability of rainfall and grazing in the Middle East (Noy-Meir & Seligman, 1979; Tielbörger et al., 2014). Under climate change, more intense drought events and a decreasing frequency of wet years (Smiatek et al., 2011) may nevertheless favour species with pronounced grazing escape traits that convergently confer high resistance to drought. Increasing abundance of escapers may lead to a decrease of forage quantity for livestock, since they produce less biomass and exhibit a shorter life cycle than tolerators. Interacting effects of intensified drought and grazing under global change will thus likely affect community composition and decrease economically important ecosystem services in areas dominated by winter annuals.

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## Author contributions

BMJE, LA, MCB, KT, and SK conceived the ideas and designed the study. SK coordinated and conducted the plant traits measurements and the grazing simulation experiment, MCB the seed dormancy assessments, and RP, KT, and SB the grazing exclosure experiments; SK analysed the data and wrote the manuscript with contributions by BMJE. All co-authors revised and commented subsequent drafts of the manuscripts and gave final approval for publication.

## Accessibility of the data

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.vhhmgqnt3 (Kurze, Bilton et al., 2021).

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# Supporting Information

**Table S1.** List of the 23 study species from the Middle East with their abbreviation and family.

**Method S1.** Details on trait measurements.

**Figure S1.** Schematic overview of the experimental design of the grazing exclosure experiment in Jordan in one site.

**Method S2.** Linear mixed models for determining species' differences in abundance responses.

**Method S3.** Random forest to assess the importance of single traits for species' abundance responses.

**Table S2.** Summary statistics for the 16 traits hypothesized to influence grazing responses (see Table 1) in the 23 annual species.

**Table S3.** Correlation matrix based on Spearman rank correlation coefficients.

**Figure S2.** Abundance responses to grazing of 20 annual species in a grazing exclosure experiment in (a) dry (south-facing) slopes and (b) moist (north-facing) slopes in Jordan.

**Figure S3.** Importance of the 16 traits hypothesized to influence grazing responses (see Table 1) and of species' fecundity responses to simulated grazing for species' abundance responses in (a) dry (south-facing) slopes and (b) moist (north-facing) slopes in a grazing exclosure experiment in Jordan.

**Figure S4.** Relation between species' annual rainfall niche (i.e. species' distribution along the large-scale rainfall gradient) and their positions along the (a) escape axis (PCA axis 1), (b) tolerance axis (inverse PCA axis 3), or (c) their fecundity responses to (simulated) grazing.

**Table S1.** List of the 23 study species from the Middle East with their abbreviation and family. Species were ordered alphabetically. * indicates the three species, which were not recorded in the grazing exclosure experiment.

| Species name | Abbreviation | Family |
|---|---|---|
| *Atractylis cancellata* | Atr can | Asteraceae |
| *Brachypodium hybridum s.l.* | Bra hyb | Poaceae |
| *Briza maxima** | Bri max | Poaceae |
| *Bromus fasciculatus* | Bro fas | Poaceae |
| *Carrichtera annua* | Car an | Brassicaceae |
| *Catapodium rigidum* | Cat rig | Poaceae |
| *Crithopsis delileana* | Cri del | Poaceae |
| *Crupina crupinastrum* | Cru cru | Asteraceae |
| *Filago desertorum** | Fil des | Asteraceae |
| *Filago palaestina** | Fil pal | Asteraceae |
| *Hedypnois rhagadioloides* | Hed rha | Asteraceae |
| *Helianthemum salicifolium* | Hel sal | Cistaceae |
| *Hippocrepis unisiliquosa* | Hip uni | Fabaceae |
| *Hymenocarpos circinnatus* | Hym cir | Fabaceae |
| *Plantago afra* | Plan afr | Plantaginaceae |
| *Plantago cretica* | Plan cre | Plantaginaceae |
| *Psilurus incurvus* | Psi inc | Poaceae |
| *Rostraria cristata* | Ros cri | Poaceae |
| *Stipa capensis* | Sti cap | Poaceae |
| *Torilis tenella* | Tor ten | Apiaceae |
| *Trifolium pilulare* | Tri pil | Fabaceae |
| *Trifolium stellatum* | Tri stel | Fabaceae |
| *Urospermum picroides* | Uro pic | Asteraceae |

## Method S1. Details on trait measurements

Plants for the trait measurements were grown in the greenhouse in Bayreuth (Germany) during winter 2017/2018 (start at the end of September) except for growth rate (winter 2018/2019) and seed dormancy (greenhouse in Tübingen in winter 2013/2014; see details below).

*Seed dormancy* (Dormancy) was determined for field-collected seeds (over-summered in screenhouses in Israel) following an established protocol (Tielbörger et al., 2012). Germination trials were conducted on moistened filter paper in Petri dishes with 14-18 seeds of each species (*Plantago cretica* with 32 seeds) replicated 13-15 times. Germinated seeds were counted and removed every two days. The proportion of germinated seeds after two weeks was averaged across all Petri dishes per species. Germination tests (including a treatment with gibberellic acid) in the following year (M. C. Bilton, unpublished data), as well as previous experiments on our study species (Tielbörger et al., 2012; Lampei et al., 2017) indicated that ungerminated seeds were dormant instead of inviable. Seed dormancy was thus defined as the proportion of ungerminated seeds (1 - germination proportion). This measure of seed dormancy has been shown to be related with species' site-specific risk of reproductive failure under natural conditions (Tielbörger et al., 2012).

*Onset of flowering* (Flowering) was assessed as the number of days between germination and the first appearance of reproductive organs (checked daily and every second day, respectively). *Leaf number at flowering start* (Leaves flower) was counted as a non-destructive assessment of plant size at reproduction onset.

*Leaf area* (LA) of individual leaves was measured with an Area-meter (Model LI 3100, Li-Cor Bioscience, Lincoln, NE, USA). For *specific leaf area* (SLA = LA/DW) and *leaf dry matter content* (LDMC = DW/FW) the saturated fresh weight (FW) of the leaves was determined after hydration overnight (app. 15 hours) and the dry weight (DW) after 48 h in a drying oven at 70°C. LA, SLA and LDMC were usually determined for two or three leaves per individual and averaged. *Leaf toughness* (Toughness), i.e. the physical strength of a leaf as force to punch, was measured with Linear Push/Pull Scales (Amatek Chatillon®, Florida, USA, two types 516-0500M [5 g precision] and 516-1000M [10 g precision]) in three points in the centre of one fully hydrated leaf per individual avoiding the midrib and primary veins, and averaged. The four leaf traits were measured 21-23 weeks after sowing on randomly selected, mature, healthy leaves.

*Maximum photosynthetic rate* ($A_{max}$) was measured with an infra-red gas analyser (Li-Cor 6400, Li-Cor, Lincoln, NE, USA). Measurements were taken between 8.30 a.m. and 11.00 a.m. at a light intensity of 2000 µmol photons/($m^2$ * s) (based on light response curves for a species subset), 25°C, and 400 ppm $CO_2$. If the leaf did not fill the measurement chamber, photosynthetic rate was re-calculated based on leaf area measurements with an Area Meter (see above). Usually, one leaf per individual was measured, but in species with very small or thin leaves (e.g. a few grasses, *Filago*, *Helianthemum*) several leaves were jointly arranged in the chamber. $A_{max}$ was determined 8-12 weeks after sowing.

The *C:N ratio* (C:N, weight-based carbon to nitrogen ratio) was determined for the leaves used in photosynthesis measurements (few exceptions in *Psilurus incurvus*, *Rostraria cristata*) with an EA-IRMS coupling (Elemental Analyzer NA 1108, CE Instruments, Milan, Italy; Interface ConFlo III, Finnigan MAT, Bremen, Germany; Isotope ratio mass spectrometer: delta S, Finnigan MAT, Bremen, Germany).

*Plant height* (Height) was measured at the end of the life cycle (start of leaf senescence) as the distance between soil surface and the highest point of the plant.

*Total biomass* and its allocation were assessed at the end of the life cycle. Plants were harvested, roots washed and the aboveground biomass separated into leaves, stems, fruits and further reproductive biomass (e.g. flowering stems, remaining parts of the inflorescence etc., plants were wrapped in organza to avoid loss of reproductive biomass). All plant organs were oven-dried at 50°C for five days except fruits, which were air-dried for two weeks (25-30°C) to avoid seed damage. Biomass allocation (*leaf*, *root*, and *reproductive mass fraction*, Leaf MF, Root MF, Rep. MF) was calculated as the proportion of the respective plant organ weight on total biomass (total seed weight was used for reproductive mass fraction).

*Absolute growth rate* (AGR) in the vegetative stage was measured over the first 16 weeks after sowing, i.e. before the peak of flowering when all species still exhibited substantial vegetative growth. Absolute growth rate was calculated as biomass increase per day, i.e. total harvested above- and belowground biomass divided by the number of days between germination and harvest.

Assessments were done for 20 species in a separate set of plants grown under similar conditions (see Plant cultivation) in winter 2018/19. Absolute growth rates for the additional three species (*Trifolium pilulare*, *Trifolium stellatum*, *Hymenocarpus circinnatus*) were extrapolated based on their growth period for total biomass at the end of their life cycle. Absolute growth rate and total biomass (see above) were only weakly positively correlated, since the period of vegetative growth differed between species.

*Compensation ability*, i.e. the ability to re-grow after simulated grazing (clipping), was determined as the standardized difference of total biomass of clipped compared with unclipped plants in each species in the grazing simulation experiment: Compensation ability = mean (log (Tot. $\text{biomass}_{\text{clipped}}$)) – mean (log (Tot. $\text{biomass}_{\text{control}}$)). The formular for compensation ability is equivalent to the widely used response ratio (Hedges et al., 1999; see details in grazing simulation experiment), except we natural log-transformed Tot. biomass before calculating the mean for each treatment (clipped *vs*. control), since data were not normally distributed. As in response ratios, less negative values indicate higher compensation ability, and positive values indicate overcompensation. We assessed compensation ability at the species rather than the individual level. Nevertheless, it can be considered as trait measurable at the individual level (see also seed dormancy).

*Total seed weight* (TSW, i.e. fecundity) was determined for each individual as the product of seed (or fruit) number and seed (or fruit) mass, depending on morphology and family. It was assessed as total seed weight in Cistaceae and Plantaginaceae, as total fruit weight in legumes, Apiaceae, Asteraceae, and Brassicaceae, and as spikelet weight in grasses, if they were dense and hardly contained any further biomass except of seeds, glumes, and awns. In four grasses (*Briza maxima*, *Crithopsis delileana*, *Psilurus incurvus*, *Stipa capensis*) seeds with their glumes and awns were removed from the infructescence to determine total seed weight. Total seed weight was used for calculating species' fecundity responses to simulated grazing (see grazing simulation experiment in the greenhouse).

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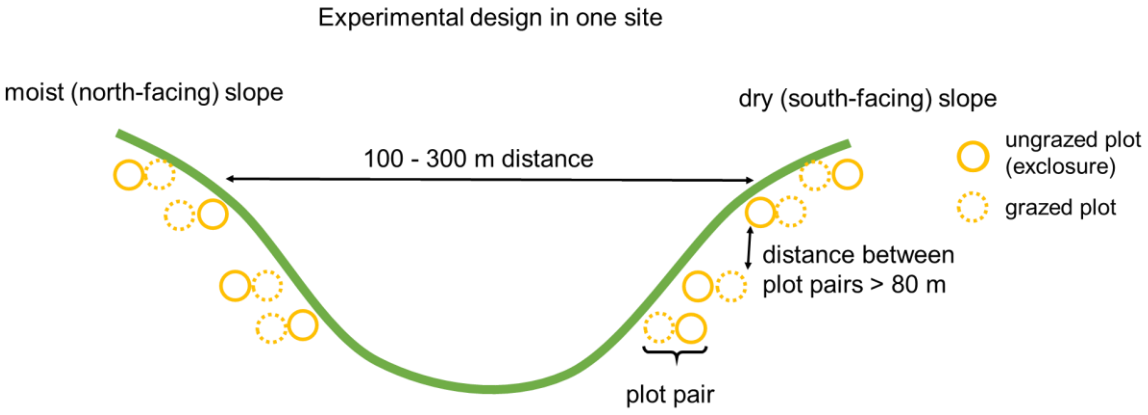

**Figure S1.** Schematic overview of the experimental design of the grazing exclosure experiment in Jordan. Shown is one of four replicated sites. Eight plot pairs were installed in each site, four on a south-facing and four on a north-facing slope (dry and moist slope, respectively) at similar elevation. Each plot pair included one ungrazed (fenced) and one grazed (unfenced) plot. Species abundance was recorded in six randomly located permanent quadrates in each plot in each spring. Our analyses of species' abundance responses to grazing in each slope focused on differences within plot pairs (grazed *vs*. ungrazed) averaged within each slope across all plot pairs, years, and sites (for details see grazing exclosure experiment in the field).

## Method S2. Linear mixed models for determining species' differences in abundance responses

Species' differences in abundance responses to grazing in each slope (dry *vs*. moist slope) were analysed with separate linear mixed models (package lme4, Bates et al., 2014). For this analysis, species' abundance responses in the plot pairs were not averaged among sites and years for each slope (see Grazing exclosure experiment in the field), but calculated for each year in each site by averaging the abundance responses of the four plot pairs (installed in each site per slope) in each year. Each linear mixed model included species as fixed explanatory variable, and site and year as random factors. The significance of the species effect was tested with a Wald F-test, the calculation of the degrees of freedom and appropriate p-values followed the Kenward-Roger approximation (packages lmertest, Kuznetsova et al., 2014; package pbkrtest, Halekoh & Højsgaard, 2014), and the proportion of explained variance by the fixed explanatory variable (marginal $R^2$, $R^2m$) was calculated according to Nagakawa and Schielzeth (2013) (package MuMIn, Barton, 2015).

