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Review Article

Responses of invasive and native plant species to drought stress and elevated CO_2 concentrations: a meta-analysis

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Abstract

Superior trait responses of invasive plant species to their native counterparts determine invasion success under various environmental conditions. To date, numerous experimental studies have compared the physiological and growth trait responses of invasive plant species to native ones in simulated drought or CO_2 enrichment conditions; however, these studies have not recently been summarised. Here, we conducted a global meta-analysis using 48 experimental studies to determine whether there are generalisable differences between invasive and native plant species in terms of their physiological and growth trait responses to drought and elevated CO_2 and which traits potentially facilitate plant invasion in these conditions. The results indicate that the magnitude of responses do not differ substantially between invasives and natives for most traits under drought or elevated CO_2. Under drought stress, the photosynthetic rate, stomatal conductance, shoot biomass and total biomass decreased in both plant groups, supporting the contention that plants, irrespective of their origin, are negatively affected in water-limited environments. By contrast, we found that elevated CO_2 increased water-use efficiency, shoot biomass and total biomass and decreased stomatal conductance in both invasives and natives, indicating that both plant groups grow vigorously in such conditions. Compared with estimates for natives, invasives were taller and invested more biomass to roots under drought and showed greater allocation to shoot biomass under elevated CO_2. Although there were no substantial differences in the magnitude of responses in most studied traits, the differential growth responses in invasives may confer an advantage over natives under decreased water availability and high CO_2 concentrations.

Key words: Effect size, environmental variation, invasion ecology, non-native plants, quantitative synthesis, trait-based comparison

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Introduction

Invasive plant species exert multifaceted effects on native biodiversity and many ecological processes (Culliney 2005; Vilà et al. 2011; Seebens et al. 2018; Smith et al. 2018; Pyšek et al. 2020). Therefore, it is of great importance to elucidate the mechanisms underlying plant invasions for the conservation of native biodiversity and restoration of native plant communities. Various plant traits, including physiological, growth and reproductive features, are thought to contribute to invasion processes (Drenovsky et al. 2012a; Divíšek et al. 2018; Mathakutha et al. 2019) and these traits often show variation along environmental gradients in different ecosystems (Zheng et al. 2009; Milanović et al. 2020; El-Barougy et al. 2021). It has been suggested that, if invasive plant species exhibit superior trait responses in physiological and morphological attributes to those of resident native species in a plant community under altered environmental conditions, then they should outperform their native counterparts (Leffler et al. 2014; Mathakutha et al. 2019; Westerband et al. 2021) and this could explain how they become widespread and abundant in resident plant communities. To date, considerable experimental research has been put forth to investigate this notion by comparing the performances of numerous invasive species to their native competitors across taxa and biomes under simulated environmental conditions (Matzek 2012; Anderson and Cipollini 2013; Funk et al. 2016; He et al. 2018; Gufu et al. 2019; Henn et al. 2019), but the findings remain controversial. Therefore, a quantitative synthesis combining the results of independent studies is essential to draw a general conclusion about whether invasive plant species outperform native species across different environments.

Until recently, only a few studies compared the performance of invasive plant species and their native counterparts in various environmental conditions at a global scale (Daehler 2003; Sorte et al. 2013; Liu et al. 2017). In their meta-analysis, Sorte et al. (2013) showed that non-native invasive and native plant species respond similarly to various water regimes and temperatures and increased CO_2 concentrations benefitted more the former plant group, while Liu et al. (2017) revealed a significant difference in performance between these two plant groups under those environmental conditions. Both of these syntheses pooled values for various traits, including physiology, morphology and fitness-related traits, into a single metric in response to various environmental gradients. However, different traits do not respond in the same direction along environmental gradients (Leffler et al. 2013; Santamarina et al. 2022) due to trade-offs and resource constraints (Grime 2006; Ramírez-Valiente et al. 2010; Lau and Funk 2023). Additionally, some traits can be more responsive than others or do not respond at all to a particular environmental condition (Richards et al. 2006; Van Kleunen et al. 2010; Palacio-López and Gianoli 2011; Funk et al. 2016). Therefore, it is imperative to synthesise existing knowledge and bridge the gap in our understanding of how similar physiological and growth traits of invasive and native species respond to drought and elevated CO_2.

