New Phytologist

Among-population variation in drought responses is consistent across life stages but not between native and non-native ranges

Dávid U. Nagy[1], Arpad E. Thoma[1], Mohammad Al-Gharaibeh[2], Ragan M. Callaway[3], S. Luke Flory[4], Lauren J. Frazee[5], Matthias Hartmann[6], Isabell Hensen[1,7], Kateřina Jandová[8], Damase P. Khasa[9], Ylva Lekberg[10,11], Robert W. Pal[12], Ioulietta Samartza[13,14], Manzoor A. Shah[15], Min Sheng[16], Mandy Slate[17], Claudia Stein[18], Tomonori Tsunoda[19] and Christoph Rosche[1,7]

[1]Institute of Biology/Geobotany and Botanical Garden, Martin Luther University Halle-Wittenberg, Halle, 06108, Germany; [2]Department of Plant Production, Faculty of Agriculture, Jordan University of Science and Technology, Irbid, 22110, Jordan; [3]Division of Biological Sciences, University of Montana, Missoula, MT 59812, USA; [4]Agronomy Department, University of Florida, Gainesville, FL 32611, USA; [5]Department of Ecology, Evolution, & Natural Resources, Rutgers University, New Brunswick, NJ 08901, USA; [6]Thünen Institute of Biodiversity, Braunschweig, 38116, Germany; [7]German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Leipzig, 04103, Germany; [8]Institute for Environmental Studies, Faculty of Science, Charles University, Prague, CZ-12801, Czech Republic; [9]Centre for Forest Research and Institute for Integrative and Systems Biology, Université Laval, Quebec, QC, G1V0A6, Canada; [10]MPG Ranch Missoula, Florence, MT 59833, USA; [11]Department of Ecosystem and Conservation Sciences, W.A. Franke College of Forestry and Conservation, University of Montana, Missoula, MT 59812, USA; [12]Department of Biological Sciences, Montana Technological University, Butte, MT 59701, USA; [13]School of Biology, Aristotle University of Thessaloniki, Thessaloniki, 54124, Greece; [14]Institute of Plant Breeding and Genetic Resources, Hellenic Agricultural Organization Demeter, Thessaloniki, 57001, Greece; [15]Department of Botany, University of Kashmir, Srinagar, Jammu & Kashmir, 190006, India; [16]College of Forestry, Northwest A&F University, Yangling, Shaanxi, 712100, China; [17]Department of Ecology and Evolutionary Biology, University of Colorado, Boulder, CO 80309, USA; [18]Department of Biology and Environmental Science, Auburn University at Montgomery, Montgomery, AL 36124, USA; [19]Bioscience and Biotechnology, Fukui Prefectural University, Fukui, 910-1195, Japan

Author for correspondence:
Dávid U. Nagy
Email: davenagy9@gmail.com

Received: *5 June 2023*
Accepted: *25 May 2024*

New Phytologist (2024) **243:** 922–935
doi: 10.1111/nph.19895

Key words: climate change, *Conyza canadensis*, drought responses, intraspecific variation, invasiveness, natural selection, ontogeny, plasticity.

Summary

- Understanding how widespread species adapt to variation in abiotic conditions across their ranges is fundamental to ecology. Insight may come from studying how among-population variation (APV) in the common garden corresponds with the environmental conditions of source populations. However, there are no such studies comparing native vs non-native populations across multiple life stages.
- We examined APV in the performance and functional traits of 59 *Conyza canadensis* populations, in response to drought, across large aridity gradients in the native (North America) and non-native (Eurasia) ranges in three experiments. Our treatment (dry vs wet) was applied at the recruitment, juvenile, and adult life stages.
- We found contrasting patterns of APV in drought responses between the two ranges. In the native range, plant performance was less reduced by drought in populations from xeric than mesic habitats, but such relationship was not apparent for non-native populations. These range-specific patterns were consistent across the life stages.
- The weak adaptive responses of non-native populations indicate that they can become highly abundant even without complete local adaptation to abiotic environments and suggest that long-established invaders may still be evolving to the abiotic environment. These findings may explain lag times in invasions and raise concern about future expansions.

Introduction

Water availability is a major determinant of plant growth, reproduction, abundance, and distribution. Plants deal with low water availability through various strategies. For example, plants can escape dry periods by altering their phenology (Rauschkolb *et al.*, 2023) or they can avoid drought by adjusting functional traits related to transpiration, such as specific leaf area, root : shoot ratio, and leaf dry matter content (Blumenthal *et al.*, 2020). However, it is still not thoroughly understood how functional traits mediate the effects of drought on plant performance, particularly at the intraspecific level (Westerband *et al.*, 2019; González de Andrés *et al.*, 2021; Dawson *et al.*, 2024). This is an issue in global change ecology because the frequency and severity of drought events are rapidly shifting through climate change (Cook *et al.*, 2018). The understanding of adaptation to drought is therefore crucial for predicting future species distributions, such as range expansions by invasive species or the persistence of plant populations experiencing climate change (Moritz, 1994; Colautti *et al.*, 2009; Pratt &

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Mooney, 2013; Rosche *et al.*, 2018a; Exposito-Alonso *et al.*, 2019).

Studies on the drivers of among-population variation (APV) have a pivotal role for our understanding of adaptation to environmental stress, such as drought. These studies often include experimental treatments (e.g. drought treatment) to study how populations that sourced from diverse environmental gradients (e.g. aridity gradient spanning from mesic to xeric conditions) differ in their responses to the treatment (Lucas *et al.*, 2024). If the responses to drought follow aridity gradients of the source populations, such experiments indicate adaptation to drought. Thus, by examining APV in drought responses, we can gain valuable insights into the adaptive potential of plant species which may help predicting how plant populations evolve to changing environmental conditions, including those driven by climate change (Montesinos-Navarro *et al.*, 2011; Alexander *et al.*, 2012; Pratt & Mooney, 2013).

There are several possible patterns of how the performance of populations originating from a gradient in aridity (mesic to xeric) can differ between dry and wet experimental treatments (Fig. 1, Supporting Information Fig. S1). Plants may grow less in dry than wet treatments but do so in the same way across the aridity gradient (i.e. purely plastic response to the treatment; Fig. 1a). Adaptive APV in drought responses would be evident if plants from mesic habitats demonstrate a large change in performance (Δ performance) between wet and dry conditions, whereas plants from xeric habitats showed a smaller Δ performance (i.e. decreasing Δ performance with increasingly xeric habitats; Fig. 1b). This would create a significant two-way interaction between the response to drought and mesic vs xeric population sources. The opposite pattern may occur when Δ performance increases with increasingly xeric habitats (Fig. 1c). However, this pattern would be unexpected as populations from xeric environments would appear to be less adapted to drought than populations from mesic environments.

To properly assess the adaptive potential to drought, it is crucial to sample across broad spatial and bioclimatic gradients. However, only a limited number of studies have undertaken global-scale samplings of APV in drought responses (Cook *et al.*, 2018; Dawson *et al.*, 2024). Among these, Exposito-Alonso *et al.* (2019) examined the effects of drought on 517 *Arabidopsis thaliana* populations. They showed that populations from the edges of the environmental limits of *A. thaliana* experienced the strongest climate-driven selection. However, the study solely included native populations, which have a long history of *in situ* evolution in arid conditions. Comparing mesic to xeric gradients in native vs non-native populations can offer insights into the evolutionary time scales of natural selection. In particular, while native populations may adapt to local environmental conditions through numerous generations, non-native populations often undergo rapid range expansions across diverse environmental conditions (Broennimann *et al.*, 2014). Thus, range expansions can lead to a more stochastic distribution of genotypes in non-native ranges as compared to a more deterministic distribution of genotypes (along environmental gradients) in native ranges (Keller & Taylor, 2008; Rosche *et al.*, 2016, 2018b; Nagy *et al.*, 2018). Non-native populations may counteract such random distribution of genotypes through rapid evolution (Callaway & Maron, 2006; Alexander *et al.*, 2009; Vandepitte *et al.*, 2014; van Kleunen *et al.*, 2018), which can result in the emergence of locally adapted genotypes over time. However, whether rapid evolution can result in comparable APV in drought responses between native and non-native ranges remains poorly understood (Dlugosch *et al.*, 2015). Mráz *et al.* (2014) found that APV in drought responses was differently pronounced in native than in non-native populations of *Centaurea stoebe*. In addition, functional traits were less correlated with environmental gradient in non-native than native populations of *Plantago lanceolata* (Villellas *et al.*, 2021), which might be due to the lack of time to adapt to the new environments in the non-native range. In the context of Fig. 1, such differences in the patterns of adaptive variation between ranges would be illustrated by a significant three-way interaction (range × drought treatment × aridity of the source populations, see Fig. 1d).