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### Method S3. Random forest to assess the importance of single traits for species' abundance responses

We assessed the importance of single traits and fecundity response for species' abundance responses to grazing in each slope (dry *vs*. moist slope) with a random forest algorithm, which allows the identification of explanatory variables in datasets with small sample size and large number of explanatory variables (Breimann, 2001; Strobl et al., 2007; Strobl et al., 2008).

Random forest combines many binary decision trees based on several bootstrap samples and chooses a random subset of explanatory variables for each tree (Genuer et al., 2010). The decision trees aim to partition a sample in subsamples to reduce variation based on a threshold value for a certain explanatory variable. This searching and partitioning approach is recursively continued until no better split emerges (Breiman, 2001). The importance value specifies the contribution of each explanatory variable separately and in multivariate interactions to changes in the prediction accuracy of the response, when the variable is randomly permuted, while others are left unchanged (Genuer et al., 2010; Liaw & Wiener, 2002; Strobl et al., 2007). The fit of the tree and the variable importance are assessed based on the data, which are not included in the bootstrap sample (Breiman, 2001). Accordingly, cross-validation with external data is not necessary (Wei et al., 2010).

We calculated 1000 conditional trees to account for correlated variables (package party, Hothorn et al., 2006; Strobl et al., 2007; Strobl et al., 2008). Each single tree based on five explanatory variables. The minimum number of observations per node necessary for splitting was five, and the minimum number of observations in each terminal node was three. We considered different values for the number of preselected explanatory variables, the minimum number of observations in each node and necessary for splitting, but the qualitative results hardly changed. Variable importance was calculated based on area-under-the-curve (AUC) estimation (Janitza et al., 2013).

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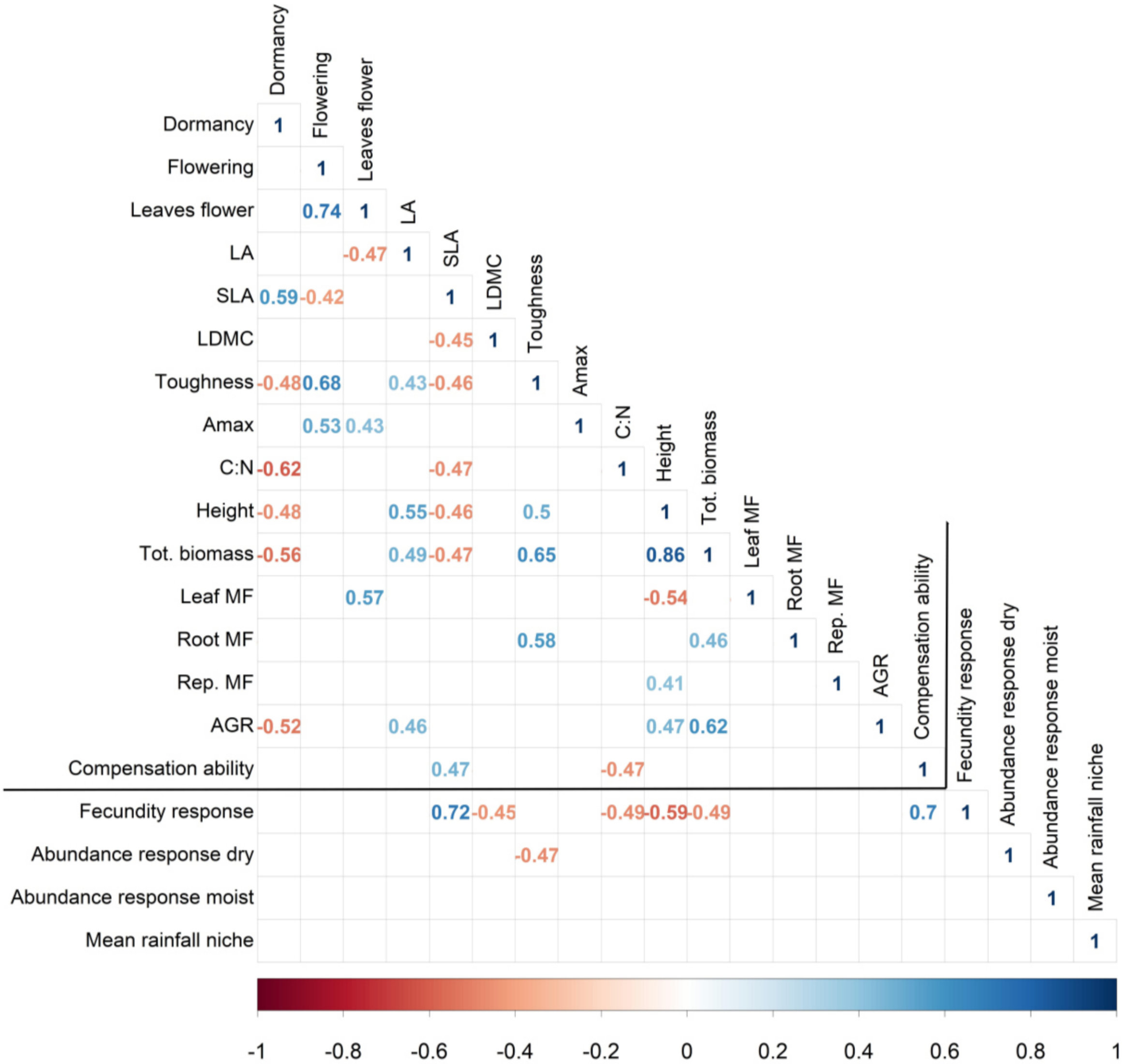
**Table S2.** Summary statistics for the 16 traits hypothesized to influence grazing responses (see Table 1) in the 23 annual species with mean ± standard deviation (std), minimum (Min) and maximum (Max) species' mean, and x-fold variation (Var) across species (Var = Max/Min). Additionally, results of linear models testing for species' differences in each trait are given (den. d.f., F-value, p-value and $R^2$). For seed dormancy, species' differences were tested with a generalised linear model with logit-link function, i.e. the F-value corresponds to a $Chi^2$-value (presented in italics). Numerator degrees of freedom were 22 for all traits (except of growth rate with 19), but denominator degrees of freedom (den. d.f.) varied between traits due to different sample sizes. Species' differences in all traits remained significant under strict Bonferroni correction of significance level to $p < 0.0033$ for 15 separate tests (traits). For trait abbreviations and units see Table 1.

| Trait | Mean ± std | Min | Max | Var | den. d.f. | F | p | $R^2$ |
|---|---|---|---|---|---|---|---|---|
| Dormancy | 0.63 ± 0.27 | 0.07 | 0.97 | 14 | - | *1848.7* | < 0.001 | 0.81 |
| Flowering | 107 ± 32 | 59 | 165 | 3 | 204 | 22.03 | < 0.001 | 0.67 |
| Leaves flower | 74 ± 87 | 12 | 418 | 34 | 204 | 22.58 | < 0.001 | 0.68 |
| LA | 6.4 ± 9.5 | 0.3 | 47.2 | 149 | 285 | 161.59 | < 0.001 | 0.92 |
| SLA | 37.5 ± 16.9 | 18.6 | 93.7 | 5 | 285 | 59.32 | < 0.001 | 0.81 |
| LDMC | 150.7 ± 50.9 | 86.5 | 250.7 | 3 | 286 | 71.06 | < 0.001 | 0.83 |
| Toughness | 0.30 ± 0.09 | 0.16 | 0.54 | 3 | 282 | 12.61 | < 0.001 | 0.46 |
| $A_{max}$ | 15.0 ± 4.7 | 7.9 | 25.6 | 3 | 243 | 7.96 | < 0.001 | 0.37 |
| C:N | 13.4 ± 3.1 | 8.7 | 19.0 | 2 | 139 | 2.58 | < 0.001 | 0.18 |
| Height | 57.7 ± 34.2 | 11.6 | 132.4 | 11 | 314 | 91.49 | < 0.001 | 0.86 |
| Tot. biomass | 12.7 ± 8.0 | 1.1 | 29.6 | 27 | 314 | 54.96 | < 0.001 | 0.78 |
| Leaf MF | 0.23 ± 0.09 | 0.09 | 0.53 | 6 | 314 | 22.54 | < 0.001 | 0.59 |
| Root MF | 0.07 ± 0.04 | 0.03 | 0.16 | 6 | 314 | 15.67 | < 0.001 | 0.49 |
| Rep. MF | 0.29 ± 0.16 | 0.02 | 0.59 | 26 | 312 | 49.49 | < 0.001 | 0.76 |
| AGR | 0.018 ± 0.011 | 0.002 | 0.048 | 27 | 156 | 24.46 | < 0.001 | 0.72 |
| Compensation ability | -0.38 ± 0.32 | -0.98 | 0.07 | - | - | - | - | - |

**Table S3.** Correlation matrix based on Spearman rank correlation coefficients including the 16 traits hypothesized to influence grazing responses (Table 1), as well as species' fecundity responses to simulated grazing, the abundance responses to grazing in the exclosure experiment in dry and moist slopes (south- and north-facing slopes, respectively), and mean annual rainfall niche (i.e. species' distribution along the rainfall gradient). Fecundity responses, abundance responses, and mean annual rainfall niche are separated by lines. 23 annual species were considered in the trait measurements in the greenhouse (except of growth rate N = 20), and 20 of these species were included in the grazing exclosure experiment. Only correlation coefficients with $p < 0.05$ are shown. For trait abbreviations see Table 1.



| | Dormancy | Flowering | Leaves flower | LA | SLA | LDMC | Toughness | Amax | C:N | Height | Tot. biomass | Leaf MF | Root MF | Rep. MF | AGR | Compensation ability | Fecundity response | Abundance response dry | Abundance response moist | Mean rainfall niche |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Dormancy | 1 | | | | | | | | | | | | | | | | | | | |
| Flowering | | 1 | | | | | | | | | | | | | | | | | | |
| Leaves flower | | 0.74 | 1 | | | | | | | | | | | | | | | | | |
| LA | | | -0.47 | 1 | | | | | | | | | | | | | | | | |
| SLA | 0.59 | -0.42 | | | 1 | | | | | | | | | | | | | | | |
| LDMC | | | | | -0.45 | 1 | | | | | | | | | | | | | | |
| Toughness | -0.48 | 0.68 | | 0.43 | -0.46 | | 1 | | | | | | | | | | | | | |
| Amax | | 0.53 | 0.43 | | | | | 1 | | | | | | | | | | | | |
| C:N | -0.62 | | | | -0.47 | | | | 1 | | | | | | | | | | | |
| Height | -0.48 | | | 0.55 | -0.46 | | 0.5 | | | 1 | | | | | | | | | | |
| Tot. biomass | -0.56 | | | 0.49 | -0.47 | | 0.65 | | | 0.86 | 1 | | | | | | | | | |
| Leaf MF | | | 0.57 | | | | | | | -0.54 | | 1 | | | | | | | | |
| Root MF | | | | | | | 0.58 | | | | 0.46 | | 1 | | | | | | | |
| Rep. MF | | | | | | | | | | 0.41 | | | | 1 | | | | | | |
| AGR | -0.52 | | | 0.46 | | | | | | 0.47 | 0.62 | | | | 1 | | | | | |
| Compensation ability | | | | | 0.47 | | | | -0.47 | | | | | | | 1 | | | | |
| Fecundity response | | | | | 0.72 | -0.45 | | | -0.49 | -0.59 | -0.49 | | | | | 0.7 | 1 | | | |
| Abundance response dry | | | | | | | -0.47 | | | | | | | | | | | 1 | | |
| Abundance response moist | | | | | | | | | | | | | | | | | | | 1 | |
| Mean rainfall niche | | | | | | | | | | | | | | | | | | | | 1 |

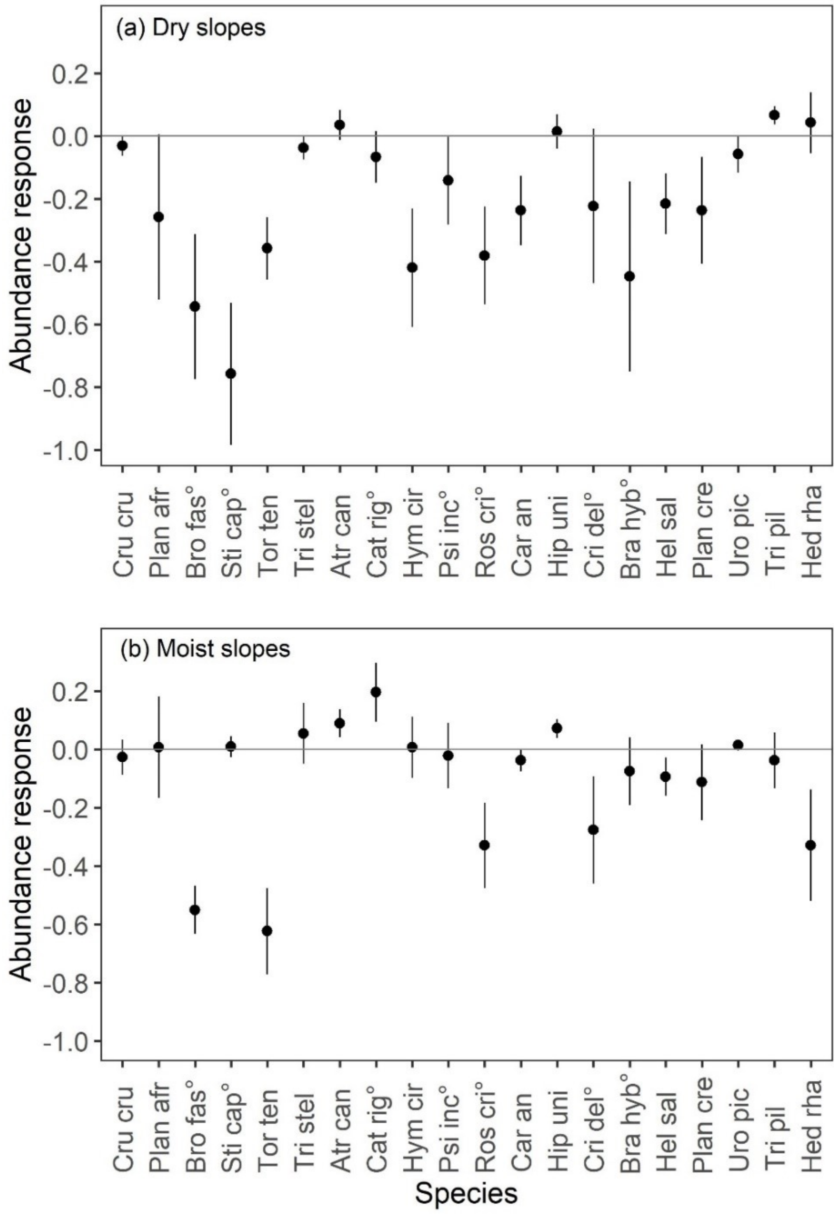


**Figure S2.** Abundance responses (mean ± 1 standard error) to grazing of 20 annual species (° indicates grasses) in a grazing exclosure experiment in (a) dry (south-facing) slopes and (b) moist (north-facing) slopes in Jordan (see Figure S1). Species were ordered according to their fecundity response to simulated grazing in the greenhouse experiment (see Figure 2). Abundance responses differed between species in dry and moist slopes (dry slopes: $F_{19,215} = 2.09$, $p = 0.006$, $R^2m = 0.13$; moist slopes: $F_{19,215} = 3.62$, $p < 0.001$, $R^2m = 0.22$) and they were more negative in grasses than forbs in dry slopes (Kruskal-Wallis test: $Chi^2 = 4.7$, $p = 0.03$), but independent from life form in moist slopes ($Chi^2 = 0.5$, $p = 0.50$).