Given the importance of understanding invasive-native trait divergence in the context of environmental variation, a good number of studies have focused on differences in physiological and growth trait responses between these two plant groups in stressful conditions (e.g. Hwang and Lauenroth (2008); Funk et al. (2016); Huang et al. (2017); El-Barougy et al. (2020)). It has been posited that, under stressful environments, characterised by limited water, nutrients or light availability, both invasive and native plant species would downregulate their physiology and growth stimulation due to the unavailability of resources (Funk and Vitousek 2007; González et al. 2010; Santamarina et al. 2022). In drought stress, in particular, decreased water availability is predicted to constrain photosynthetic carbon assimilation because of decreased stomatal openness and other physiological adjustments in plants (DeFalco et al. 2003; Casper et al. 2006; Godoy et al. 2011; Drenovsky et al. 2012b). Accordingly, numerous studies have reported that, in water-limited environments, plants show decreases in the net photosynthetic rate and stomatal conductance, irrespective of species origin, thereby resulting in a shift in biomass investment or overall reduction in plant growth (Drenovsky et al. 2012b; Larson and Funk 2016; Santamarina et al. 2022). However, comparative studies have also shown that invasive plant species often exhibit various attributes that confer some drought tolerance, such as thick leaves and greater allocation to below-ground structures in conditions where water is limited (Funk and Vitousek 2007; Grotkopp and Rejmánek 2007; Van Kleunen et al. 2010), but see Cavaleri and Sack (2010). Further, decreased water availability can be advantageous for invasive plant species over their native counterparts because the former could have a wide range of physiological niches and greater tolerance to environmental stresses (Funk and Vitousek 2007; Davidson et al. 2011; Funk 2013). Therefore, in some regions, particularly in arid and semi-arid systems, limited water availability may put many native plant species at a disadvantage, as demonstrated by Ding et al. (2021) and Drenovsky et al. (2012a, b). However, a general relationship between drought stress and the increased dominance of invasive plant species over native ones has yet to be established. Recently, some evidence also has suggested that drought stress has larger detrimental effects on growth, physiology and reproductive traits of some invasive species than the native ones within recipient communities (Valliere et al. 2019; Kelso et al. 2020; Liu et al. 2024).

The patterns in trait differences between invasive and native species may change with environmental conditions. It has widely been suggested that many invasive plant species will thrive in high-resource environments because invasive plant species, by virtue of their traits, tend to have fast resource use strategies and that attribute often becomes even faster in resource-rich non-native areas (Davis et al. 2000; Ordonez and Olff 2013; Sardans et al. 2017; El-Barougy et al. 2020). Therefore, environments with high CO_2 concentrations, which is a source of carbon fertilisation for plants, may favour invasive species over resident native species because the former have advantageous traits (e.g. high potential photosynthetic rate, high specific leaf area, high growth rate etc.) that facilitate rapid carbon assimilation and use (Vilà et al. 2007; Raizada et al. 2009; Anderson and Cipollini 2013). In agreement with this assumption, many earlier studies reported that atmospheric CO_2-enrichment benefits invasive species more by promoting their physiological functions, such as photosynthetic carbon assimilation and water-use efficiency and by accelerating their growth performance such as height and biomass accumulation than those of their native counterparts growing in common conditions (Vilà et al. 2007; Song et al. 2010; Lei et al. 2011; Blumenthal et al. 2013). However, several previous studies that support that elevated CO_2 concentrations would improve the growth and fitness of invasive species over those of natives, also suggest that many native species can profit equally as invasives in such conditions because the effect of elevated CO_2 concentration is more closely related to the species than to the origin of the species (Vilà et al. 2007; Song et al. 2010; Lei et al. 2011; Tooth and Leishman 2013). Therefore, a relevant question is whether co-existing invasive species would outperform natives, as many predict, under elevated CO_2 concentrations. Understanding whether invasive and native species have different or similar responses to elevated CO_2 concentrations would help predict future risks from invasions under such conditions.