So far, the studies on annual species that sampled broad bioclimatic gradients focused exclusively on adult plants. On smaller bioclimatic scales, there are studies that investigated APV at early life stages (e.g. Al-Gharaibeh *et al.*, 2017; Birkeli *et al.*, 2023). However, we are not aware of studies that compared APV in drought responses across several life stages. This comparison may be important because the impact of drought can significantly differ between seedlings and adults, likely with stronger effects observed at the seedling stage (Niinemets, 2010; Coe *et al.*, 2021). Investigating ontogenetic variation may also help understanding whether and how selection pressure on functional traits related to drought vary across different life stages (Mitchell & Bakker, 2014; Zirbel & Brudvig, 2020; Havrilla *et al.*, 2021).

To address the apparent research gaps, we studied APV in drought responses for 30 native and 29 non-native populations of *Conyza canadensis* (Canadian fleabane) collected across broad aridity gradients in both the native and the non-native ranges. In a green house, three complementary experiments were conducted in which plants of the (1) recruitment (i.e. germination and early seedling development), (2) juvenile, and (3) adult life stages were subjected to wet and dry treatments. We hypothesize that:

(**1**) Due to adaptation along the aridity gradient, populations from xeric habitats exhibit greater resistance to drought than populations from mesic habitats, resulting in evolutionary expected patterns of APV in drought responses (i.e. decreasing Δ performance in Fig. 1b).

(**2**) Because of a longer timeframe for evolution, such relationship is more pronounced in native populations than in non-native populations, resulting in significant three-way interactions between range, aridity gradient, and the drought treatment (i.e. differently expressed Δ performance between rages in Fig. 1d).

(**3**) Because seedlings are less drought resistant than adults, adaptive responses to drought are more pronounced at the seedling and juvenile stages than for adults.

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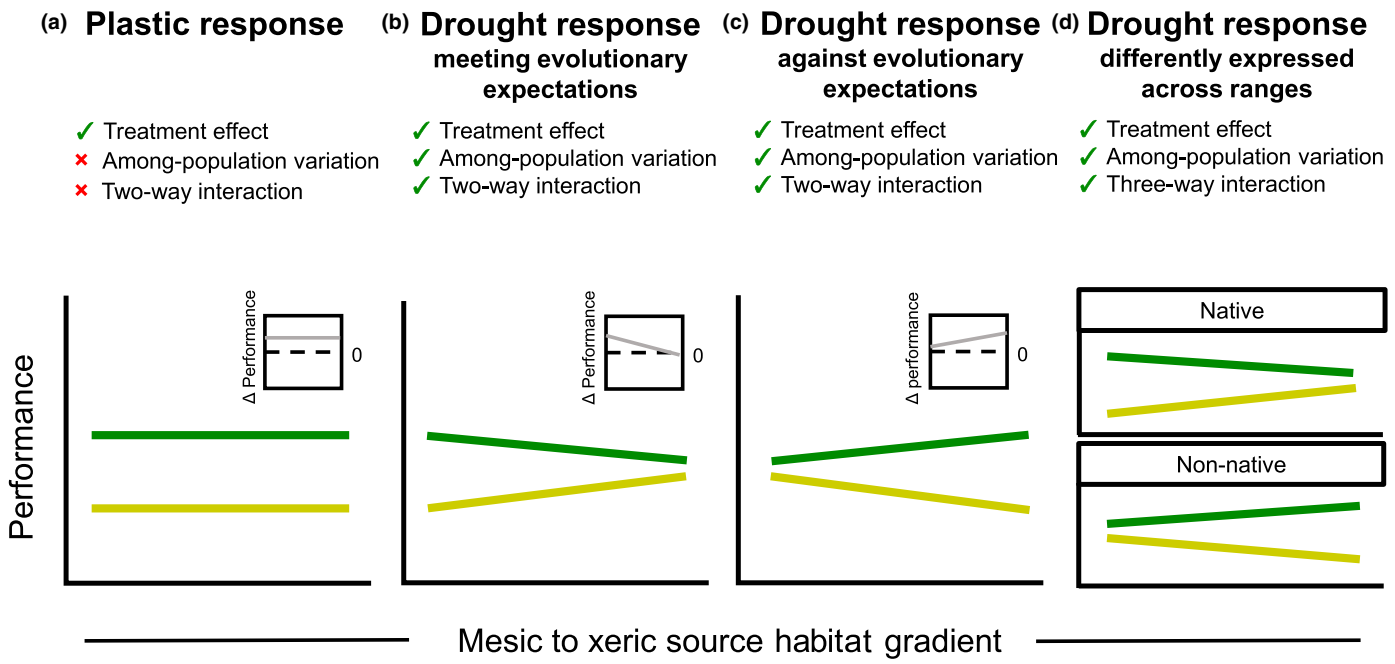

Fig. 1 Predictions for the performance of *Conyza canadensis* populations under wet (green lines) and dry experimental conditions (yellow lines) along a gradient in how often and severe drought occurs in the source populations (i.e. aridity gradient from mesic to xeric source habitats). This conceptual figure illustrates potential scenarios of change in performance (Δ performance) between wet and dry treatments across the aridity gradient, aiming to demonstrate its change along the gradient, though not explicitly depicting all possible scenarios of wet and dry lines. For the sake of clarity, the populations have not been included (e.g. as dots) but only their linear response for the two drought treatments along the aridity gradient (Supporting Information Fig. S1 for a more detailed figure including populations). In (a), drought affects plant Δ performance, but the aridity gradient does not (constant Δ performance). In (b, c), treatment affects plant performance and the aridity gradient affects Δ performance (i.e. among-population variation in drought response can be explained by the aridity gradient). Out of these two scenarios, (b) meets evolutionary expectations where increasing aridity of the source populations results in decreasing Δ performance, whereas (c) presents the opposite response (increasing Δ performance), that is, against evolutionary expectations. In (d), drought response is differently expressed between native and non-native ranges. Note that this pattern represents one example out of the many possible three-way interactions, which would indicate that native populations follow evolutionary expectations whereas non-native populations do not. Another possible scenario is when performance does not respond to the experimental drought (not presented in the figure), but in that case, the experiment would not fulfill the condition to test our hypotheses.

Materials and Methods

Study species

Conyza canadensis (L.) Cronq. is an annual, selfing species in the Asteraceae family with a short life cycle (6–12 months). The species primarily colonizes ruderal habitats and is also growing as a weed of arable lands (Weaver, 2001). Its native range covers much of North America and its non-native range includes most of the rest of the Northern Hemisphere. *Conyza canadensis* was introduced to Europe *c.* 350 yr ago, to China *c.* 150 yr ago, and to Kashmir just *c.* 80 yr ago (Shah *et al.*, 2014). In some parts of this non-native range, *C. canadensis* can be invasive by suppressing native biodiversity (Shah *et al.*, 2014).