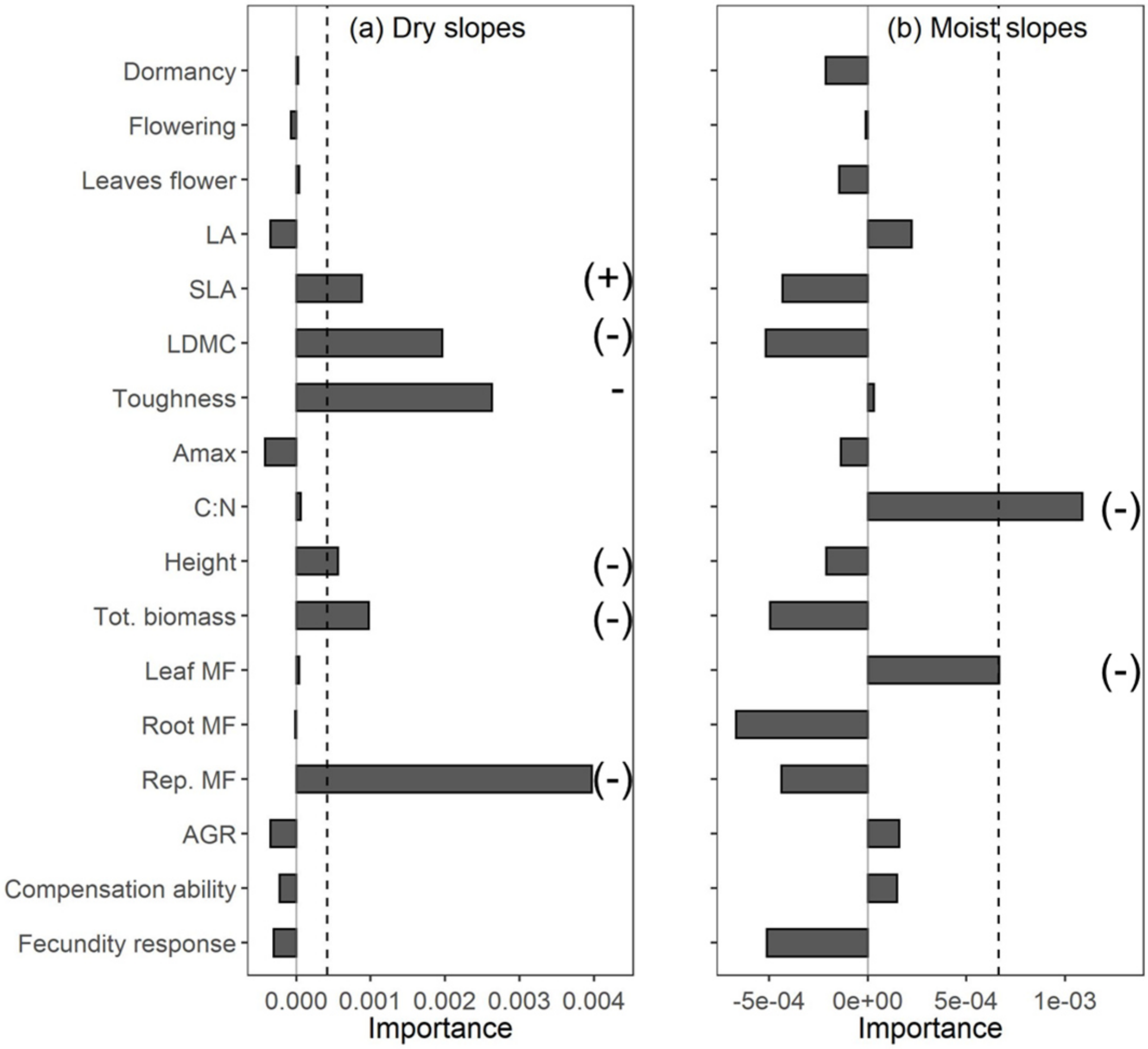


**Figure S3.** Importance of the 16 traits hypothesized to influence grazing responses (see Table 1) and of species' fecundity responses to simulated grazing for species' abundance responses in (a) dry (south-facing) slopes and (b) moist (north-facing) slopes in a grazing exclosure experiment in Jordan. Importance values were based on a random forest algorithm. Traits with values higher than the dashed, vertical line (corresponding to the maximum random noise in the dataset) were classified as important (see Holmes et al., 2015). Directions were derived from Spearman rank correlation coefficients: + indicates positive relation between explanatory variable and abundance response, – indicates a negative relation between explanatory variable and abundance response, () indicates that correlation was not significant. Note that variable importance values are useful to compare relative trait contributions within a data set, but cannot be compared across data sets.

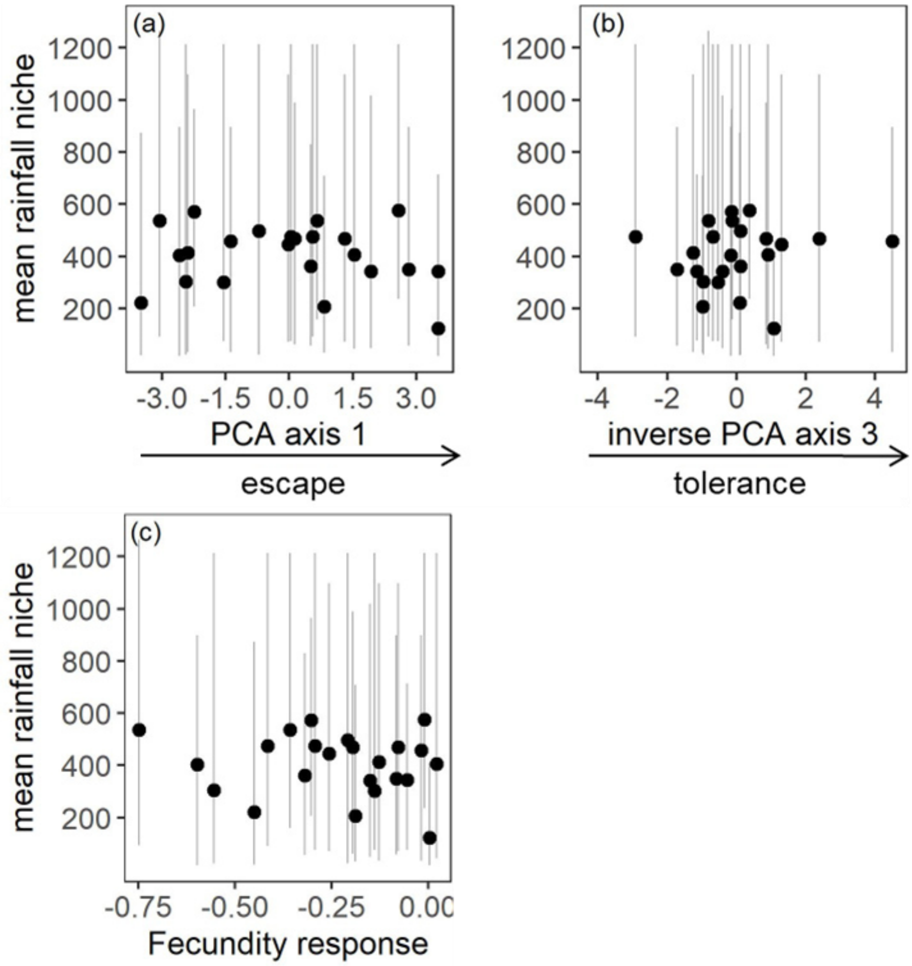


**Figure S4.** Relation between species' annual rainfall niche (i.e. species' distribution along the large-scale rainfall gradient) and their positions along the (a) escape axis (PCA axis 1), (b) tolerance axis (inverse PCA axis 3), or (c) their fecundity responses to (simulated) grazing. The lines reflect the distribution range (minimum to maximum annual rainfall niche), and the points the mean annual rainfall niche of each species. Relations with the mean (see Figure 5) as well as with the minimum and maximum annual rainfall niche were not significant.

## Reference

Holmes, N. D., Griffiths, R., Pott, M., Alifano, A., Will, D., Wegmann, A. S., & Russell, J. C. (2015). Factors associated with rodent eradication failure. *Biological Conservation, 185,* 8–16. http://dx.doi.org/10.1016/j.biocon.2014.12.018

# Manuscript 3:

# Rethinking the plant economics spectrum for annuals - a multi-species study

**Susanne Kurze[1*], Bettina M. J. Engelbrecht[1,2], Mark C. Bilton[3,4], Katja Tielbörger[4], Leonor Álvarez-Cansino[1]**

[1] University of Bayreuth, Functional and Tropical Plant Ecology, Bayreuth Centre of Ecology and Environmental Research (BayCEER), Universitätsstraße 30, 95447 Bayreuth, Germany

[2] Smithsonian Tropical Research Institute, Apartado 0843-03092, Balboa, Ancón, Panama

[3] Namibia University of Science and Technology (NUST), Department of Agriculture and Natural Resources Sciences, 13 Jackson Kaujeua Street, Private Bag 13388, Windhoek, Namibia

[4] University of Tübingen, Plant Ecology Group, Institute of Evolution and Ecology, Auf der Morgenstelle 5, 72076 Tübingen, Germany

* Corresponding author

Susanne.Kurze@uni-bayreuth.de

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Annual species, Drylands, Growth rate, Life-history strategy, Leaf structure, Rainfall gradient, Resource-use strategy, Root morphology

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## Abstract

The plant economics spectrum hypothesizes a correlation among resource-use related traits along one single axis, which determines species' growth rates and their ecological filtering along resource gradients. This concept has been mostly investigated and shown in perennial species, but has rarely been tested in annual species. Annuals evade unfavourable seasons as seeds and thus may underlie different constraints, with consequences for interspecific trait-trait, trait-growth and trait-environment relations. To test the hypotheses of the plant economics spectrum in annual species, we measured twelve resource-use related leaf and root traits in 30 winter annuals from Israel under controlled conditions. Traits and their coordinations were related to species' growth rates (for 19 species) and their distribution along a steep rainfall gradient. Contrary to the hypotheses of the plant economics spectrum, in the investigated annuals traits were correlated along two independent axes, one of structural traits and one of carbon gain traits. Consequently, species' growth rates were related to carbon gain traits, but independent from structural traits. Species' distribution along the rainfall gradient was unexpectedly neither associated with species' scores along the axes of carbon gain or structural traits nor with growth rate. Nevertheless, root traits were related with species' distribution, indicating that they are relevant for species' filtering along rainfall gradients in winter annuals. Overall, our results showed that the functional constraints hypothesized by the plant economics spectrum do not apply to winter annuals, leading to unexpected trait-growth and trait-rainfall relations. Our study thus cautions to generalize trait-based concepts and findings between life-history strategies. To predict responses to global change, trait-based concepts should be explicitly tested for different species groups.

# Introduction

Trait-based schemes, such as the plant economics spectrum, characterize general combinations and trade-offs among functional traits and their relations to environmental conditions (e.g. Grime, 1977; Westoby et al., 2002; Wright et al., 2004; Reich, 2014). They are widely used for assessing and predicting community assembly and ecosystem functioning under current and future conditions (e.g. Westoby et al., 2002; Wright et al., 2004; Reich, 2014). However, the plant economics spectrum has been mainly developed and tested for woody and perennial herbaceous species (reviewed in Reich, 2014), whereas investigations of this concept in annual species are virtually missing (but see Brouillette et al., 2014). The universality of the plant economics spectrum to reflect functional constraints and interspecific trait-environment relations across life-history strategies (annuals *vs*. perennials) therefore remains unclear.

Annual species substantially contribute to species diversity, primary production, and ecosystem services in many dryland ecosystems worldwide (Noy-Meir, 1973; Ruppert et al., 2015; Tielbörger et al., 2014). These ecosystems have been characterized as particularly vulnerable to global change (Sala et al., 2000; Schröter et al., 2005), underscoring the relevance of assessing and predicting species' responses to climate and land-use change. Environmental changes may affect annual plant communities even faster than perennial ones due to their short life cycle. Understanding interspecific trait-trait relations and the ecological filtering of annuals is therefore timely and of practical relevance.