In this meta-analysis including the past and most recent literature data, we aim to compare the responses of invasive and native plant species in terms of their physiological and growth traits to drought stress and elevated CO_2 concentrations. Although many different traits may determine the success of invasive plant species, we focused on a subset of traits associated with physiology (i.e. net photosynthetic rate, stomatal conductance and water-use efficiency) and growth (i.e. height, specific leaf area, shoot biomass, root biomass, total biomass and root-shoot ratio). We included only these above-mentioned traits in the current synthesis because these physiological and growth traits were more frequently investigated in the retrieved studies. Given the substantial importance of plant attributes in shaping invasion success in resident communities, if a consistent difference in various physiological and growth traits between these two plant groups can be identified where invasive species exhibit significantly higher values for a suite of traits than the native ones, this may provide insight into which traits potentially can facilitate plant invasions in drought stress and in environments with high CO_2 concentrations in various ecosystems. We hypothesised that drought stress will constrain physiological and growth trait responses in both invasive and native plant species, but invasive species would still show greater tolerance to drought because of their higher plasticity and as they are more efficient at using limiting resources relative to native species adapted to such systems (Davidson et al. 2011; Heberling and Fridley 2013; Funk et al. 2016). We also hypothesised that an elevated CO_2 concentration would stimulate physiological and growth trait responses in both invasive and native plant species, as performance typically improves in resource-rich environments, irrespective of species origin; however, invasives will benefit more due to their ability to quickly take up available resources and their inherent faster growth than the native species (Tecco et al. 2010; Godoy et al. 2011).

Methods

Literature survey

A literature survey was conducted to obtain peer-reviewed articles and thesis papers that report the responses of invasive and native plant species to drought stress and/or elevated CO_2 concentrations. For the purpose of the current study, a 'native' plant species was defined as a species that is not invasive in the study area or elsewhere and an 'invasive' plant species was defined as a species that was introduced and became invasive in the study area. To retrieve a large sample of studies, Science Direct, PQDT (ProQuest Dissertations and Theses) Global, Springer Archive, Wiley Online Library, Oxford University Press, JSTOR (Biological Science), Proquest (Natural Science Collection) and Google Scholar were used as literature sources. The following keywords or phrases were used in various combinations to search for relevant papers: "climate change or environmental change or environmental fluctuation or environmental stress or extreme climatic event or drought or drought stress or water stress or precipitation variability or elevated carbon dioxide or elevated CO_2 or carbon dioxide enrichment" AND "invasive or alien invasive or non-native invasive or non-native invasive" AND "native". Relevant literature was also retrieved by scrutinising the reference lists of papers identified by this search and from prior meta-analyses conducted on the topic (Sorte et al. 2013; Liu et al. 2017). In a few papers, it was not clear whether the introduced species was invasive or not from the description. In such cases, an additional search on the web was performed to confirm the status of those species. Our survey only included studies published in English.

Study inclusion and data extraction criteria

All retrieved studies were assessed individually. Studies were included in the meta-analysis if the following three criteria were met: 1) The study included at least one invasive and one native plant species in the same experiment. If a study involved several invasive and native plant species and they were not presented invasive-native pairwise, they were paired for the purpose of invasive-native comparison, based on their phylogenetic relatedness and/or shared growth forms. In some studies, several individual species were presented as an invasive or native plant group. Such groups were considered as an individual entity and included in the meta-analysis. All the experiments carried out in growth chambers, greenhouses, open top chambers (OTC), free air CO_2 enrichment (FACE) systems, mesocosms and field conditions were included; 2) The experimental plants were exposed to at least two treatment levels (i.e. control and treatment) for drought stress or elevated CO_2; 3) The study reported at least one of the following physiological or growth traits: net photosynthetic rate, stomatal conductance, water-use efficiency, specific leaf area, height, shoot biomass, root biomass, root-shoot ratio or total biomass of invasive and native plant species.