Aridity experienced in the field was shown to be the most important environmental determinant of both field and green house plant growth performance (Rosche *et al.*, 2019). Recent precipitation experiments have indicated that drought could indirectly promote invasion success when increasing the abundance of *C. canadensis* relative to native competitors (Mojzes *et al.*, 2020). This observation aligns with the findings in Rosche *et al.* (2019), suggesting that the ability to respond drought might play an important role in the invasive success of *C. canadensis*. More generally, *C. canadensis* serves as an excellent model species for studying the drivers of APV due to its remarkable potential for rapid adaptation to diverse environmental conditions (Bajwa *et al.*, 2016; Rosche *et al.*, 2019) and biotic interactions (Sheng *et al.*, 2022), which is likely attributable to its annual life cycle and self-pollinating reproduction (Peischl *et al.*, 2015; Rosche *et al.*, 2019). The very low genetic variability within *C. canadensis* populations enables estimating APV with a small number of individuals per population (Rosche *et al.*, 2019; Sheng *et al.*, 2022).

Sample populations

We sampled 30 native and 29 non-native populations from 17 different geographical regions across the Northern Hemisphere (Fig. 2a; Table S1). In each region, populations were separated by a minimum of 10 km. The populations occurred across a broad climatic gradient, including six out of the nine Whittaker biomes (Fig. 2b). From each population, we sampled matured seeds from five individuals (in total 295 plants). These plants

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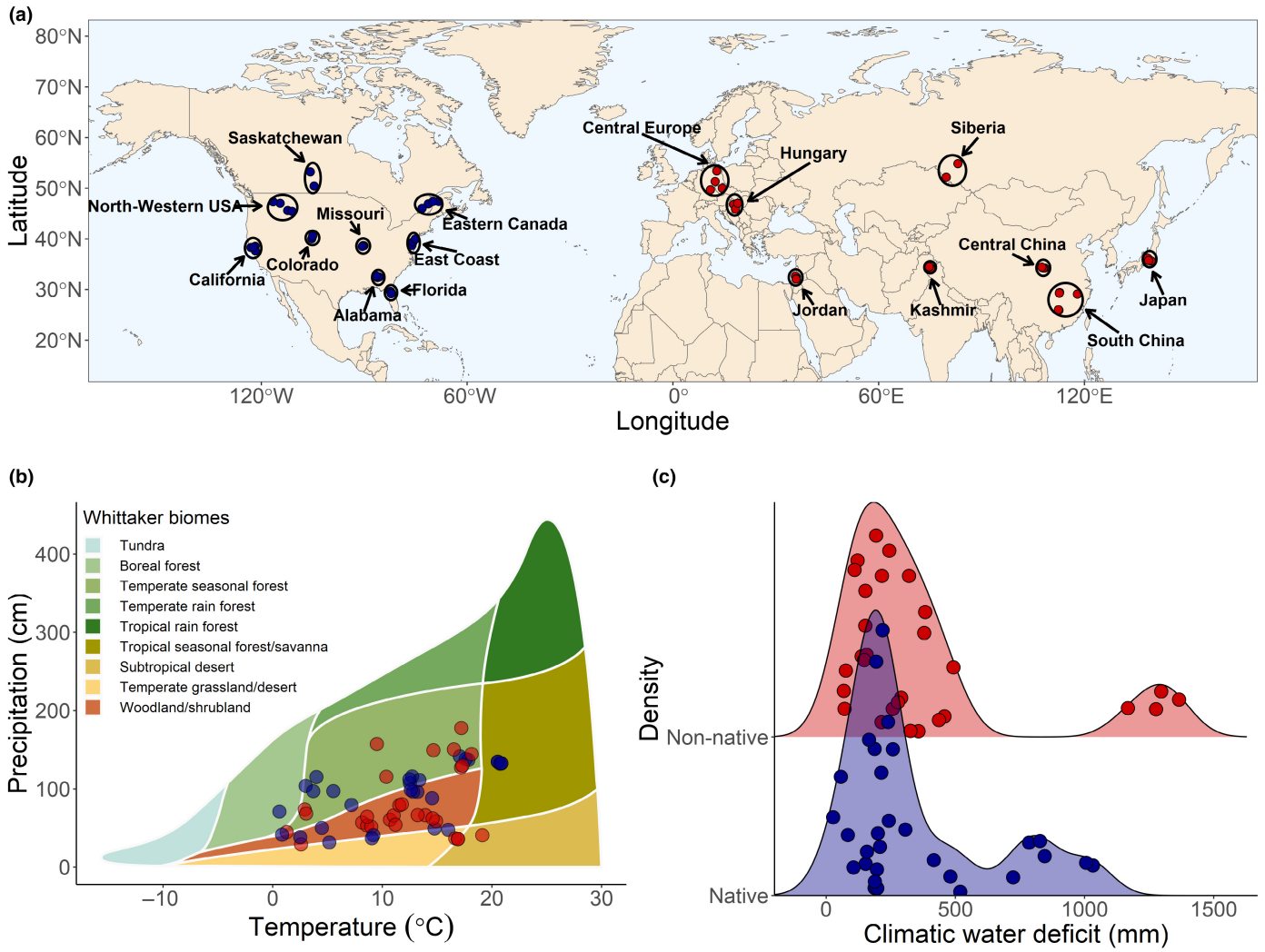

Fig. 2 Spatial and bioclimatic distribution of 30 native (blue) and 29 non-native (red) *Conyza canadensis* populations used in the present study. In panel (a), geographical distribution of the populations across nine native and eight non-native regions are presented. In panel (b), populations are plotted according to their mean annual temperature and precipitation on a Whittaker diagram, illustrating the wide bioclimatic gradients where the species can occur. In panel (c), the comparison of climatic water deficit (CWD) between native and non-native populations is presented. Climatic water deficit data were downloaded from the TerraClimate database (Abatzoglou *et al*., 2018). Precipitation and temperature data were downloaded from the CliMond database (Kriticos *et al*., 2012).

were selected randomly across an area that was *c*. 30 × 30 m in size, keeping at least 5 m distance among the sampled individuals. To estimate the aridity patterns experienced by populations (i.e. local aridity regime), monthly climatic water deficit (CWD) data were obtained for each population, using the TerraClimate dataset (Abatzoglou *et al*., 2018) at a spatial resolution of 1/24° (*c*. 4 km). The CWD quantifies unmet evaporative demand by calculating the difference between actual and potential evapotranspiration. Thus the CWD represents the missing water that would be needed to maximize plant growth (Young *et al*., 2021), and with that captures the local aridity conditions of the source populations. The populations from the native and non-native ranges were sampled from comparable gradients (Fig. 2c; *t*-test: df = 58, $t = 0.025$, $P = 0.989$). The variation in CWD was higher among regions (SD: ±319.11 mm) than within regions (SD: ±79.03 mm).

General experimental design

To avoid immediate maternal effects from the field, a potential bias in offspring fitness in common garden experiments (de Villemereuil *et al*., 2016), F1 offsprings were produced. To do so, offspring from the five seed families collected in the field were raised by covering inflorescences with a mesh bag until achenes were mature to prevent cross-pollination. Of the 295 seed families sampled, 270 produced seeds as F1 generation (the 25 seed families that failed to produce seeds were evenly distributed across populations and regions).

To compare the effects of drought across life stages, three separate experiments were conducted in parallel, focusing on (1) seeds and seedlings (recruitment life stage), (2) juveniles (3 wk after germination), and (3) adult plants (2 months after germination). In each experiment, 540 plants were included (270 seed

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families × 2 drought treatments (wet, dry)), using independent seeds from the same seed families.

In each experiment, three performance and three functional traits were assessed (Fig. 3). The performance traits included the above- and belowground biomasses as well as a transition trait. The latter was a binomial measure on the proportion of individuals that successfully passed the respective life stage, including germination in the recruitment life stage, survival in the juvenile life, and flowering in the adult life stage. The functional traits included specific leaf area (SLA = leaf area/leaf dry biomass), leaf dry matter content (LDMC = leaf dry biomass/leaf fresh biomass), and root : shoot ratio (RSR = shoot dry biomass/root dry biomass).