The plant economics spectrum hypothesizes an interspecific trade-off between trait attributes conferring rapid resource acquisition (i.e. acquisitive or fast attributes, e.g. high assimilation rate and nutrient concentrations, low tissue density, Table 1) and those conserving resources (i.e. conservative or slow attributes, e.g. low assimilation rate and nutrient concentrations, high tissue density) at the whole plant level, i.e. among and within leaves, stems, and roots (Reich, 2014). Due to functional constraints to avoid resource shortage or excess, interspecific variation of resource-use related leaf, stem and root traits should thus be coordinated along one single axis of variation (Freschet et al., 2010; Reich, 2014).

According to the plant economics spectrum, the trade-off among resource-use related traits should influence species' growth rates and their ecological filtering along resource gradients (Reich, 2014). Species with acquisitive trait attributes should exhibit high growth rates under high resource availability, but exhibit low performance under resource-poor conditions because of their higher resource demand (Reich, 2014). In contrast, species with conservative trait attributes minimize performance losses under resource-poor conditions (i.e. they exhibit high stress resistance) but at the cost of lower growth rates (Reich, 2014). The resulting interspecific growth-stress resistance trade-off should lead to ecological filtering of species along resource gradients, with acquisitive/fast species predominating under high resource availability and conservative/slow species under low resource availability (Grime & Hunt, 1975; Reich, 2014).

**Table 1.** Studied resource-use related traits, and relative growth rate with their abbreviation (Abb.), unit, and hypothesized association with the resource-use strategy according to the plant economics spectrum. a and c, respectively, indicate whether a high trait value is considered to be associated with an acquisitive or conservative resource-use strategy as the opposite extremes along a continuum.

| Trait | Abb. | Unit | Association with resource-use strategy |
|---|---|---|---|
| Specific leaf area | SLA | $mm^2/mg$ | a |
| Leaf dry matter content | LDMC | mg/g | c |
| Leaf tissue density | LTD | $g/cm^3$ | c |
| Leaf thickness | Lthick | mm | c |
| Area-based photosynthetic rate | $A_{area}$ | $\mu mol/(m^2 * s)$ | a |
| Area-based nitrogen content | $N_{area}$ | $mg/mm^2$ | a |
| Mass-based photosynthetic rate | $A_{mass}$ | $\mu mol/(g * s)$ | a |
| Mass-based nitrogen content | $N_{mass}$ | mg/g | a |
| Mass-based carbon content | $C_{mass}$ | mg/g | c |
| Specific root length | SRL | m/g | a |
| Root tissue density | RTD | $g/cm^3$ | c |
| Root diameter | Rdia | mm | c |
| Relative growth rate | RGR | g/(g * day) | a |

The interspecific trait-trait, trait-growth and trait-environment relations expected by the plant economics spectrum have been demonstrated in woody and perennial herbaceous species from various ecosystems (reviewed in Reich, 2014). Only a few studies showed trait-trait or trait-environment relations deviating from the hypotheses of this concept (Baraloto et al., 2010; Fortunel et al., 2012; Kramer-Walter et al., 2016). However, these few studies are significant, because they indicate that the plant economics spectrum may not be universally applicable across different ecosystems, life forms, and/or life-history strategies.

In contrast to perennial species, annuals are characterized by early reproduction at small vegetative size, a short lifespan, high reproductive allocation, and especially annuals from drylands by a pronounced between-year seed dormancy, acting as bet-hedging mechanism against unpredictable reproductive failure (Grime, 1977; Kooyers, 2015; Philippi & Seger, 1989). Additionally, annuals have been assumed and shown to exhibit pronounced acquisitive trait attributes and high growth rates (Garnier & Laurent, 1994; Grime, 1977; Kooyers, 2015; Roumet et al., 2006). This trait combination enables them to evade unfavourable conditions in time, i.e. annuals exhibit an escape strategy (*sensu* Kooyers, 2015; Levitt, 1980). Although all annuals show this strategy, they differ in their trait attributes and occur in a wide range of environmental conditions (Bilton et al., 2016; Blumenthal et al., 2020; Li & Shipley, 2017). The consequences of annual's life history on interspecific trait-trait, and trait-growth relations, and on their ecological filtering along resource gradients, however, remain almost unexplored.

To our knowledge, interspecific studies testing the plant economics spectrum in annuals are missing. Intraspecifically, one study has addressed differences of resource-use related leaf traits along a rainfall and nutrient gradient in an annual desert forb (Brouillette et al., 2014). Populations showed the expected trait-trait correlations, but contrary to the assumptions of the plant economics spectrum, acquisitive trait attributes were associated with low resource availability (dry and nutrient-poor habitats) and conservative attributes with high resource availability (wetter, nutrient-rich habitats) (Brouillette et al., 2014). However, to rigorously test the applicability of the plant economics spectrum in annuals, we need multi-species studies that directly link comparative trait assessments across species with their growth rates and their distribution along resource gradients.

In the present study, we addressed this gap and tested interspecific trait-trait, trait-growth, and trait-environment relations in winter annuals from rangelands in Israel. Israel is characterized by a high diversity of annual species (Tielbörger et al., 2014) and by steep rainfall gradients, ranging from arid conditions (short growing season, low, unpredictable rainfall) to mesic-Mediterranean conditions (longer growing season, high, predictable rainfall). The region thus provides an ideal study system to investigate the variation of traits and growth rates across annual species, and to relate them to their distribution along rainfall gradients to assess species' ecological filtering.

Winter annuals grow and reproduce in the mild, rainy season (winter) and survive the dry, hot season (summer) as seeds, i.e. they escape the dry season. Accordingly in winter annuals, arid (i.e. resource poor) conditions should favour species with pronounced escape traits, which are considered to be associated with acquisitive trait attributes and high growth rates (see above, Grime, 1977; Kooyers, 2015). This trait combination should enable them to grow and reproduce within the short rainfall season. Towards the opposite, moist side of rainfall gradients, resource availability and competition intensity increase, but rainfall season is still interrupted by occasional dry spells (Noy-Meir, 1973; Schiffers & Tielbörger, 2006; Ziv et al., 2014). Under these conditions, annuals with sufficient drought resistance to withstand dry spells in the vegetative and reproductive phase should be favoured, since they can utilize the whole length of the growing season to attain larger heights for an increased competitive effect. Higher stress (drought) resistance is associated with conservative trait attributes and slow growth according to the hypotheses of the plant economics spectrum (Reich, 2014). Ecological filtering in winter annuals should favour species with acquisitive (instead of conservative) traits in arid conditions and species with conservative (instead of acquisitive) traits in more mesic Mediterranean conditions. The expected interspecific trait changes along rainfall gradients in winter annuals are thus opposite to the predictions of the plant economics spectrum and the patterns in perennials (Reich, 2014), but consistent with the findings on intraspecific trait variation in an annual forb (Brouillette et al., 2014).

In the present study, we measured twelve traits that are considered relevant for resource-use by the plant economics spectrum (Table 1) in 30 winter annual species from Israel under common, controlled conditions. We analysed trait-trait relations, as well as the relations of traits to species' growth rates (for 19 species) and to their distribution across a steep regional rainfall gradient. Specifically, we addressed the following hypotheses:

(1) Resource-use related leaf and root traits are correlated along one main axis of variation, reflecting a trade-off between acquisitive and conservative trait attributes.

(2) Species' growth rates are influenced by their trait combinations, i.e. their positions along the main trait axis. Species with acquisitive traits exhibit high growth rates, while species with conservative traits exhibit low growth rates.

(3) Species' distributions along a rainfall gradient are related with their trait combinations and growth rates. Fast-growing annuals with acquisitive traits are associated with arid conditions, whereas slow-growing species with conservative traits are associated with wetter conditions.

# Material and Methods

## Study system

Israel in the Eastern Mediterranean Basin comprises steep regional rainfall gradients from both east-west (across 50 km) and north-south (across 350 km) with high and more predictable mean annual rainfall (MAR) in mesic-Mediterranean areas in the north and west (up to 800 mm/year ± 18 %, mean ± CV) and less, very unpredictable rainfall in the desert in the south (20 mm/year ± 55 %) and towards the Dead Sea (east). The length of the rainfall season, which corresponds to the main growing season, as well as primary productivity and competition intensity decrease towards arid conditions, while average temperature hardly changes (Schiffers & Tielbörger, 2006; Tielbörger et al., 2014). The region is characterised by semi-arid shrublands with mostly winter annual species dominating the inter-shrub matrix. They account for up to 90 % of species diversity, and between 55-99 % of net primary production (Tielbörger et al., 2014).

## Study species and plant material

The study focused on 30 winter annual species comprising 22 forbs (including six legumes) and eight grasses (Table S1). Species selection considered the following criteria: (1) high abundance in the region, (2) inclusion of several plant families, (3) wide differences in their distribution along the rainfall gradients (based on BioGIS, 2018), and (4) seed availability. The 30 species belonged to 27 genera and seven families, and all had C3 photosynthesis. Seeds were collected in the mid-range of the regional rainfall gradient from natural habitats in two sites that are about 40 km apart from each other (Lahav, N 31°23' E 34°54', 300 mm MAR and Matta, N 31°42' E 35°3', 540 mm MAR; for details see Tielbörger et al., 2014) in April 2012. The sampling comprised at least 50 plants per species distributed in an area of 1.0-1.5 km$^2$.

The field-collected seeds were germinated and grown under common conditions with natural light and ample water supply in a greenhouse in Tübingen (Germany) during winter 2013/2014 to produce F1 seeds (inbred lines) with homogenized parental effects. F1 seeds were over-summered for two months (mid-June to mid-August) in a greenhouse in Bayreuth (Germany) to break summer dormancy before the start of the experiments (see Tielbörger et al., 2012). The plants for trait measurements were grown from F1 seeds under common conditions in a greenhouse in Bayreuth (Germany) during winter 2017/2018 (except for growth rate, grown in 2018/2019 under similar conditions). The comparative approach focused on trait differences across species, the level considered in the plant economics spectrum, and allowed to exclude intraspecific trait variation introduced by phenotypic plasticity or ecotypic differentiation.

## Plant cultivation in the greenhouse

Plants were germinated and grown in cylindrical pots (1 l volume, diameter 6.5 cm, depth 36 cm, Deepot Cells, Stuewe & Sons, Oregon, US) with a 1:1 mixture of sand and compost supplemented with 5 g of amorphous silicon (Aerosil 300, Evonik Industries AG, Essen, Germany). Temperature was set to 20-23°C in winter and 20-26°C in spring. Natural light was supplemented by artificial lights, and day length was adapted to natural variation in Israel for unbiased phenology. All plants received water in ample supply and were fertilized several times with Wuxal Super (NPK fertilizer 8-8-6, Wilhelm Haug GmbH & Co) to preclude nutrient limitation. The pots with the different species were randomly distributed in the greenhouse and rearranged every second week. Plants were grown until the end of their life cycle (31-34 weeks after sowing) indicated by leaf senescence in most of the species.

## Trait measurements

Twelve resource-use related traits, including leaf and root traits as well as structural and carbon gain related traits, were measured on 5-14 individuals per species (Table S2). Leaf traits were assessed on one randomly chosen, healthy, mature leaf per plant 8-12 weeks after sowing. Root traits were measured 14-20 weeks after sowing.

To determine specific leaf area (SLA = LA/DW) and leaf dry matter content (LDMC = DW/FW, LDMC is the inverse of leaf water content, LWC in mg/g, LWC = 1000-LDMC), we measured saturated fresh weight (FW) of the leaf after hydrating plants overnight (approx. 15 hours), and dry weight (DW) after oven-drying. Leaf area (LA) was quantified with an Area-meter (Model LI 3100, Li-Cor Bioscience, Lincoln, NE, USA). Leaf thickness (Lthick) was measured with a micrometer (Mitutoyo M110-25, graduation 0.01 mm) at three points in the centre of the leaf blade, avoiding the midrib and primary veins, and averaged. Leaf tissue density (LTD) was calculated as ratio of dry weight to leaf volume (leaf volume = LA * Lthick).

Maximum photosynthetic rate per leaf area ($A_{area}$) was measured with an infra-red gas analyser Li-Cor 6400 (Li-Cor, Lincoln, NE, USA) between 8.30 a.m. and 11.00 a.m. at a light intensity of 2000 µmol * photons/($m^2$ * s) (based on light response curves for a species subset), 25°C, and 400 ppm $CO_2$. If the leaf did not fill the measurement chamber, photosynthetic rate was re-calculated based on leaf area measurements with an Area Meter (see above). Usually, one leaf per individual was measured, but in species with very small or thin leaves (e.g. a few grasses, *Filago*, and *Helianthemum*) several leaves were jointly arranged in the measurement chamber. The leaves used for photosynthesis measurements (few exceptions in *Psilurus incurvus*, *Rostraria cristata*) were oven-dried and ground to analyse their mass-based nitrogen content ($N_{mass}$) and carbon content ($C_{mass}$) with an EA-IRMS coupling (Elemental Analyzer NA 1108, CE Instruments, Milan, Italy; Interface ConFlo III, Finnigan MAT, Bremen, Germany; Isotope ratio mass spectrometer: delta S, Finnigan MAT, Bremen, Germany). Photosynthetic rate and nitrogen content were converted to their area- or mass-based equivalent ($A_{mass}$, $N_{area}$) via SLA based on species' average values.

Morphological root traits were determined on three subsamples of fine roots (diameter < 2 mm, stored in 35 % ethanol before the measurements) from the upper, middle and lower part of the root (except whole roots in *Filago* and *Helianthemum salicifolium*). The root samples were stained with toluidine blue (0.2 g/L) and scanned (Scanner Epson Perfection V800/V850 photo scanner, 600 dpi). Images were analysed with WinRHIZO © Reg 2017 (Regent Instruments Inc., Quebec, Canada) to determine mean diameter (Rdia), volume and length of the scanned root sample.