Mean values, sample sizes and variances (i.e. standard deviation or standard error) were extracted for the selected traits directly from texts or tables for all studies meeting the eligibility criteria. The web-based tool WebPlotDigitizer (Rohatgi 2014) was used for extracting the preceding information from studies in which they were shown in graphs or figures. In studies in which the measure of variance was expressed as standard error, it was converted to standard deviation to meet the effect size calculation criteria. Standard deviation was derived from standard error according to the following equation: standard deviation = standard error × $\sqrt{n}$, where n is the sample size. Data were extracted and compiled for a focal trait based on the following rules: 1) When experimental plants were grown in both monoculture and polyculture (competition), data were extracted only from monoculture because the targeted plants may perform differently under competition, influencing the results for focal treatments; 2) When a study had more than two levels for a focal treatment, data for the control and the highest level of manipulation relative to the control were extracted; 3) When experimental plants were subjected to other treatments alongside the focal treatments in a factorial design, data from the control condition were extracted only for the non-focal treatments; 4) When data were presented for multiple sampling dates, data were extracted only from the latest sampling date; 5) When a study reported ranges for the sample size, the lowest sample size within a range was obtained; 6) When data were presented in various measurement units for a specific trait across studies, they were converted to a common unit; 7) For photosynthetic rate, stomatal conductance or water-use efficiency, when a study presented data for any two of the three traits, values for the third trait were derived using the following equation: water-use efficiency = photosynthetic rate/stomatal conductance (Anderson and Cipollini 2013; He et al. 2018); 8) For total biomass, shoot biomass or root biomass, when a study presented data for any two of the three traits, values for the third trait were derived using the following equation: total biomass = shoot biomass + root biomass; 9) For shoot biomass, root biomass or root-shoot ratio, when a study presented data for any two of the three traits, values for the third trait were derived using the following equation: root-shoot ratio = root biomass/shoot biomass.

Effect size calculation and meta-analysis

The effect sizes were computed and meta-analyses were performed using the MetaWin statistical programme (Rosenberg et al. 2000a). In this synthesis, natural log response ratio (ln*R*) was used as the effect size metric which estimates proportionate changes between experimental and control groups (Hedges et al. 1999; Palacio-López and Gianoli 2011). The ln*R* was preferred over other measures of effect size calculation because the current meta-analysis included plant species of various growth forms (i.e. herbs, shrubs and trees) and the proportionate changes between experimental and control groups minimise the influence of plant size (Hedges et al. 1999; Palacio-López and Gianoli 2011). Firstly, ln*R* was computed for each specific trait in each invasive and native species in response to drought stress or elevated CO_2 concentrations. The ln*R* was calculated using the following equation (Hedges et al. 1999): $\ln R = \ln(X_t) - \ln(X_c)$, where X_t and X_c represent the mean values of the samples measured in the treatment and control groups, respectively. The variances associated with ln*R*(V) were calculated as follows (Hedges et al. 1999): $V = S_t^2/N_tX_t^2 + S_c^2/N_cX_c^2$, where N_t and N_c denote the number of samples and S_t and S_c indicate the standard deviations in the treatment and control groups, respectively. In a few studies, neither the standard error nor standard deviation was reported. In such cases, the average value of X_t/S_t or X_c/S_c in other studies was calculated to derive a reference S_t or S_c value, respectively (Van Groenigen et al. 2011; Sun et al. 2020).

To understand the overall mean effect of drought stress or elevated CO_2 on a specific trait in invasive or native plant species, meta-analyses were conducted separately for each focal trait using the individual effect sizes and variances computed above. Mixed-effects models were preferred to perform the analyses with the assumption that there can be true random variation amongst the effect sizes originating from different studies (Rosenberg et al. 2000b; Borenstein et al. 2010). In our final models, species status (invasive or native) was used as a fixed factor and the selected studies included in the synthesis were used as a random factor to estimate the mean effect of drought stress or elevated CO_2 on the response variables (physiological and growth traits). The response of a specific trait to drought stress or an elevated CO_2 concentration was considered significant if the 95% confidence interval of the mean effect size estimate (calculated, based on 999 permutations) did not intersect with zero. A positive or negative mean effect size estimate indicates that the effect of drought stress or an elevated CO_2 concentration increased or decreased the response of a specific trait, respectively. Whether the response of a particular trait under drought stress or elevated CO_2 concentrations differs significantly between invasive and native plant species was also evaluated using the test statistic Q_B and associated *p*-values as a guide (Gurevitch and Hedges 2020). The Q_B statistic follows a chi-square (χ^2) distribution under the null hypothesis with *m*-1 degrees of freedom, where *m* is the number of subgroups in the meta-analysis (Rubio-Aparicio et al. 2017; Spineli and Pandis 2020). Publication bias was evaluated using funnel plots, which are widely used in meta-analyses, with a symmetrical distribution of scattered points around the zero-effect size indicating the absence of bias (Light and Pillemer 1986; Borenstein et al. 2021). The funnel plots were generated by plotting the effect sizes calculated, based on ln*R* on the x-axis and precision (1/SE) on the y-axis (Suppl. material 1: figs S1, S2). A visual inspection of the funnel plot showed minimal evidence of asymmetry.