Development at the recruitment stage A germination trial was performed to investigate how plant performance and functional traits at the recruitment life stage responded to drought and how these responses correlated with CWD across native vs non-native ranges. Due to the need for precise control over experimental conditions, we conducted this experiment in Petri dishes (Winkler *et al.*, 2024). To determine a suitable osmotic potential of the dry treatment (i.e. that affects but not inhibits germination and seedling development), a preliminary experiment was performed. In this preliminary experiment, we used six seed families from six randomly selected populations and tested their response in germination and early seedling performance traits to six different mannitol concentrations ranging from 0 MPa (tap water) to −1 MPa. Based on the results of this preliminary experiment (Fig. S2), two treatments were chosen for the main experiment, that is tap water for wet conditions (*c.* 0 MPa) and mannitol solution for dry conditions (−0.8 MPa). The main experiment was performed with the 270 seed families. Ten seeds per seed family and treatment were germinated in Petri dishes, on filter paper (Whatman No. 1). Dishes were sealed with Parafilm, daily re-saturated with tap water to maintain consistent concentrations, and kept in a germination chamber at 20°C at 12 h day (176 µmol m^{-2} s^{-1}) and 10°C at 12 h night. Positions of Petri dishes were randomized daily. Germination (i.e. when radicle breaks through seed coat) was recorded daily with a stereomicroscope. The germination trial ended when no new germination had occurred for five consecutive days.

To assess traits at the recruitment life stage of *C. canadensis*, one seedling per seed family and treatment was transferred to another Petri dish and maintained under the same experimental conditions (0 vs −0.8 MPa). After 10 d, the roots (hypocotyl) were separated from the shoots (epicotyl). One leaf was immediately weighed for fresh weight, and the leaf area was scanned using WinFolia software (Regent Instruments, Quebec, QC, Canada). Roots and shoots were then placed separately in paper bags and dried (48 h at 60°C) to record dry mass.

Growth of juveniles A green house experiment was performed during the spring and summer of 2021 to investigate how performance and functional traits at the juvenile life stage responded to the wet vs dry experimental treatments and how these responses correlated with CWD across both ranges. Temperature was set between 20°C and 25°C at day and 10–15°C at night. Artificial light (between 07:00–09:00 and 16:00–18:00 h; 334 µmol m^{-2} s^{-1}) was provided during the first month of the experiment. Five hundred and forty pots (Stuewe and Sons, Tangent, OR, USA; Deepot, D40H, 6.3 × 25 cm, 650 ml) were filled with a water-saturated mixture of sand and local field soil

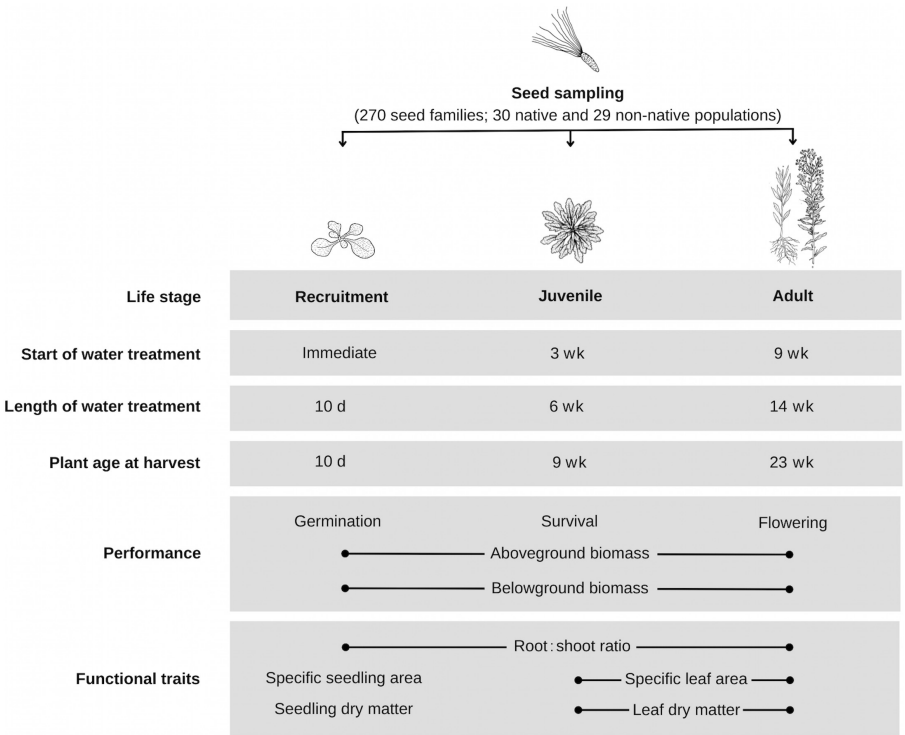

Fig. 3 Flowchart illustrating the design of the three experiments and data collection. The drought response of *Conyza canadensis* was tested with two levels using wet vs dry conditions.

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in a 1 : 1 ratio until a total weight of 600 g. From each seed family, seeds were sown in two pots (2 treatments × 270 seed families = 540 pots). After germination, individuals were randomly thinned out, leaving one individual per pot. Pots were watered equally every 2 d until the pots were transferred to either the wet or dry treatment, which was when the rosette diameter reached an average of 2 cm.

To have comparable conditions at the start of the treatment, all pots for both the wet and dry treatments were again watered until saturation (*c.* 30% soil water content measured with Theta Probe Typ ML2x Soil Moisture Device (Delta T Devices, Cambridge UK)). After that saturation, the treatment was applied in the following way: Every Monday, Wednesday, and Friday, 59 randomly chosen pots (one from each population) from the wet treatment were weighed. The average pot weight was then subtracted from the average pot weight at saturation (600 g). This difference was the average water loss. This amount of water in mL was added individually to each pot in the wet treatment using a bottle-top dispenser, while the dry treatment pots received 25% of the water added in the wet treatment. Treatments corresponded to the mean precipitation of the humid South Chinese populations and dry Northwestern USA populations in May (details on the added amount of water are in Table S2). The position of single pots within trays and the position of the trays within the green house were randomized weekly.

At harvest, an average size leaf from each individual was collected and measured for fresh biomass and leaf area with WinFolia software. Roots and shoots were also harvested and, together with leaf samples, dried for 2 d at 60°C, and then weighed.

Growth of adults Another green house experiment was performed under the same conditions as for the juvenile experiment. This experiment investigated how performance and functional traits at the adult life stage respond to wet vs dry treatments and how these responses correspond with range and CWD. Five hundred and forty pots (1450 ml; Lamprecht-Verpackungen GmbH, Göttingen, Germany, 11 × 11 × 12 cm) were set up in the green house. The pots were filled with a water-saturated mixture of sand and local field soil in a 1 : 1 ratio, weighing 1300 g. From each seed family, seeds were sown in two pots (2 treatments × 270 seed families = 540 pots). Pots were watered equally with a sprayer every 2 d until they were transitioned to either the wet or dry treatment, which was 2 months after peak germination, that is the same time at which pots with juveniles were harvested. Treatments were performed the same way as the juvenile experiment. Treatments corresponded to the mean precipitation of the humid Alabama populations and dry Northwestern USA populations in May–July (details on the added amount of water are in Table S2).

Plants were harvested 14 wk after the watering treatment was initiated, at the peak of the flowering. During the harvest, an average size leaf of each individual was collected and measured for fresh biomass and leaf area with WinFolia software. Roots and shoots were also harvested and together with the leaf samples dried for 2 d at 60°C, after which dry mass was recorded. To keep the measured performance traits comparable across life stages, we did not weigh the reproductive biomass, even though it could serve as a proxy of reproductive fitness.

Monitoring the effects of the drought treatment

To monitor the soil moisture as an effect of the applied treatment, 118 additional pots (59 populations × 2 treatments) were set up in parallel to the experimental pots. These 118 monitoring pots have been installed in both the juvenile and the adult experiment separately. Soil moisture was measured in these additional pots every Monday for the juvenile experiment and every second Monday for the adult experiment, using a Theta Probe Typ ML2x Soil Moisture Device (Delta T Devices) (Fig. S3a,b). In parallel to the soil moisture measures, the weight of the 118 pots was recorded (Fig. S3c,d). It is important to note that these 118 additional pots were treated equally to the experimental pots but were solely used for the purpose of monitoring. The additional pots were not used for any of the abovementioned trait measurements, because the soil moisture measures cause disturbance that could influence plant performance (e.g. through harming the roots).