Samples were oven-dried to measure dry weight, and to calculate specific root length (SRL = root length/root dry weight) and root tissue density (RTD = root mass/root volume). Calculations of SRL and RTD considered diameter heterogeneity by using summed root length and volume from 40 diameter classes (see Rose, 2017), respectively.

Species' average relative growth rate (RGR) was assessed in 19 species (see Table S1) in a separate plant set that was grown under similar conditions (see Plant cultivation) in winter 2018/19. RGR was calculated based on species-specific averages of aboveground biomass (AB) in week 16 (t1) and week 22-23 (t2) after sowing as: RGR = (AB 2 – AB 1)/(AB 1 * (t2-t1)).

## Species' distribution along rainfall gradients

Species' distribution along the regional rainfall gradients in Israel was characterized based on their occurrences (presence/absence data) in independent biological records (BioGIS, 2018). The BioGIS database provides the mean annual rainfall niche of each species, which is modelled as the average of local mean annual rainfall across all occurrence sites of a respective species. Our study species covered mean annual rainfall niches between 120 mm/year (association with arid conditions) and 580 mm/year (association with Mediterranean conditions, Table S1).

## Statistical analyses

Trait differences across species were tested with F-tests on linear models (LM) with species' identity as explanatory factor. Traits (except Rdia and $C_{mass}$) were natural log-transformed to improve normality and homoscedasticity. Pairwise trait correlations were calculated with Spearman rank correlation coefficients based on species' average values.

The main axes of correlations among the resource-use related traits were assessed with a principal component analysis (PCA) at the plant level (i.e. combining leaf and root traits) based on species' average trait values. Since mass- but not area-based traits are explicitly included in the leaf economics spectrum (Wright et al., 2004), we equivalently considered only $A_{mass}$, $N_{mass}$, and $C_{mass}$ in the PCA. The main trait correlations though were similar between a PCA with these mass-based traits and a PCA considering instead $A_{area}$, $N_{area}$, and $C_{area}$ (Pearson correlation coefficients among species' scores along the trait axes $|0.48| \leq r \leq |0.87|$). We also calculated PCAs separately for leaf and for root traits. The trait coordinations in leaf and root traits were similar to those observed at the whole plant level (Table S3). Species' scores along the principal components (PC, in the following referred to as trait axes) calculated for the whole plant level were therefore used to characterize species' trait combinations.

We tested for differences among life forms (i.e. grasses, non-legume forbs, legumes) in species' scores along the main trait axes (PC 1, PC 2) with F-tests on LMs separately calculated for each trait axis and Tukey post-hoc tests. Additionally, the main axes of trait correlations were separately assessed for forbs (including legumes) and grasses with PCAs as described above for all species. Trait correlations within life forms were similar to the ones among all species (Pearson correlation coefficients among species' scores along the trait axes $|0.60| \leq r \leq |0.98|$). The relations between species' scores along the trait axes or single traits, species' growth rate, and distribution were therefore calculated for the whole species set.

The relations between species' scores along the main trait axes (PC 1, PC 2, i.e. species' trait combinations) and their relative growth rates were tested with F-tests on LMs separately calculated for each trait axis. The relations between the species' scores along the trait axes and relative growth rates did not qualitatively differ depending on whether the species' scores were derived from a PCA with the full species set (30 species, Figure 1) or from a PCA with the species set with growth rate measurements (19 species, Figure S1). For consistency among all analyses, we therefore presented the findings with the PCA based on the full species set. Relations between single traits and relative growth rates were also tested with F-tests on LMs separately calculated for each trait. Relative growth rates were natural log-transformed in the LM with $C_{mass}$ to improve normality and homoscedasticity.

The relations of species' scores along the main trait axes (PC 1, PC 2, i.e. species' trait combination) or single traits with species' distribution along the rainfall gradient (i.e. mean annual rainfall niche) were tested with F-tests on LMs separately calculated for each axis or trait. Relations were also calculated with minimum and maximum rainfall niche based on BioGIS (2018), but qualitative results hardly changed (results not shown).

Adjusted significance level according to Holm-Bonferroni sequential correction (Gaetano, 2013; Holm, 1979) was applied to the multiple tests for species' differences in the traits, and for trait (axes) relations to species' growth rates and distribution. Since we tested only pre-planned hypotheses (see Table 1), we interpreted the results based on unadjusted significance level (see Armstrong, 2014).

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

## Results

The twelve resource-use related traits differed significantly across the 30 winter annuals, with almost 2 to 5 fold variation, and in relative growth rate with about 26 fold variation, respectively (F-values between 2.4-93.2, all $p < 0.001$, Table S2). The attribute range of several leaf traits in the studied annuals almost corresponded to 60-80 % of the globally documented trait ranges in plant species from different ecosystems and life forms worldwide (Kattge et al., 2020, see details in Table S2). In all traits, the values of the investigated annuals fall within the acquisitive end of the global trait range (e.g. high SLA, $N_{mass}$, Table S2).

Traits were correlated along two PCs, instead of one as we had expected (Figure 1, Table 2). PC 1 corresponded in positive direction with Rdia and Lthick, and in negative direction with LDMC, SRL, RTD, and LTD (Figure 1, Table 2). PC 1 thus summarized structural leaf and root traits (in the following referred to as structural trait axis). PC 2 was highly negatively correlated with $A_{mass}$, $N_{mass}$, $C_{mass}$ and SLA, four traits associated with carbon gain (in the following referred to as carbon gain trait axis, Figure 1, Table 2). The independence between structural and carbon gain traits was also reflected in the pairwise trait correlations (Table S4).

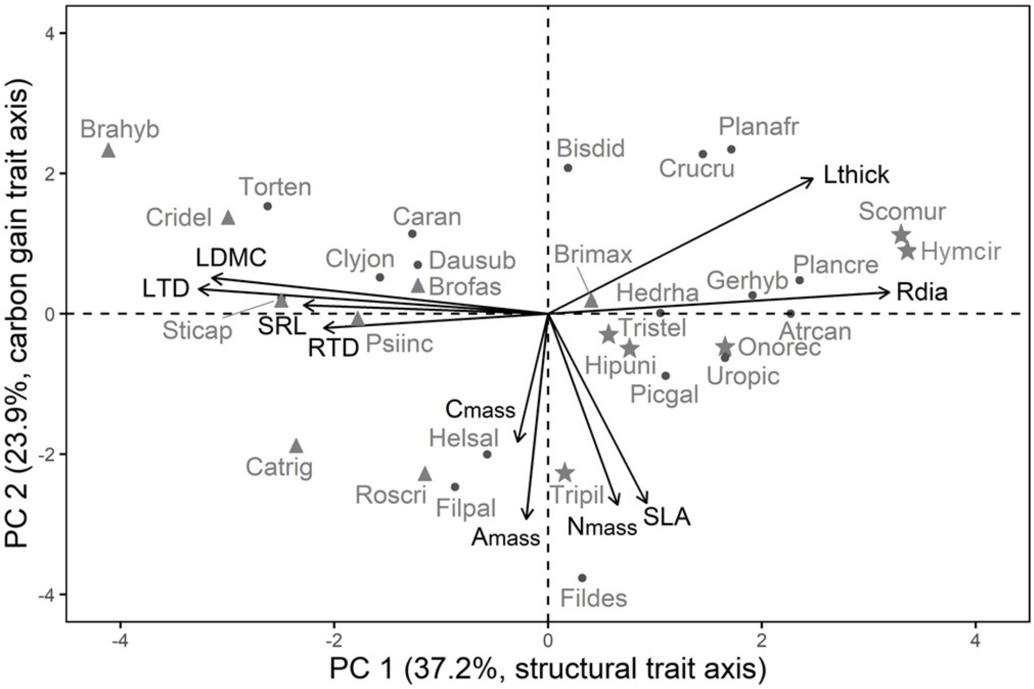

**Figure 1.** Resource-use related traits are correlated along two axes in 30 winter annual species, the first axis corresponds to structural traits (PC 1), and the second to carbon gain traits (PC 2). Trait abbreviations and trait loadings are given in Table 1 and Table 2, and species abbreviations are given in Table S1, respectively. Symbols indicate life form: triangles for grasses, points for non-legume forbs, asterisks for legumes. Grasses differed from non-legume forbs and legumes in their species' scores along PC 1, but not along PC 2.

Grasses differed from non-legume forbs and legumes in their scores along the structural trait axis (PC 1, LM statistics $F_{2,27} = 11.23$, $p < 0.001$, $R^2 = 0.41$) with higher LTD and LDMC in grasses, but not along the carbon gain axis (PC 2, $F_{2,27} = 0.12$, $p = 0.89$, Figure 1). Non-legume forbs and legumes exhibited similar scores along both trait axes (Figure 1). The trait correlations along PC 1 and PC 2 within each life form (i.e. forbs *vs*. grasses) were similar to the ones among all species (Figure S2).

**Table 2.** Trait loadings on the first two principal components (PC) of a PCA with ten resource-use related traits in 30 winter annual species (see Figure 1). The table shows the eigenvalues, the proportion of explained variance of both PCs, and the loadings of the traits. Traits were ordered according to their |loading| on PC 1. Trait loadings > |0.4| are marked in bold.

| | PC 1 | PC 2 |
|---|---|---|
| Eigenvalue | 3.71 | 2.39 |
| Explained variance [%] | 37.1 | 23.9 |
| LTD | **-0.47** | 0.06 |
| LDMC | **-0.45** | 0.09 |
| Rdia | **0.46** | 0.06 |
| Lthick | 0.36 | 0.35 |
| SRL | -0.33 | 0.02 |
| RTD | -0.30 | -0.04 |
| SLA | 0.13 | **-0.49** |
| $N_{mass}$ | 0.09 | **-0.49** |
| $C_{mass}$ | -0.04 | -0.33 |
| $A_{mass}$ | -0.03 | **-0.53** |

Species' scores along the carbon gain trait axis (PC 2) were related to relative growth rate, i.e. species with higher $A_{mass}$, $N_{mass}$, $C_{mass}$, and SLA grew faster, but scores on the structural trait axis were unrelated to relative growth rate (Figure 2, Table S5). Among single traits, only $A_{mass}$ and $A_{area}$ were positively related with relative growth rate (Table S5).

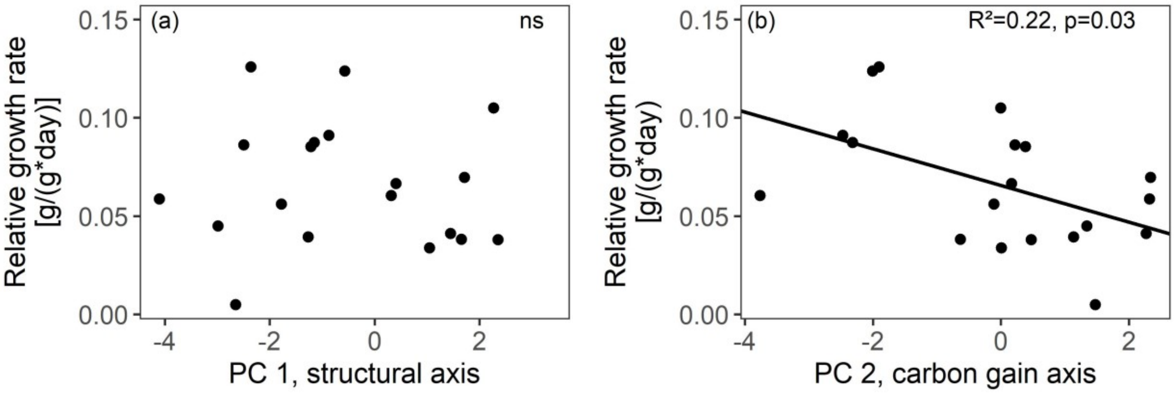

**Figure 2.** Relations between relative growth rate and species' scores along the two main trait axes of resource-use related traits: (a) structural trait axis (PC 1) and (b) carbon gain trait axis (PC 2) in 19 winter annual species. $R^2$ values and significance are given (ns not significant, for details see Table S5). Species' scores were based on the PCA in Figure 1 with 30 species.

Species' scores along the carbon gain and structural trait axes (PC 1, PC 2) as well as relative growth rates were independent from their distribution along the rainfall gradient (mean annual rainfall niche) (Figure 3 a-c, Table S6). However, among single traits, root traits were related with species' distribution. Species with higher RTD and smaller Rdia were associated with arid conditions (Figure 3 d-e, Table S6).