Results

Based on the study selection criteria, we identified 48 empirical studies published from 1991 to 2022 (Suppl. material 1: table S1). The majority of the studies were conducted in North America and Asia, notably in the United States (31%) and China (27%), whereas studies from Europe (10%), South America (9%) and Africa (4%) were under-represented. Studies were mainly carried out in the greenhouses (58%), followed by mesocosms (15%), growth chambers (13%) and field conditions (6%) (Suppl. material 1: table S1). Potting soil was preferred as a substrate material in the majority of the experiments (67%), while field soil was used in the remaining studies (33%) (Suppl. material 1: table S1). Across studies, 74 invasive and 94 native plant species were exposed to either drought stress or elevated CO_2 concentration and most of the plants were herbaceous (86%). Our full dataset comprised 308 pairs of cases for comparisons between invasive and native plant species (drought stress: 157; elevated CO_2 concentration: 151) distributed across different physiological and growth traits (Figs 1, 2). We found that the most common plant attribute used to compare the performance between invasive and native plant species was total biomass in both drought stress (22%) and CO_2 enrichment (30%) treatments. Other common attributes that were studied were the root-shoot-ratio, specific leaf area and shoot biomass under drought stress and photosynthetic rate, stomatal conductance and specific leaf area under elevated CO_2 concentrations.

Our meta-analyses indicate that drought stress had negative effects on physiological functions and growth performance in both invasive and native plant species (Fig. 1). Compared with estimates in control individuals, plants subjected to water constraint exhibited a significantly lower photosynthetic rate (invasive: *lnR* = -0.32, CI = -0.55 to -0.09; native: *lnR* = -0.40, CI = -0.61 to -0.19), stomatal conductance (invasive: *lnR* = -1.73, CI = -2.46 to -0.99; native: *lnR* = -2.14, CI = -2.65 to -1.64), shoot biomass (invasive: *lnR* = -0.48, CI = -0.65 to -0.31; native: *lnR* = -0.68, CI = -0.86 to -0.51) and total biomass (invasive: *lnR* = -0.60, CI = -0.72 to -0.48; native: *lnR* = -0.60, CI = -0.72 to -0.48), regardless of their species origin (Fig. 1). In response to drought stress, a significant reduction was also detected in height growth (*lnR* = -0.25, CI = -0.35 to -0.15) and root biomass production (*lnR* = -0.36, CI = -0.46 to -0.25), but only in native plant species (Fig. 1). In native plant species, however, decreased water availability led to a significant increase in the root-shoot ratio (*lnR* = 0.25, CI = 0.13–0.36) (Fig. 1). When the magnitudes of the performance responses were compared between invasive and native plant species under drought stress, we found significant differences in height growth (Q_B = 5.87, df = 1, p = 0.015) and root biomass accumulation (Q_B = 19.19, df = 1, p = 0.000); native species showed greater decreases in height and allocation of biomass to the root system than those in invasive counterparts (Fig. 1, Table 1). Under decreased water availability, we also detected a marginally significant difference in the root-shoot ratio (Q_B = 3.56, df = 1, p = 0.059) between these two groups of plant species (Fig. 1, Table 1). In other studied traits, no significant differences were detected between invasive and native plant species, although water-limited conditions tended to have greater negative effects on photosynthetic carbon assimilation, stomatal conductance and shoot biomass production in native species than invasives (Fig. 1, Table 1).