In addition, we measured the stomatal conductance and recorded the leaf $\delta^{13}C$ isotope ratio in 120 random individuals from both juvenile and adult experiments at harvest. These measures served to record the effects of drought on *C. canadensis* individuals at the end of the experiment and were measured on experimental plants (Fig. S3e–h). Measuring stomatal conductance and leaf $\delta^{13}C$ isotope ratio provides direct physiological indicators of plant response to water stress, offering insights into water use efficiency (Mininni *et al.*, 2022). These trait data were solely used to test the efficacy of the applied treatment and were not used to test our main concept (i.e. the three-way interaction).

The stomatal conductance was measured on the largest leaf of each plant using an AP4 Porometer (Delta T Devices). The porometer was calibrated before each measurement. The $\delta^{13}C$ isotope ratio was determined from grounded leaf samples with an elemental analyzer Flash 2000 with a TCD detector that was coupled to a Conflo IV and mass spectrometer Delta V Advantage (Thermo Fisher Scientific, Bremen, Germany). The carbon isotope ratio is expressed as follows: $\delta^{13}C = (R_{sample}/R_{standard} - 1) \times 1000$, where R is the relative abundance of the carbon isotopes ($R = {}^{13}C/{}^{12}C$). The isotope ratio was normalized by using international standards. In addition to the repeated measurements of a series of international standards (e.g. IAEA-CH3, IAEA-CH6, and IAEA-600), a glycine standard was run after every 10th sample to calibrate the elemental composition determinations and to quality control for the isotopic measurements. The carbon isotope ratios were reported using the Vienna Pee Dee Belemnite (VPDB) scale. The analytical precision was within ±0.2‰ for the isotope ratios.

Statistical analyses

Performance and functional trait analyses were conducted with linear mixed-effects models using the R package lme4 v.1.1-29 (Bates *et al.*, 2015). Random factors were as follows: (1) seed family nested within population nested within region, (2)

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population nested within region, and (3) region. Explanatory variables were the interactive effects of range, treatment, and transformed (centered) CWD. To assess significance of the explanatory variables, we employed stepwise backward model selection, based on chi-square and Akaike information criterion (AIC) values. Both methods provided consistent results. Variables remained untransformed, except for the aboveground and belowground biomasses which were log-transformed. Germination, survival, and flowering were analyzed as binomial response variables with generalized linear mixed-effects models.

With respect to the local CWD estimate, we initially sought a suitable proxy by examining whether the responses to drought were more closely associated with annual or seasonal CWD values in the sampled populations. Specifically, we compared the model performance of the annual CWD and four seasonal CWDs for 3-month-long periods (spring: March–May, summer: June–August, autumn: September–November, and winter: December–February). Based on AIC and chi-square values, we found that annual CWD values consistently showed the best model performances across the 18 response variables (Table S3).

Germination was also analyzed in terms of timing using a time-to-event analysis performed with mixed-effects Cox models, using the R package COXME v.2.2-16 (Therneau, 2012). The same model structure (explanatory variables and random effects) as for the mixed-effects models above was used, again applying stepwise backward model selection based on chi-square and AIC values. Cox proportion hazards were checked via Kaplan–Meier plots and multicollinearity was checked via variance inflation factor (VIF) for each model individually (McNair *et al.*, 2012).

In addition to analyzing the recorded absolute values of performance and functional traits, we calculated plasticity indices for every trait to evaluate plasticity in response to drought. To do so, we adopted the simplified Relative Distance Plasticity Index (RDPI), a commonly used metric to assess plasticity in response to environmental conditions (Valladares *et al.*, 2006). Valladares *et al.* (2006) originally proposed the usage of relative distances per individual to calculate RDPIs, which involves comparing the trait values of individuals within populations. Because populations differed in the number of deaths and how these were distributed across the seed families, we calculated population mean plasticity indices instead of using individual seed family values. RDPIs for a given trait were calculated as:

$$\mathrm{RDPIs} = \frac{|\mathrm{Tw} - \mathrm{Td}|}{\mathrm{Tw} + \mathrm{Td}}$$

where Tw and Td represented mean trait values for each population in the wet and dry treatments, respectively. The RDPI values were then tested for differences between ranges with linear mixed-effects setting region as a random effect.

To investigate whether the effect of drought on performance traits was determined by functional traits, we tested for Pearson correlations between the RDPI values of the measured performance traits and the values of the functional traits of the respective population in the dry treatment. These correlations were recorded separately for each of the three life stages.

In addition, we used log-response ratios to quantify the effect size of the treatment. Log-response ratios are frequently used in ecological research because they allow comparing differences in the magnitude of treatment effects across diverse variables. They are calculated by taking the natural logarithm of the ratio of the response variable (e.g. aboveground biomass) in the treatment group (e.g. dry treatment) to that in the control group (e.g. wet treatment). To test whether the effects of drought were consistent across the life stages, four separate linear mixed-effects models were run, using the log-response ratios of each performance traits, setting population nested within region, and region. The maximal models included the following: (1) the three-way interactions of range × centered CWD × life stage, (2) the two-way interactions of centered CWD × life stage, (3) range × life stage, and (4) the main effect of life stage. To compare the individual trait values across the life stages, each trait values were standardized within life stages.

We also assessed the extent of spatial autocorrelation in our models on the performance traits. Our data showed evidence for spatial autocorrelation due to the regional structuring of the data and we found that setting population nested within region, and region as random effects appropriately accounted for this spatial autocorrelation (for more details see Notes S1; Table S4).

Results

Effects of drought on performance and functional traits

The applied treatment affected eight out of nine performance traits (three measurements × three life stages, Fig. 4, for details of the models, see Table S5). Plants grown in the wet treatment produced 50–450% more above- and/or belowground biomass than plants in dry treatments, demonstrating significant variation in biomass across different performance traits across life stages. Germination rate was the only trait not affected by the treatment (Fig. 4a). However, the time-to-event analysis suggested a greater and faster germination through time in wet compared with dry conditions: on average, seeds in the wet treatment germinated 1 d earlier than seeds in the dry treatment ($\chi^2_{(1)} = 348.58$, $P < 0.01$; Table S6; Fig. S4).

The treatment affected functional traits in eight out of nine cases (Table S7; Fig. S5). Only LDMC at the adult life stage was not affected by the treatment (Fig. S5i). There was a shift in functional traits toward increased growth and resource acquisition by plants in the wet treatment: They showed a 14–30% higher SLA and 22–33% lower LDMC than in the dry treatment plants (Fig. S5g,h). Moreover, plants in the wet treatment had 16–32% higher RSR than plants in the dry treatment (Fig. S5a–c).

Correlations between functional traits and the RDPI values of the performance traits were not significant for any of the 27 possible cases (Fig. S6).

Differences between native and non-native ranges in drought responses

Five out of nine performance traits showed significant three-way interactions among range, treatment, and CWD (Fig. 4;