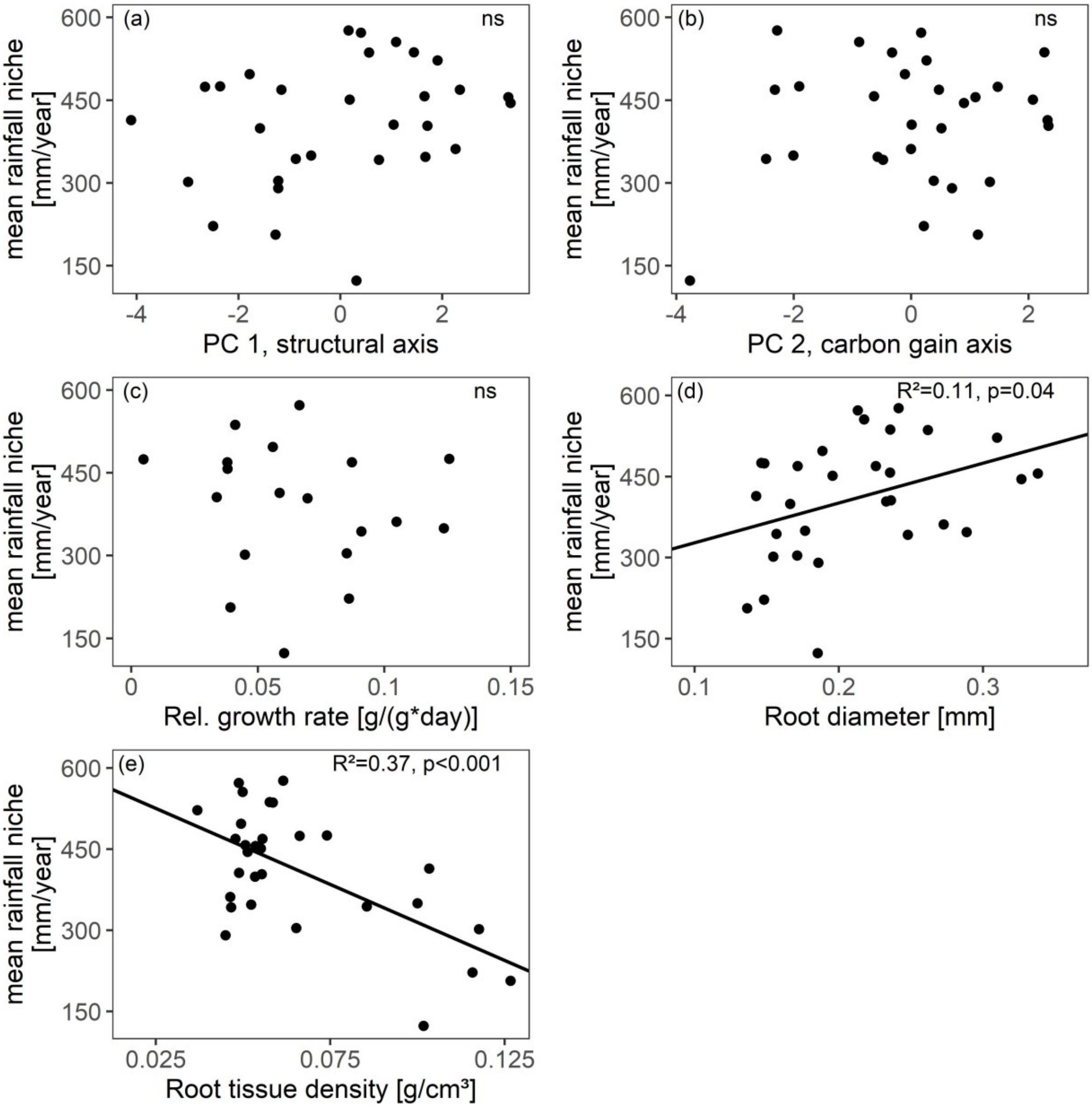

**Figure 3.** Relations between species' mean annual rainfall niche (i.e. species' distribution along the rainfall gradient) and (a, b) their scores along the two main axes of resource-use related traits (PC 1, PC 2), (c) relative growth rate, (d) root diameter, and (e) root tissue density in 30 winter annual species. Relative growth rate was only assessed in 19 species. R² values and significance were given (ns not significant, for details see Table S6). Further single traits were unrelated to species' mean annual rainfall niche (see Table S6).

## Discussion

The main premise of the plant economics spectrum is that resource-use related traits are correlated along a single axis, comprising both structural and carbon gain traits, as well as traits of different plant organs (Reich, 2014). In contrast, in the investigated winter annuals structural and carbon gain traits were decoupled, and correlated along two independent axes. The unexpected decoupling contradicts the predictions of the plant economics spectrum and had pervasive consequences on trait relations to growth rates and species' distributions along the rainfall gradient that were also inconsistent with the hypotheses of the plant economics spectrum.

### Trait-trait relations: Structural and carbon gain traits are independent

The decoupling between structural and carbon gain traits we found in the investigated winter annuals has, to our knowledge, not been observed in perennial herbaceous or woody species. Instead, perennial herbaceous or woody species predominantly show the expected correlation of resource-use related traits along a single axis (e.g. de la Riva, Tosto et al., 2016; Freschet et al., 2010; Liu et al., 2010). In perennials, variation of leaf structure, especially of leaf tissue density and thickness, is mainly due to differences in carbon content (de la Riva, Olmo et al., 2016; Roderick et al., 1999). Higher carbon contents are associated with a higher proportion of sclerenchyma, thicker mesophyll layers and/or thicker mesophyll cell walls (de la Riva, Olmo et al., 2016; Onoda et al., 2017). This leaf structure leads to lower mass-based photosynthetic rate due to higher diffusion resistance to carbon dioxide, shading of chloroplasts, or lower proportion of mass-based nitrogen content (Niinemets, 1999; Onoda et al., 2017; Shipley et al., 2005). In the studied winter annuals, however, structural trait variation (i.e. the structural trait axis) was independent from carbon content. The unexpected decoupling between structural and carbon gain traits implies that structural trait variation is due to components that do not constrain photosynthetic rate.

Our study species exhibited high water contents, leaf hairiness, and silicon accumulation. These traits are assumed to increase species' ability to cope with the environmental conditions in drylands by maximizing water storage, reflecting sunlight, decreasing transpiration, and deterring grazing herbivores (Ehleringer & Mooney, 1978; Katz, 2019; Sack et al., 2003; Woodman & Fernandes, 1991). They have additionally been proposed to dilute the relations between mass-based nitrogen content and structural leaf traits expected by the leaf economics spectrum (Grubb, 2016). Consistently, they influenced leaf tissue density and thickness in our study species. Leaf tissue density was strongly influenced by silicon instead of carbon content (Table S4, Method S1); and in forbs, high tissue density was additionally associated with long and/or dense leaf hairs (pers. obs.). Similarly, high leaf thickness mainly resulted from high water content and was negatively associated with carbon content (Table S4). Despite their influence on leaf structure, silicon content, leaf water content, and leaf hairiness did not affect mass-based photosynthetic rate since they did not constrain the proportion of mass-based nitrogen content (Table S4), nor the diffusion resistance to carbon dioxide. Decoupling between structural and carbon gain traits, which is in contrast to the hypothesis of the plant economics spectrum, thus might not be restricted to winter annuals, but should also emerge in other species groups, in which traits other than carbon content lead to leaf structure variation, e.g. in perennial grasses with high silicon accumulation or succulent perennials (compare to Grubb, 2016).

Despite the decoupling of structural and carbon gain traits, the structural traits of roots and leaves were correlated in the studied winter annuals (SRL, RTD, Rdia, and LTD, LDMC, Lthick, respectively), consistent with findings in perennials (de la Riva, Tosto, et al., 2016; Freschet et al., 2010; Reich, 2014). The structural analogy between leaves and roots thus is not a consequence of the correlation of resource-use related traits along one axis, but might result from tissues pervading the entire plant, such as xylem and phloem vessels (Hummel et al., 2007; Wahl & Ryser, 2000).

### Trait-growth relations: Growth rate is independent from structural traits

The plant economics spectrum proposes that species' positions along the single axis of resource-use related traits determine their growth rates (Reich, 2014). Consistent with this hypothesis, winter annuals with higher carbon gain trait attributes exhibited higher relative growth rates. However, structural traits were unrelated to relative growth rate, reflecting their uncoupling from carbon gain. Winter annuals with a wide variation of structural traits thus exhibited similar relative growth rates in contrast to the findings in perennials and the hypothesis of the plant economics spectrum (Lambers & Poorter, 1992; Reich, 2014).

The structural traits should, however, influence species' stress resistance. In our study species, the structural trait axis was associated with silicon content and leaf hairiness (see above), traits assumed to deter grazing herbivores (Katz, 2019; Woodman & Fernandes, 1991), as well as with turgor loss point, i.e. the water potential at which leaves lose turgor (Figure S3, Method S1). Turgor loss point is considered as a major physiological determinant of species' drought response (Bartlett et al., 2012; Sun et al., 2020). A relation between structural traits and species' drought and grazing resistance has also been indicated across life forms in semi-arid ecosystems (Blumenthal et al., 2020).

Independence between growth rate and structural traits thus implies that the assumptions of the growth-stress resistance trade-off (see Grime & Hunt, 1975; Reich, 2014) do not apply to the studied winter annuals. Growth rates indeed turned out to be independent of species' stress resistance (to grazing and drought) in our study species (Kurze et al., in review). Similar findings emerged in a few studies of perennial herbaceous species (Fernández & Reynolds, 2000; Jung et al., 2020).

### Trait-environment relations: Species' filtering along the rainfall gradient is only reflected in root traits

We expected that arid conditions favour winter annuals with acquisitive trait attributes and high growth rates due to their ability to reproduce within a short period and thus to escape drought (see Kooyers, 2015; Levitt, 1980). However, in the investigated annuals, species' distribution along the rainfall gradient was unrelated to their scores along the structural and carbon gain trait axis and to growth rate. It is improbable that this unanticipated result is due to our focus on trait variation across species, which did not consider ecotypic variation. Ecotypic trait variation is usually considerably smaller than interspecific variation (Garnier et al., 2001; Kazakou et al., 2014; Siefert et al., 2015). This has been also shown in some of our study species (Bergholz et al., 2017; Kurze et al., 2017; Álvarez-Cansino et al. unpublished data). Additionally, at the intraspecific level, resource-use related leaf traits did not show directional changes along the rainfall gradient in our study system (Bergholz et al., 2017; Kurze et al., 2017).

Rather, this unexpected finding likely emerged from the independence of growth rate and stress resistance, which facilitates similar ecological success of species with alternative trait combinations and supports the co-occurrence of annuals with a wide range of structural and carbon gain traits and growth rates along the rainfall gradient. Theoretical models (Marks & Lechowicz, 2006) and studies on interspecific variation of leaf traits in woody and perennial herbaceous species support that different trait combinations can be successful in the same environment (Cernusak et al., 2011; Forrestel et al., 2017; Muir et al., 2017; Wright et al., 2004). In our study species, the structural trait axis was associated with traits related to both drought and grazing resistance (e.g. turgor loss point, leaf silicon content, leaf hairiness, see above), which should be differentially filtered along the rainfall gradient and may offset each other (Carmona et al., 2012; Rota et al., 2017). Similarly, fast and slow growth rates may confer species a high competitive effect and high competitive response under wetter conditions (Goldberg & Landa, 1991; Liancourt et al., 2009). Consequently, contrary to the expectations of the plant economics spectrum, neither species' trait combinations along the structural or carbon gain trait axis nor growth rates led to ecological filtering along the rainfall gradient in winter annuals.

Nevertheless, fine root traits were associated with species' distribution along the rainfall gradient in the studied annuals. Fine root traits should be more directly related to species' drought resistance than the combination of structural traits (reflected in the structural trait axis), which comprised traits of both drought and grazing resistance. Root traits have indeed previously been shown to be more strongly related to the drought survival of annual species than leaf traits (Harrison & LaForgia, 2019). In our study species, root diameter decreased and root tissue density increased with increasing species' association to arid conditions. Species with these trait attributes are assumed to exhibit higher drought resistance, since thin and dense roots decrease the resistance to radial water inflow and are less prone to cavitation due to smaller xylem vessels (Comas et al., 2013; Wahl & Ryser, 2000). Woody species with these root trait attributes have been shown to be favoured under low water availability (de la Riva et al., 2018; Nicotra et al., 2002). The root trait changes along the rainfall gradient observed in our study species thus imply that the low water availability during the growing season imposes an ecological filter under arid conditions. Arid conditions thus favour winter annuals with high drought resistance in the vegetative phase conferred by root traits but not with acquisitive traits or high growth rate to escape drought, as we initially expected.

### Conclusion

Our findings showed that the functional constraints hypothesized by the plant economics spectrum do not apply to winter annuals. Winter annuals can thus not be ranked along a single axis of resource-use related traits from acquisitive (or fast) to conservative (or slow), as proposed by the plant economics spectrum (Reich, 2014). The limited applicability of the plant economics spectrum to winter annuals cautions to generalize functional constraints, trait-growth, or trait-environment relations among life-history groups. Explicitly testing and establishing these relations for species groups that may be subjected to different constraints is a precondition for using trait-based approaches to understand and predict species' performance, community composition, or ecosystem functioning.

## Author contributions

SK conceived the ideas for this manuscript, and LA, BE, SK, MB, and KT designed the study. SK coordinated and conducted the trait measurements, analysed the data, and wrote the manuscript with contributions by LA and BE. All co-authors commented subsequent drafts of the manuscripts and gave final approval for publication.

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# Supporting Information

**Table S1.** List of the 30 studied winter annual species from Israel with their abbreviation, family, and mean annual rainfall niche.

**Table S2.** Attributes of the resource-use related traits, relative growth rate, and leaf silicon content across the 30 studied winter annual species, and comparison with the global trait range.

**Table S3.** Trait correlations separately analysed for leaf and for root traits in 30 winter annual species based on principal component analyses.

**Figure S1.** Trait correlations in the subset of 19 winter annual species for which relative growth rates were measured based on a principal component analysis.

**Table S4.** Pairwise correlations among the twelve resource-use related traits and leaf silicon content based on Spearman rank correlation coefficients in 30 winter annual species.

**Figure S2.** Trait correlations separately analysed in forbs and grasses based on principal component analyses.

**Table S5.** Relations between species' relative growth rate and species' scores along the main trait axes (PC 1, PC 2), or single traits in 19 winter annual species.

**Table S6.** Relations between species' mean annual rainfall niche and species' scores along the main trait axes (PC 1, PC 2), relative growth rate, or single traits.