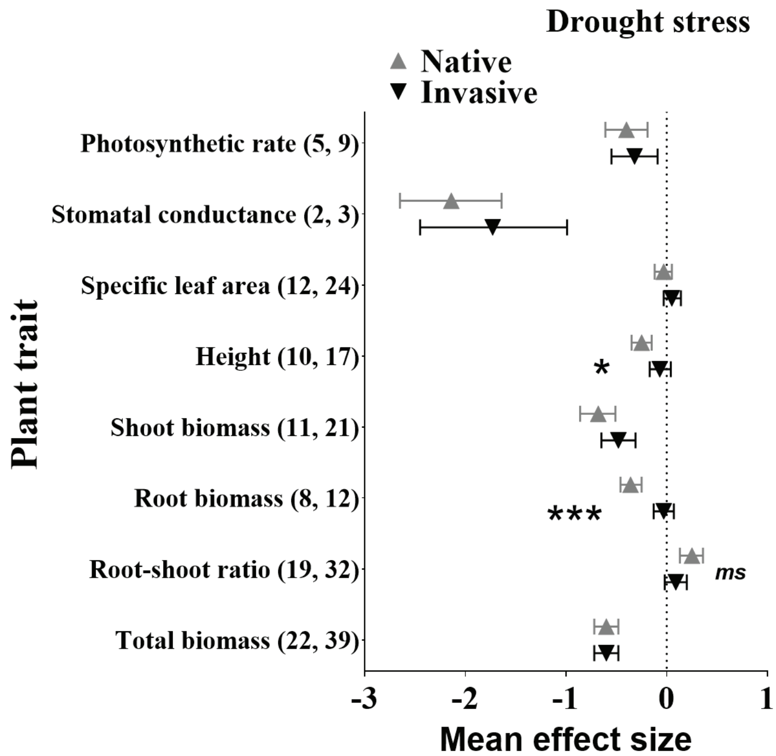

Figure 1. Mean effect sizes of drought stress on the physiological and growth trait responses of invasive and native plant species. Error bars represent 95% confidence intervals around the mean effect sizes. The numbers in parentheses indicate the number of studies included in the meta-analyses and the number of individual effect sizes used to calculate the mean effect sizes, respectively. Asterisks denote a statistically significant difference between invasive and native plant species and *ms* indicates a marginally significant difference.

Table 1. Results of a meta-analysis of the effect of drought stress on the physiological and growth trait responses of invasive and native plant species. Q_B statistics and associated *p*-values for the difference in the magnitude of the response between invasive and native plant species subjected to drought stress are presented.

Trait	Species group	Effect sizes			Q_B tests		
		Mean	Lower 95% CI	Upper 95% CI	Q_B	df	*p*
Photosynthetic rate	Invasive	-0.32	-0.55	-0.09	0.28	1	0.599
	Native	-0.40	-0.61	-0.19			
Stomatal conductance	Invasive	-1.73	-2.45	-0.99	0.84	1	0.359
	Native	-2.14	-2.65	-1.64			
Specific leaf area	Invasive	0.05	-0.03	0.14	1.92	1	0.166
	Native	-0.03	-0.12	0.05			
Height	Invasive	-0.07	-0.17	0.04	5.87	1	0.015
	Native	-0.25	-0.35	-0.15			
Shoot biomass	Invasive	-0.48	-0.65	-0.31	2.69	1	0.101
	Native	-0.68	-0.86	-0.51			
Root biomass	Invasive	-0.03	-0.13	0.07	19.19	1	0.000
	Native	-0.36	-0.46	-0.25			
Root-shoot ratio	Invasive	0.09	-0.02	0.20	3.56	1	0.059
	Native	0.25	0.13	0.36			
Total biomass	Invasive	-0.60	-0.72	-0.48	0.00	1	0.988
	Native	-0.60	-0.72	-0.48			