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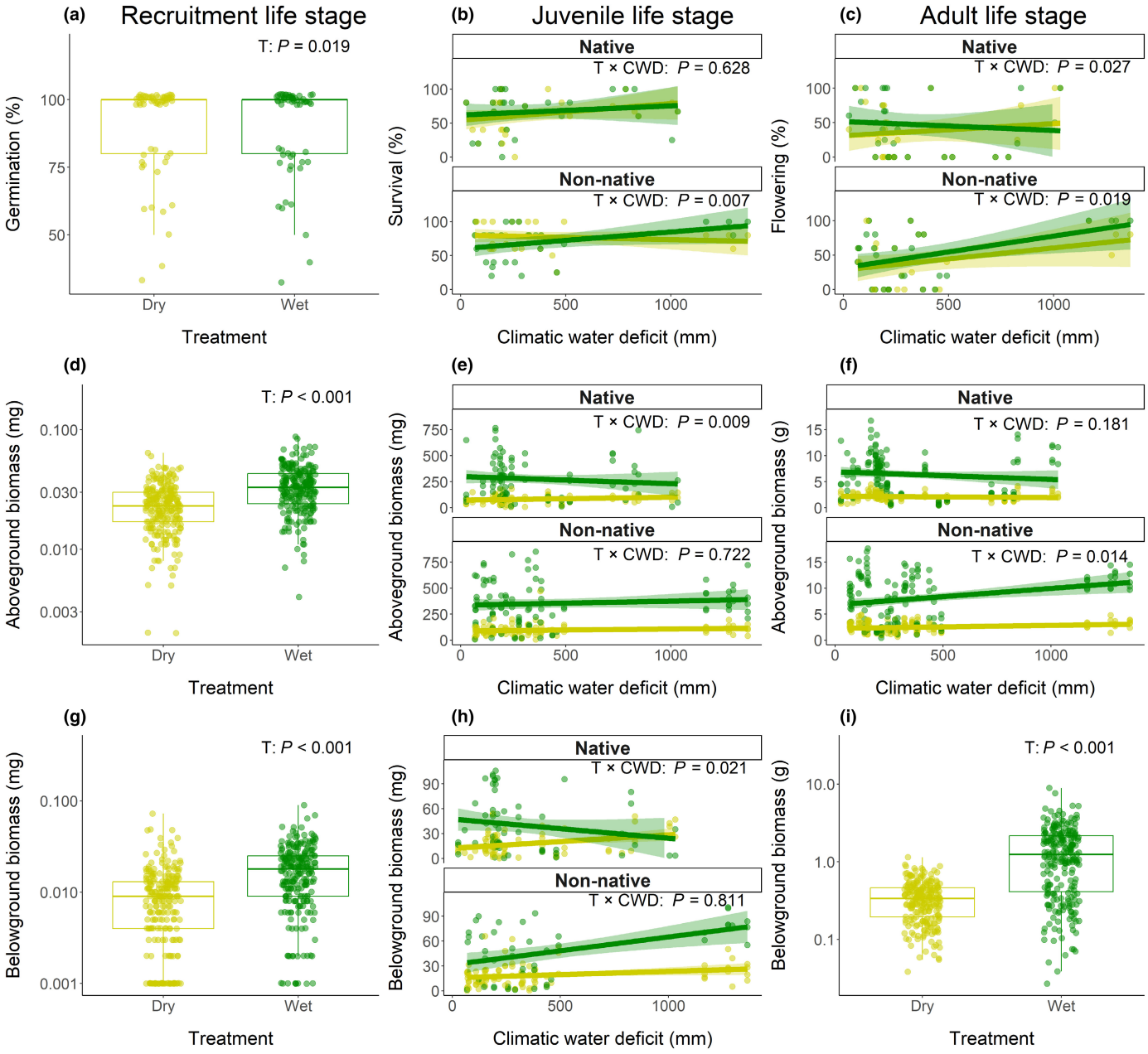

Fig. 4 Interactive effects of the applied treatment (T: dry vs wet), climatic water deficit (CWD), and range affiliation (native vs non-native) on the performance of *Conyza canadensis* for germination (a), survival (b), and flowering (c), aboveground biomasses (d–f), and belowground biomasses (g–i). Performance traits were recorded across three experiments focusing on the following life stages: recruitment life stage (a, d, g), juvenile life stage (b, e, h), and adult life stage (c, f, i). The panels represent the results of the respective minimum adequate models (i.e. including only significant terms), except for the response variables where none of the three tested explanatory factors or their interactions had a significant effect (here: germination rate (a)). For germination, survival, and flowering rate, data were analyzed at the individual level (binomial), but population means were plotted as percentages for the sake of clarity. Coloring is based on the applied treatment (dry: yellow, wet: green). Boxplots show the interquartile range with the solid line indicating the median, and whiskers the max and min values without outliers (calculated as 1.5 times the interquartile range). The confidence intervals of the lines are presented as shadings. Details on the models and results are found in Supporting Information Table S5. Increasing CWD refers to more arid conditions. In case of significant three-way interactions, we ran two separate models to test the interaction between T and CWD for native and non-native ranges (presented in the figure).

Table S5). However, if the three-way interaction was not significant, there was also no two-way interaction between CWD and treatment. In other words, whenever APV in the response to drought was present (e.g. Fig. 1b or c), the patterns differed between native and non-native ranges (as in Fig. 1d). In particular, in the native range, the performance of populations from xeric habitats was less reduced by drought than that of mesic populations for adult flowering rate ($\chi^2_{(1)} = 4.82$, $P = 0.03$;

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Fig. 4c), and the aboveground ($\chi^2_{(1)} = 6.76$, $P = 0.01$; Fig. 4e) and belowground biomasses of juveniles ($\chi^2_{(1)} = 5.70$, $P = 0.02$; Fig. 4h). By contrast, for non-natives, no such relationships were found for the mentioned performance traits. For non-natives, APV in drought responses was present for juvenile survival ($\chi^2_{(1)} = 7.25$, $P = 0.01$; Fig. 4b), adult flowering ($\chi^2_{(1)} = 5.49$, $P = 0.02$; Fig. 4c) and aboveground biomass of adults ($\chi^2_{(1)} = 6.09$, $P = 0.01$; Fig. 4f), but they did not follow the evolutionary expectations because Δ performance (performance difference between wet and dry treatments) increased with aridity of the source populations. For the abovementioned responses, however, there was no APV in drought responses in the native populations.

Notably, as main effects, none of the nine performance traits differed between native and non-native populations (e.g. non-natives did not grow bigger, see Table S5). Furthermore, plasticity in response to drought did not differ between native and non-native populations for any of the nine performance traits (Fig. S7). This result means there were no mean differences between native and non-native populations in performance traits and their response to drought, yet how the aridity gradient of the source populations affected drought responses differed strongly across the ranges.

APV in the responses of functional traits to drought

Functional traits did not show a consistent pattern of APV in drought responses across life stages. Only for the SLA of adults (Fig. S5f), there was a significant three-way interaction ($\chi^2_{(1)} = 5.86$, $P = 0.02$) showing that APV in the response to drought differed between native and non-native ranges. Seedling dry matter content was the only trait with a significant two-way interaction ($\chi^2_{(1)} = 6.43$, $P = 0.01$) between drought and CWD (Fig. S5g). With range as a main effect, none of the nine functional traits differed between native and non-native populations, nor did plasticity in response to drought differ between native and non-native populations for any of the nine functional traits (Fig. S8).

Differences among life stages in the response to drought

For each of the three performance trait categories (i.e. transition traits, aboveground, and belowground biomasses), there was a significant difference among the life stages in how strongly the traits were affected by drought as a main effect (Table S8). There were overall smaller log-response ratios for the recruitment life stage than for the juvenile life stage (by 48.1–95.8%) and the adult life stage (by 41.7–95.5%). However, when comparing the standardized, individual trait values between wet and dry-treated plants, we found consistent patterns across all life stages (Fig. 5). In particular, germination, survival, and flowering did not differ between treatments across all life stages, but aboveground and belowground biomass was 50–450% greater in the wet than in the dry treatment across all life stages. More importantly, log-response ratios were not affected by the interaction between life stage and CWD or life stage and range or their three-way interactions (Table S8). These results indicate that the patterns of APV in drought responses were similar among the life stages.

Discussion

This research investigated APV in response to drought across three life stages while studying broad biogeographical scales in both native and non-native ranges. Drought affected performance and functional traits consistently at all life stages and across both ranges. According to our first hypothesis, native populations from xeric habitats were less inhibited by drought than mesic populations, displaying the evolutionarily expected pattern of APV in drought responses. By contrast, non-native populations did not follow this pattern confirming our second hypothesis. Patterns of drought responses were consistent across the life stages, contradicting our third hypothesis.