**Method S1.** Measurement of leaf silicon content and turgor loss point.

**Figure S3.** Relation between species' positions along the structural trait axis (PC 1) and turgor loss point.

**Table S1.** List of the 30 studied winter annual species from Israel with their abbreviation, family, and mean annual rainfall niche (from BioGIS, 2018). The 19 species with relative growth rate measurements are marked with *. Species are ordered alphabetically.

| Species name | Abbreviation | Family | Rainfall niche [mm/year] |
|---|---|---|---|
| *Atractylis cancellata** | Atrcan | Asteraceae | 361.2 |
| *Biscutella didyma* | Bisdid | Brassicaceae | 450.9 |
| *Brachypodium hybridum** | Brahyb | Poaceae | 413.5 |
| *Briza maxima** | Brimax | Poaceae | 572 |
| *Bromus fasciculatus** | Brofas | Poaceae | 303.7 |
| *Carrichtera annua** | Caran | Brassicaceae | 206 |
| *Catapodium rigidum** | Catrig | Poaceae | 475 |
| *Clypeola jonthlaspi* | Clyjon | Brassicaceae | 398.8 |
| *Crithopsis delileana** | Cridel | Poaceae | 301.5 |
| *Crupina crupinastrum** | Crucru | Asteraceae | 536.7 |
| *Daucus subsessilis* | Dausub | Apiaceae | 290.1 |
| *Filago desertorum** | Fildes | Asteraceae | 122.8 |
| *Filago palaestina** | Filpal | Asteraceae | 343.5 |
| *Geropogon hybridus* | Gerhyb | Asteraceae | 521.7 |
| *Hedypnois rhagadioloides** | Hedrha | Asteraceae | 405.6 |
| *Helianthemum salicifolium** | Helsal | Cistaceae | 349.4 |
| *Hippocrepis unisiliquosa* | Hipuni | Fabaceae | 341.8 |
| *Hymenocarpos circinnatus* | Hymcir | Fabaceae | 444.7 |
| *Ononis reclinata* | Onorec | Fabaceae | 346.9 |
| *Picris galilaea* | Picgal | Asteraceae | 555.3 |
| *Plantago afra** | Planafr | Plantaginaceae | 403.4 |
| *Plantago cretica** | Plancre | Plantaginaceae | 468.9 |
| *Psilurus incurvus** | Psiinc | Poaceae | 496.8 |
| *Rostraria cristata** | Roscri | Poaceae | 468.9 |
| *Scorpiurus muricatus* | Scomur | Fabaceae | 455.2 |
| *Stipa capensis** | Sticap | Poaceae | 221.7 |
| *Torilis tenella** | Torten | Apiaceae | 474.2 |
| *Trifolium pilulare* | Tripil | Fabaceae | 576.1 |
| *Trifolium stellatum* | Tristel | Fabaceae | 535.9 |
| *Urospermum picroides** | Uropic | Asteraceae | 457 |

**Table S2.** Attributes of the resource-use related traits, relative growth rate, and leaf silicon content ($Si_{mass}$, see Method S1) across the 30 studied winter annual species, and comparison with the global trait range. Given are the mean ± standard deviation (std) across species, minimum (Min) and maximum (Max) species' mean, their x-fold variation (Var = Max/Min), and the number of replicates measured in each species (N). Given are also the results of linear models testing for species' differences in each trait (den. d.f., F-value, p-value and $R^2$). Traits significantly differed across species (all $p < 0.001$), and species' differences in all traits remained significant after Holm-Bonferroni correction. Global trait ranges based on the TRY database (Kattge et al., 2020) are given with minimum (Min) and maximum (Max) species' means (min and max represent the 2.5 and 97.5 percentile of global trait variation, respectively), their x-fold variation among species (Var) as well as the percentage of the global trait range covered by the investigated annuals (cov. annuals [%] = (trait range annuals/trait range global) * 100). See Table 1 for trait abbreviations.

| Trait | Unit | 30 annual species | | | | | | | | | global data set | | | Cov. annuals |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Mean ± std | Min | Max | Var | N | den. d.f. | F | p | $R^2$ | Min | Max | Var | |
| SLA | $mm^2$/mg | 33.51 ± 9.34 | 20.65 | 57.56 | 2.8 | 9-14[a] | 323 | 12.27 | < 0.001 | 0.48 | 4.04 | 45.9 | 11.4 | 88.4 |
| LDMC | mg/g | 129.36 ± 46.27 | 66.87 | 291.32 | 4.4 | 9-14[a] | 323 | 27.14 | < 0.001 | 0.68 | 121 | 518 | 4.3 | 58.0 |
| LTD | $g/cm^3$ | 0.17 ± 0.07 | 0.08 | 0.30 | 4.0 | 9-14[a] | 323 | 17.73 | < 0.001 | 0.58 | 0.13 | 0.64 | 5.0 | 44.1 |
| Lthick | mm | 0.23 ± 0.09 | 0.12 | 0.47 | 3.8 | 9-14[a] | 323 | 43.42 | < 0.001 | 0.78 | 0.11 | 0.73 | 6.9 | 54.8 |
| $A_{area}$ | µmol/($m^2$ * s) | 14.41 ± 4.42 | 6.51 | 25.64 | 3.9 | 7-14[a] | 292 | 7.32 | < 0.001 | 0.36 | 2.07 | 28.89 | 14.0 | 71.2 |
| $N_{area}$ | $mg/mm^2$ | 0.001 ± 0.0003 | 0.0006 | 0.0018 | 2.7 | 1 | - | - | - | - | 0.0006 | 0.004 | 6.7 | 35.4 |
| $A_{mass}$ | µmol/(g * s) | 0.46 ± 0.13 | 0.25 | 0.76 | 3.1 | 1 | - | - | - | - | 0.02 | 0.45 | 23.5 | 119.4 |
| $N_{mass}$ | mg/g | 34.23 ± 6.68 | 23.17 | 50.47 | 2.2 | 5-9[a] | 173 | 2.41 | < 0.001 | 0.17 | 8.10 | 41.27 | 5.1 | 81.4 |
| $C_{mass}$ | mg/g | 397.13 ± 22.66 | 355.33 | 444.50 | 1.3 | 5-9[a] | 173 | 3.34 | < 0.001 | 0.25 | - | - | - | - |
| SRL | m/g | 579.46 ± 231.86 | 211.54 | 1105.18 | 5.2 | 8-9[a] | 208 | 32.34 | < 0.001 | 0.79 | 245 | 27722 | 113.2 | 3.3 |
| RTD | $g/cm^3$ | 0.07 ± 0.02 | 0.04 | 0.13 | 3.4 | 8-9[a] | 208 | 29.04 | < 0.001 | 0.77 | 0.067 | 0.697 | 10.4 | 14.3 |
| Rdia | mm | 0.21 ± 0.06 | 0.14 | 0.34 | 2.5 | 8-9[a] | 208 | 93.16 | < 0.001 | 0.92 | 0.17 | 1.32 | 7.7 | 17.5 |
| RGR[b] | g/(g * day) | 0.07 ± 0.03 | 0.005 | 0.126 | 25.8 | 1 | - | - | - | - | - | - | - | - |
| $Si_{mass}$ | mg/g | 16.98 ± 20.01 | 1.89 | 91.69 | 48.5 | 7-11[a] | 213 | 191.53 | < 0.001 | 0.96 | - | - | - | - |

[a] exceptions are *Daucus subsessilis* (n = 4-6), *Ononis reclinata* (n = 5-8), [b] for 19 species

**Table S3.** Trait correlations separately analysed for leaf and for root traits in 30 winter annual species based on principal component analyses. Given are the trait loadings on the first two principal components (PC) of PCAs either calculated with the seven resource-use related leaf traits or the three resource-use related root traits. The table shows the eigenvalues, the proportion of explained variance of both PCs, and the loadings of the traits. Traits were ordered according to their |loading| on PC 1. Species' scores along both PCs of leaf traits and along PC 1 of root traits were highly correlated (Pearson correlation coefficient $r > |0.81|$) with the species' scores along the PCs of the PCA calculated for the whole plant level (Figure 1, Table 2).

| | PC 1 | PC 2 |
|---|---|---|
| Eigenvalue | 2.50 | 2.34 |
| Explained variance [%] | 35.7 | 33.4 |
| Leaf traits | | |
| LDMC | -0.55 | -0.23 |
| LTD | -0.54 | -0.26 |
| SLA | 0.41 | -0.31 |
| $N_{\text{mass}}$ | 0.35 | -0.36 |
| $A_{\text{mass}}$ | 0.24 | -0.47 |
| Lthick | 0.22 | 0.55 |
| $C_{\text{mass}}$ | 0.06 | -0.35 |
| Root traits | | |
| Eigenvalue | 1.92 | 1.03 |
| Explained variance [%] | 64.0 | 34.4 |
| Rdia | -0.71 | 0.0 |
| SRL | 0.52 | 0.67 |
| RTD | 0.47 | -0.74 |

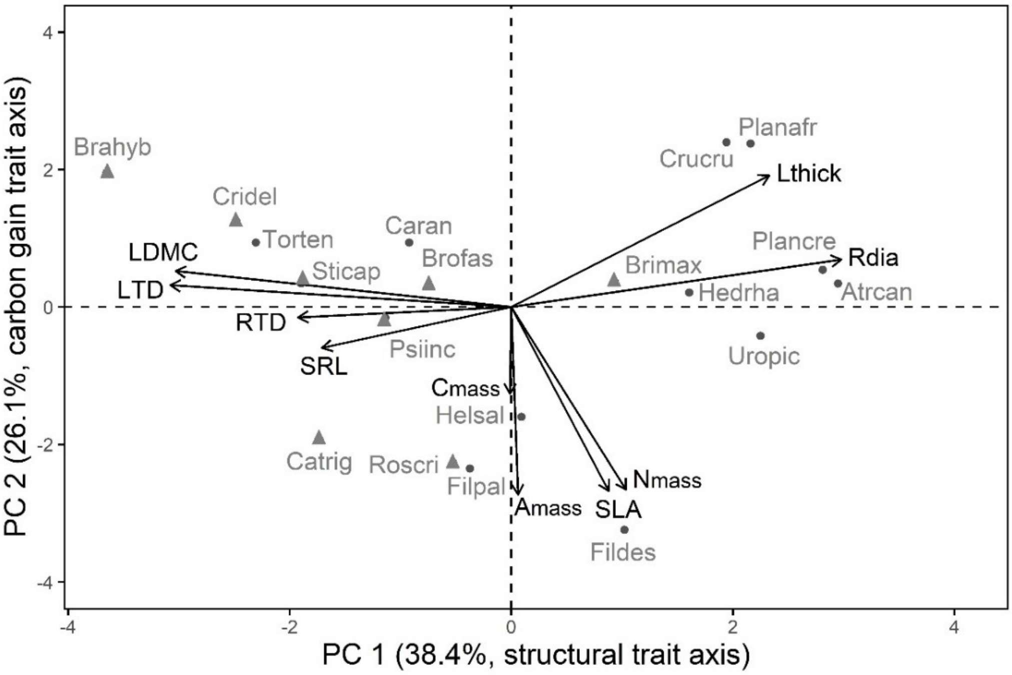
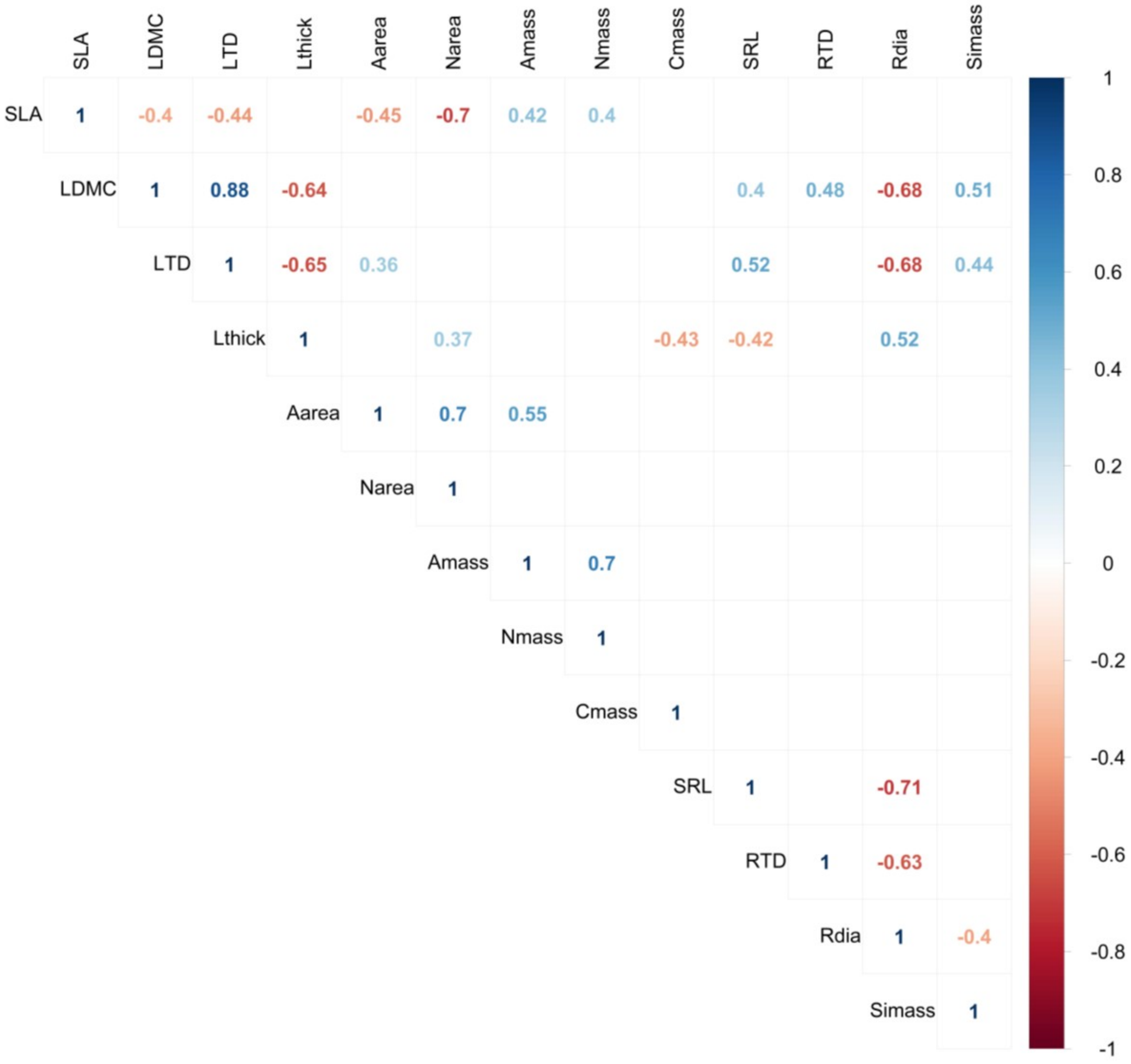


**Figure S1.** Trait correlations in the subset of 19 winter annual species for which relative growth rates were measured based on a principal component analysis. Symbols indicate life form: points for forbs, triangles for grasses. Species' scores along the main trait axes were correlated with species' scores along the main trait axes in the PCA with the full species set (N = 30, Figure 1, Table 2, Pearson correlation coefficient r ≥ |0.99|), indicating that trait coordinations were similar between both species sets. See Table 1 and Table S1 for trait and species abbreviations, respectively.