Effects of drought on performance and functional traits

Drought had consistent strong effects on plant performance traits across all life stages, setting the stage for testing our predictions. In terms of functional traits, drought decreased SLA and increased LDMC which is a common response of plants to increase stress tolerance by reducing fast growth (Balachowski & Volaire, 2018). Root : shoot ratio was reduced by drought, which was consistent across life stages but is not consistent with many other studies (e.g. Knight *et al.*, 2006; Qi *et al.*, 2019). However, investing resources in increasing RSR under drought may be more advantageous for perennial plants than for short-lived annuals, as the developed root system may be more cost-effective in multiple years than in a single season (Mokany *et al.*, 2006). Instead, *C. canadensis* may invest more into shoot growth in order to more quickly complete its annual life cycle under drought stress (Brandenburger *et al.*, 2022), therefore essentially escaping periods of drought (Volaire, 2018).

The weak relationships between functional traits and the response of performance traits to drought suggest that the measured functional traits have either weak or complex effects on how *C. canadensis* copes with drought stress. Also, previous studies estimating the relationship between plant functional traits and fitness have shown mixed results, with some predicting variation in performance, while others have not (Caruso *et al.*, 2020). Drought stress may require multidimensional responses that may not be captured by single functional traits (Kooyers, 2015). Moreover, different functional traits may be subject to contrasting climate selection pressures, and trait correlations and ecological trade-offs may prevent functional traits from adapting linearly to distinct climatic gradients (Ahrens *et al.*, 2020).

Performance and plasticity in native vs non-native ranges

There were no general differences in performance traits in the common garden between native and non-native populations, which contrasts with many studies of other invasive species (reviewed by Parker *et al.*, 2013; Callaway *et al.*, 2022), and a

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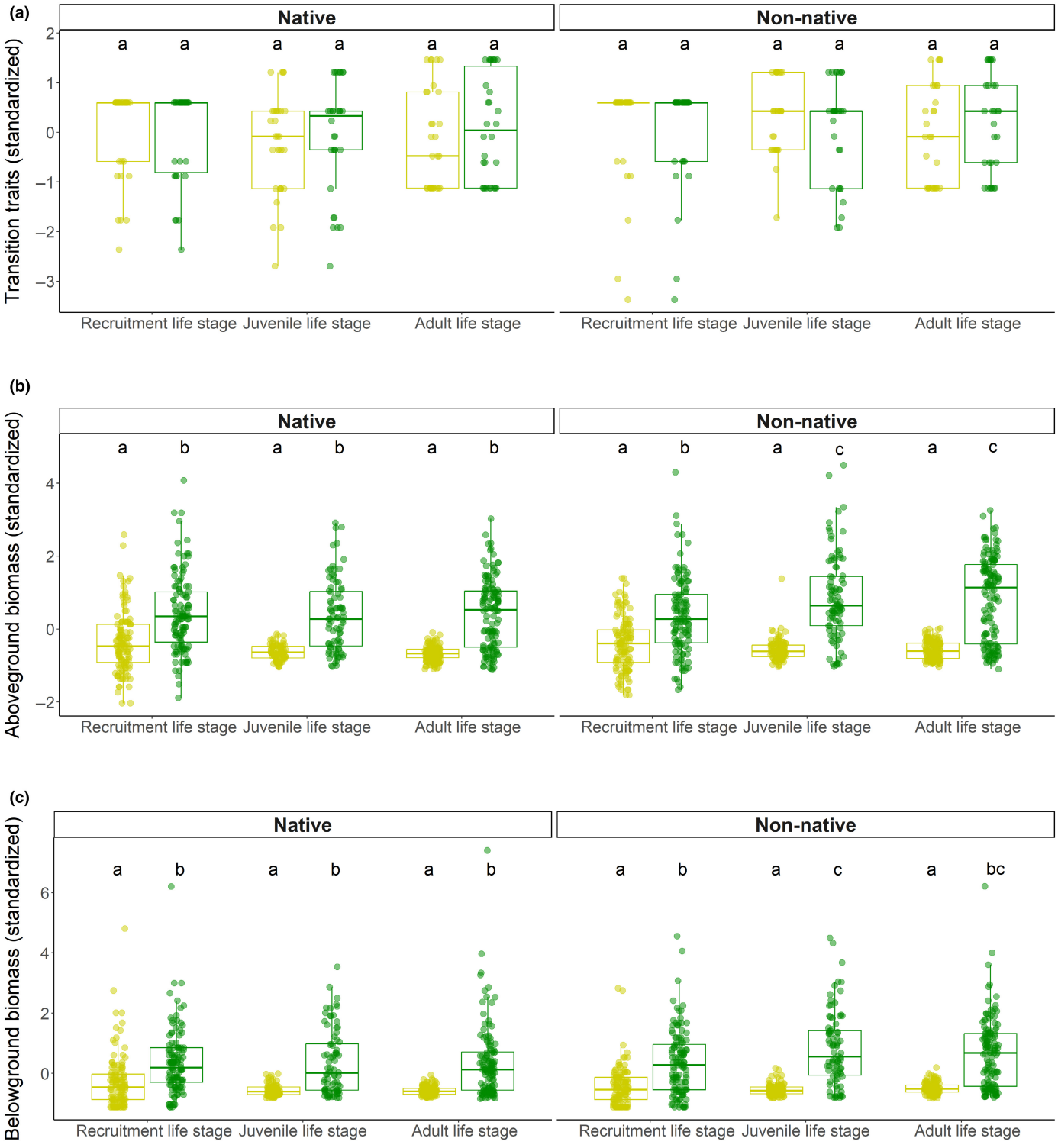

Fig. 5 Life stage (recruitment, juvenile, and adult) and their interactive effects with range and treatment (dry: yellow, wet: green) on performance of *Conyza canadensis*, namely the binomial transition traits (germination, survival, and flowering) (a), aboveground biomass (b), and belowground biomass (c). The models tested the differences in log-response ratios; however, the plot aimed to visualize the comparable effect of experimental drought across life stages. To reduce the effect of scale differences among life stages (e.g. biomass variation), all variables were standardized across life stages. For transitional traits, binomial data were analyzed but population means were plotted for the sake of clarity. Details on the models and results are found in Supporting Information Table S7. Coloring is based on the applied treatment (dry: yellow, wet: green). Boxplots show the interquartile range with the solid line indicating the median, and whiskers the max and min values without outliers (calculated as 1.5 times the interquartile range). Lowercase letters refer to the groupings tested with *post hoc* analyses (Tukey honestly significant difference) performed on the standardized data.

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study that found the opposite for *C. canadensis* (Abhilasha & Joshi, 2009). One possible explanation could be that differences between native and non-native ranges may not be present when very large and comparable environmental gradients in both ranges are considered, as recently demonstrated for *C. canadensis* (Rosche *et al.*, 2019; Sheng *et al.*, 2022).

The plasticity of the responses to drought was comparable between the two ranges. This result does not match the assumption that increased plasticity of non-native populations is an important factor for invasion success in general (Hiatt & Flory, 2020) and in response to climatic conditions (Turner *et al.*, 2015). Apparently, high-performance genotypes or greater plasticity in non-native populations are not the primary reason for the overwhelming colonization success of *C. canadensis* in the Northern Hemisphere. Instead, shifts in biotic interactions such as with root-colonizing fungi (Sheng *et al.*, 2022) or plant competitors (Shah *et al.*, 2014; Nagy *et al.*, 2020, 2022) are more likely to drive the success of non-native *C. canadensis* populations.

Drought responses in native vs non-native ranges

Five out of nine performance traits showed APV in response to drought. Although we did not explicitly test for local adaptation, our results indicate that *C. canadensis* shows large adaptive variation to climate, which may have facilitated its ability to occur across the unusually large climatic gradient of its cosmopolitan distribution (see also Rosche *et al.*, 2019). However, the patterns differed in all five cases between the two ranges. The response of native populations to drought met evolutionary expectations in the native range – populations from xeric habitats were less suppressed by the dry treatment than populations from mesic habitats. Such relationships were not apparent in non-native populations, as non-native populations from arid habitats exhibited less increases in performance under dry but maintained and/or increased performance under wet conditions.

Our results on range-specific APV are consistent with studies of *C. stoebe* (Mráz *et al.*, 2014) and *P. lanceolata* (Villellas *et al.*, 2021). In the latter, similar, but weaker patterns of APV were observed in the non-native as compared to the native ranges of *P. lanceolata*. Together, these two and our studies suggest generality in range-specific APV. We postulate three mutually non-exclusive mechanisms that may explain why non-native populations may not have locally adapted, or perhaps yet, to variation in water supply.

First, non-native populations, while not strictly locally adapted, possess traits that enable them to thrive in wet conditions throughout the year. This flexibility might be advantageous, contributing to the success of non-native populations in diverse environments (Donelson *et al.*, 2019). Second, non-native populations have been introduced to their current climatic regimes much more recently (Yan *et al.*, 2020) and did not necessarily match their previous adaption to climate. Thus, non-native populations may have not experienced enough time to adapt to their new abiotic environments. Third, the relative importance of different selection regimes may differ between ranges. For example, fundamentally altered biotic interactions – as Sheng *et al.* (2022) found evolution toward enhanced mutualism in non-native ranges – may be more important for the non-native *C. canadensis* populations than a 'perfect adaptation' to local aridity (see also Callaway *et al.*, 2011; Pal *et al.*, 2020; Villasor *et al.*, 2024). Such basic evolutionary research questions need to be addressed with more complex experimental designs that simultaneously manipulate abiotic and biotic conditions. For example, studying competitive interactions simultaneously with responses to drought for many native vs non-native populations across large geographic distributions could enhance our mechanistic understanding of rapid evolution (Lucas *et al.*, 2024).

Irrespective of these mechanisms, our results have two important implications. First, assuming that the highly successful *C. canadensis* is not yet fully adapted to climate, the spread and impact of this species might become even more pronounced in the future. Second, because *C. canadensis* is present in non-native ranges for centuries and is actually known for rapid responses to environmental changes (Rosche *et al.*, 2019), our findings raise questions about how other plant species can adapt quickly to contemporary climate change. In other words, if this species has not fully established its response to drought in non-native ranges, the ability of other plants to cope with such rapid changes remains uncertain. Such interpretation is concerning with a view on global change scenarios and calls for further investigations in comparable future studies.

Drought responses across life stages

Drought had weaker effects in the recruitment life stage than in the other two life stages. This suggests that plants may respond less plastically at the recruitment stage where they must either grow very rapidly or die as found for *Solidago gigantea* (Nagy *et al.*, 2018). From the perspective of performance traits, above- and belowground biomass was reduced, but transition traits not affected for all life stages. In addition, range-specific responses to drought were also similar across life stages. It is unclear whether this pattern arises because plants allocate the same energy between life stages in response to drought stress. Further physiological investigations including studies on energy allocation strategies used by plants in different life stages would be needed to reveal the mechanisms behind our observations.

Similarly pronounced drought responses across life stages could be particularly important under climate change, which likely leads to more extreme weather events, such as unpredictable droughts at any life stage (Parmesan & Hanley, 2015). If a plant species responds similarly to these different weather conditions across all life stages, it will be better able to adapt and survive (Garzón *et al.*, 2011; Moran *et al.*, 2016; Welles & Funk, 2021). This may have several positive effects for the colonization of large ranges and adaptive strategies to the resilience of species to changing climatic conditions.

Conclusions

Our study shed light on the adaptation of invasive species in new environments, and the speed of adaptation to drought. We

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suggest that invaders can thrive even in the absence of complete adaptation to new abiotic environments, indicating their remarkable resilience in the face of changing global conditions. Furthermore, our findings suggest that long-established invaders may continue to evolve in response to the dynamic abiotic environment. Future research is needed to test the generality of these findings with focus on (1) the implications for the adaptive potential of plant populations under ongoing climate change, (2) whether invasion success of some non-native species become even more pronounced once they are fully adapted to the local climate in the novel ranges, and (3) the relative importance of abiotic and biotic selection drivers for rapid evolution in non-native plants.

Acknowledgements

The project was supported by the Deutsche Forschungsgemeinschaft (DFG, German Research Foundation; project no.: RO 6418/1-1 to CR), an MLU|BioDivFund grant (R02020830-29 to CR), and an NSERC grant (RGPIN-2022-05262 to DPK). MAS acknowledges the support through the Ministry of Education, Government of India. IH and CR gratefully acknowledge the support of iDiv funded by DFG (FZT 118, 202548816). We express our gratitude to the MPG Ranch for hosting a workshop. We thank Rachel Draude, Dr Heidi Hirsch, Katrin Kittlaus, and Anne Sophie Winkler for their help during the experiments and manuscript visualization. We also thank Prof. Helge Bruelheide for important discussions on the application of our drought treatment. Dr Sasha Reed and four anonymous reviewers provided very helpful criticisms on previous versions of the manuscript. Open Access funding enabled and organized by Projekt DEAL.

Competing interests

None declared.

Author contributions

DUN and CR designed and planned the experiments. DUN, MA-G, SLF, LJF, MH, DPK, YL, RWP, MAS, M Sheng, M Slate, CS, TT and CR conducted the fieldwork and sampling. DUN, MH and CR analyzed the data. DUN, AET, KJ, IS and CR performed the experiments. DUN, RMC, SLF, IH, YL and CR wrote the manuscript with input from all co-authors.

ORCID

Mohammad Al-Gharaibeh https://orcid.org/0000-0001-9242-4262
Ragan M. Callaway https://orcid.org/0000-0001-7342-4312
S. Luke Flory https://orcid.org/0000-0003-3336-8613
Lauren J. Frazee https://orcid.org/0000-0001-5248-8763
Matthias Hartmann https://orcid.org/0000-0001-9721-0925
Isabell Hensen https://orcid.org/0000-0001-6470-9359
Kateřina Jandová https://orcid.org/0000-0002-3166-9175
Damase P. Khasa https://orcid.org/0000-0002-9336-7770
Ylva Lekberg https://orcid.org/0000-0003-1033-8032
Dávid U. Nagy https://orcid.org/0000-0001-7742-4459
Robert W. Pal https://orcid.org/0000-0003-2843-8517
Christoph Rosche https://orcid.org/0000-0002-4257-3072
Ioulietta Samartza https://orcid.org/0009-0007-3627-2947
Manzoor A. Shah https://orcid.org/0000-0003-2639-3167
Min Sheng https://orcid.org/0000-0003-1858-1387
Mandy Slate https://orcid.org/0000-0002-4026-7952
Claudia Stein https://orcid.org/0000-0002-9586-8587
Arpad E. Thoma https://orcid.org/0009-0001-5518-9969
Tomonori Tsunoda https://orcid.org/0000-0002-1163-2893

Data availability

The data that support the findings of this study are available in the Supporting Information of this article (see Dataset S1).

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Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article.

Dataset S1 Raw performance, biomass, and trait data, along with stomatal conductance and isotope ratio measurements, used in this study.

Fig. S1 Concept of clinal variation in the experiment.

Fig. S2 Results of germination and early seedling traits in a pre-experiment.

Fig. S3 Monitoring the effects of drought, during the juvenile and adult life stages.

Fig. S4 Kaplan–Meier plot for germination success.

Fig. S5 Interactive effects of drought, climatic water deficit, and range affiliation on plant functional traits.

Fig. S6 Details of the analyses investigating the correlation among performance and functional traits.

Fig. S7 Effects of range affiliation on plasticity of performance traits.

Fig. S8 Effects of range affiliation on plasticity of functional traits.

Notes S1 Spatial autocorrelation in the used dataset.

Table S1 Geographical location and climatic water deficit of 30 native and 29 non-native *Conyza canadensis* populations.

Table S2 Summary table of the drought treatment in the juvenile and adult experiments.

Table S3 Model selection by Akaike information criterion and Chi-square values testing how seasonal and annual climatic water deficit influence the models.

Table S4 Details of the linear mixed-effects models on regional comparisons.

Table S5 Details of the linear mixed-effects models on performance traits.

Table S6 Details of the linear mixed-effects Cox model.

Table S7 Details of the linear mixed-effects models on functional traits.

Table S8 Details of the linear mixed-effects models on log-response ratios.

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