**Table S4.** Pairwise correlations among the twelve resource-use related traits and leaf silicon content ($Si_{mass}$, see Method S1) based on Spearman rank correlation coefficients in 30 winter annual species. Only significant ($p \leq 0.05$) correlation coefficients are shown. Note that LDMC is the inverse of leaf water content (LWC in mg/g, LWC = 1000-LDMC).



| | SLA | LDMC | LTD | Lthick | Aarea | Narea | Amass | Nmass | Cmass | SRL | RTD | Rdia | Simass |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| SLA | 1 | -0.4 | -0.44 | | -0.45 | -0.7 | 0.42 | 0.4 | | | | | |
| LDMC | | 1 | 0.88 | -0.64 | | | | | | 0.4 | 0.48 | -0.68 | 0.51 |
| LTD | | | 1 | -0.65 | 0.36 | | | | | 0.52 | | -0.68 | 0.44 |
| Lthick | | | | 1 | | 0.37 | | | -0.43 | -0.42 | | 0.52 | |
| Aarea | | | | | 1 | 0.7 | 0.55 | | | | | | |
| Narea | | | | | | 1 | | | | | | | |
| Amass | | | | | | | 1 | 0.7 | | | | | |
| Nmass | | | | | | | | 1 | | | | | |
| Cmass | | | | | | | | | 1 | | | | |
| SRL | | | | | | | | | | 1 | | -0.71 | |
| RTD | | | | | | | | | | | 1 | -0.63 | |
| Rdia | | | | | | | | | | | | 1 | -0.4 |
| Simass | | | | | | | | | | | | | 1 |

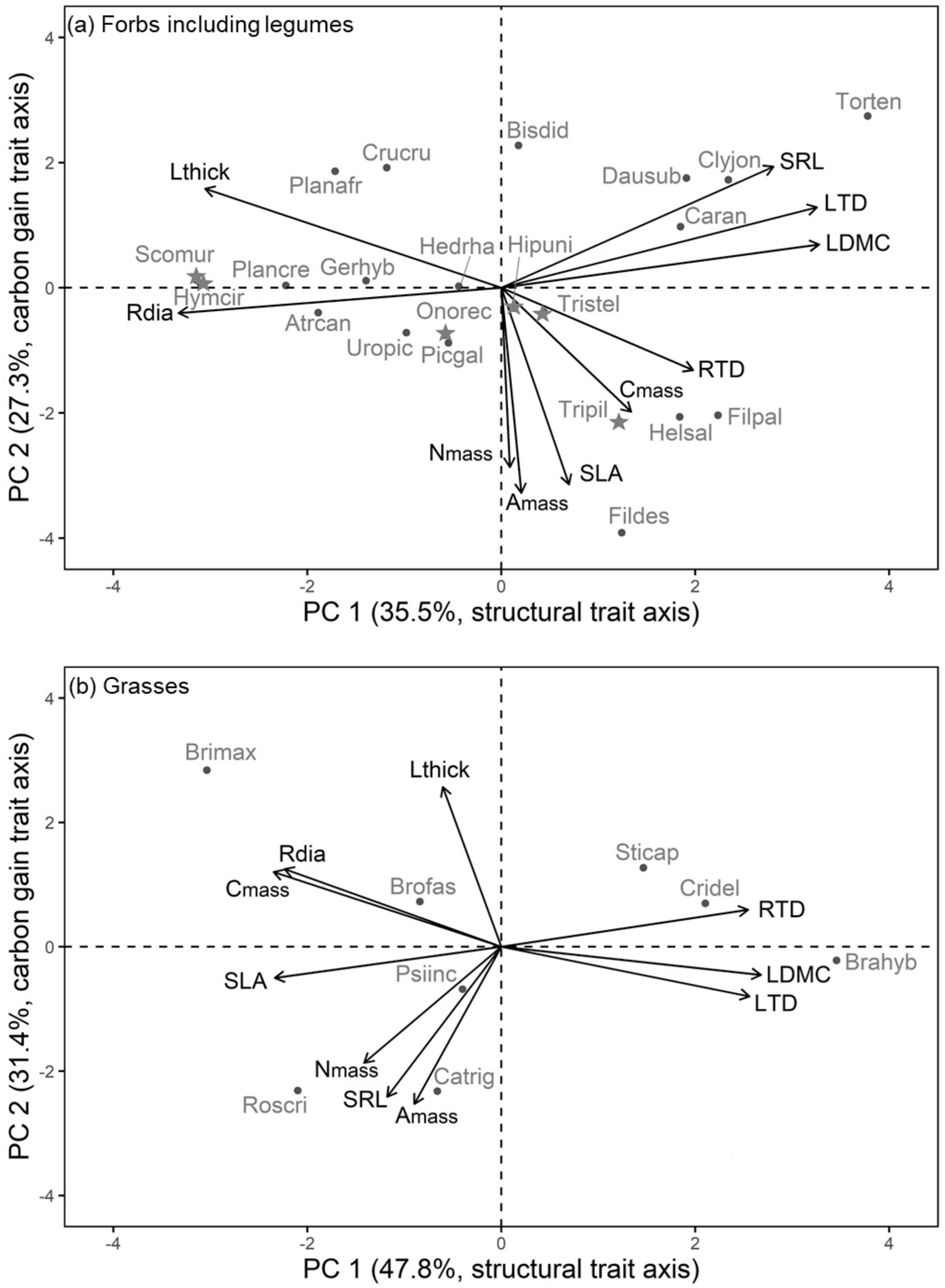


**Figure S2.** Trait correlations separately analysed in (a) forbs (22 species, including 6 legumes, indicated by asterisks) and (b) grasses (8 species) based on principal component analyses. In both life forms, traits were correlated along a structural trait axis (PC 1) and carbon gain trait axis (PC 2) as in the whole species set. See Table 1 and Table S1 for trait and species abbreviations, respectively.

**Table S5.** Relations between species' relative growth rate and species' scores along the main trait axes (PC 1, PC 2), or single traits in 19 winter annual species. Given are the results of linear models. Traits significantly related to relative growth rate are highlighted in bold; traits remaining significant after Holm-Bonferroni correction for 14 tests (traits) are indicated with *. For trait abbreviations see Table 1.

| Trait | $F_{1,17}$ | p | $R^2$ |
|---|---|---|---|
| PC 1 (structural trait axis) | 0.08 | 0.786 | -0.05 |
| **PC 2 (carbon gain trait axis)** | **5.95** | **0.026** | **0.22** |
| SLA | 0.57 | 0.461 | -0.02 |
| LDMC | 0.07 | 0.792 | -0.05 |
| LTD | 0.01 | 0.910 | -0.06 |
| Lthick | 0.70 | 0.416 | -0.02 |
| **$A_{area}$**[a] | **4.61** | **0.046** | **0.17** |
| $N_{area}$ | 0.18 | 0.673 | -0.05 |
| **$A_{mass}$*** [a] | **15.19** | **0.001** | **0.44** |
| $N_{mass}$ | 2.34 | 0.144 | 0.07 |
| $C_{mass}$[a] | 1.46 | 0.243 | 0.03 |
| SRL | 0.17 | 0.687 | -0.05 |
| RTD | 0.09 | 0.770 | -0.05 |
| Rdia | 0.15 | 0.707 | -0.05 |

[a] were influenced by *Torilis tenella*, the species with by far the lowest relative growth rate; without *Torilis tenella*: $A_{area}$ $F_{1,16} = 2.78$, $p = 0.115$, $R^2 = 0.09$; $A_{mass}$ $F_{1,16} = 10.77$, $p = 0.005$, $R^2 = 0.36$; $C_{mass}$ $F_{1,16} = 4.16$, $p = 0.058$, $R^2 = 0.16$

**Table S6.** Relations between species' mean annual rainfall niche (i.e. species' distribution along the rainfall gradient) and species' scores along the main trait axes (PC 1, PC 2), relative growth rate, or single traits. Given are the results of linear models. Traits significantly related to mean annual rainfall niche are highlighted in bold; traits remaining significant after Holm-Bonferroni correction for 15 tests (traits) are indicated with *. All traits were measured in 30 species ($F_{1,28}$) except of relative growth rate measured in 19 species ($F_{1,17}$). For trait abbreviations see Table 1.

| Trait | F | p | $R^2$ |
|---|---|---|---|
| PC 1 (structural trait axis) | 2.25 | 0.145 | 0.04 |
| PC 2 (carbon gain trait axis) | 0.50 | 0.486 | -0.02 |
| RGR | 0.31 | 0.587 | -0.04 |
| SLA | 0.63 | 0.434 | -0.01 |
| LDMC | 0.56 | 0.460 | -0.02 |
| LTD | 0.65 | 0.426 | -0.01 |
| Lthick | 0.89 | 0.353 | 0.0 |
| $A_{area}$ | 0.04 | 0.837 | -0.03 |
| $N_{area}$ | 0.02 | 0.882 | -0.03 |
| $A_{mass}$ | 0.00 | 0.967 | -0.04 |
| $N_{mass}$ | 0.69 | 0.413 | -0.01 |
| $C_{mass}$ | 0.12 | 0.734 | -0.03 |
| SRL | 0.01 | 0.940 | -0.04 |
| **RTD*** | 17.96 | < 0.001 | 0.37 |
| **Rdia** | 4.48 | 0.043 | 0.11 |

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**Method S1. Measurement of leaf silicon content and turgor loss point.**

Both leaf silicon content ($Si_{mass}$) and turgor loss point were assessed in all 30 investigated annuals on 6-11 individuals per species.

Leaf silicon content ($Si_{mass}$) was determined on the total leaf biomass harvested at the end of the plant's life cycle. Silicon was extracted by an alkaline method using 30 mg of oven-dried, grounded leaf material (bulk sample) and 30 ml of 0.1 M sodium carbonate solution ($Na_2CO_3$) in a water bath for five hours (see Struyf et al., 2010). The solution was subsequently passed through a 0.2 µm syringe filter (ChromafilXtra CA-20/25) and its silicon concentration was determined with inductively coupled plasma optical emission spectrometry (ICP-OES) using a Varian Vista-Pro Radial element analyser (Varian Inc., Palo Alto, USA).

Turgor loss point was calculated based on osmotic potential at full turgor determined with an osmometer (Vapor Model 5600, Wescor, Logan, Utah, USA) on leaf discs (one disc per plant) from plants fully hydrated overnight 8-12 weeks after sowing following Bartlett et al. (2012) and Sun et al. (2020).

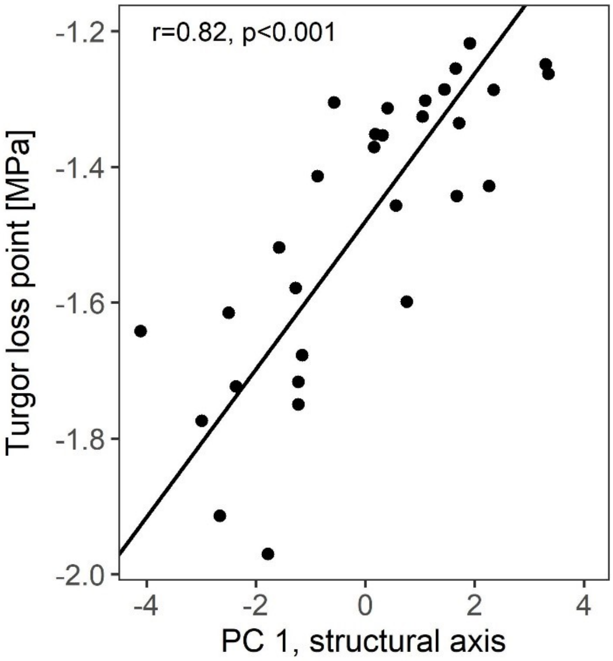

**Figure S3.** Relation between species' scores along the structural trait axis (PC 1) and turgor loss point (see Method 1). Relation was analysed with Spearman rank correlation coefficient (r).

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Sun, S., Jung, E., Gaviria, J., & Engelbrecht, B. M. J. (2020). Drought survival is positively associated to high turgor loss points in temperate perennial grassland species. *Functional Ecology, 34,* 788–798. https://doi.org/10.1111/1365-2435.13522

## List of additional manuscripts not included in this thesis

Klotz, M., Schaller, J., Kurze, S., & Engelbrecht, B. M. J. (2021). Variation of foliar silicon concentrations in temperate forbs: effects of soil silicon, phylogeny and habitat. *Oecologia, 196,* 977–987. https://doi.org/10.1007/s00442-021-04978-9

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