An elevated CO_2 concentration promoted changes in the physiological and growth traits in both invasive and native plant species, irrespective of their origin (Fig. 2). In both invasive and native plant species, the water-use efficiency (invasive: *lnR* = 0.23, CI = 0.08–0.39; native *lnR* = 0.19, CI = 0.03–0.34), shoot biomass (invasive: *lnR* = 0.52, CI = 0.45–0.59; native: *lnR* = 0.31, CI = 0.22–0.41) and total biomass (invasive: *lnR* = 0.28, CI = 0.19–0.36; native: *lnR* = 0.18, CI = 0.10–0.27) were significantly higher under CO_2 enrichment than in ambient conditions (Fig. 2). Further, a high CO_2 concentration significantly increased the photosynthetic rate (*lnR* = 0.15, CI = 0.04–0.26), height (*lnR* = 0.15, CI = 0.06–0.25) and root biomass production (*lnR* = 0.27, CI = 0.11–0.43) in invasive species (Fig. 2). However, our meta-analyses indicated that stomatal conductance (invasive: *lnR* = -0.20, CI = -0.35 to -0.05; native: *lnR* = -0.38, CI = -0.53 to -0.22) declined significantly in both invasive and native plant species subjected to elevated CO_2 concentrations (Fig. 2). While CO_2 enrichment benefitted both invasive and native plant species with respect to physiological and growth traits, there was a significant difference in shoot biomass accumulation (Q_B = 11.43, df = 1, p = 0.001), based on species origin (Fig. 2, Table 2). In response to elevated CO_2 concentrations, invasive species exhibited significantly greater above-ground biomass production than that of their native counterparts. Moreover, we detected a marginally significant difference in photosynthetic carbon assimilation (Q_B = 2.86, df = 1, p = 0.091) between these two plant groups grown in environments with high CO_2 concentrations (Fig. 2, Table 2). However, the magnitude of responses of most studied traits did not differ significantly between invasive and native plant species, although we observed a trend towards more positive effects of elevated CO_2 concentrations on invasive species (Fig. 2, Table 2).

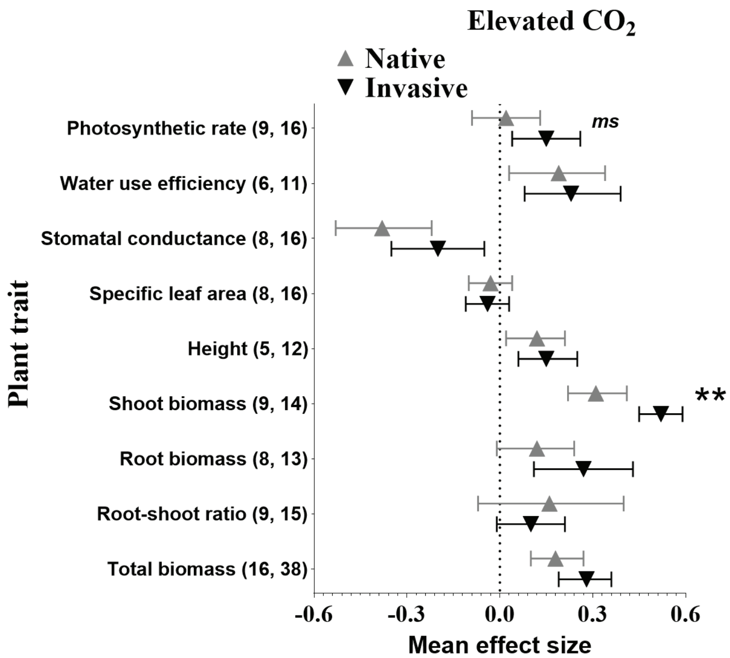

Figure 2. Mean effect sizes of elevated CO_2 concentrations on the physiological and growth trait responses of invasive and native plant species. Error bars represent 95% confidence intervals around the mean effect sizes. The numbers in parentheses indicate the number of studies included in the meta-analyses and the number of individual effect sizes used to calculate the mean effect sizes, respectively. Asterisks denote a statistically significant difference between invasive and native plant species and *ms* indicates a marginally significant difference.

Table 2. Results of a meta-analysis of the effect of elevated CO_2 concentrations on the physiological and growth trait responses of invasive and native plant species. Q_B statistics and associated *p*-values for the difference in the magnitude of response between invasive and native plant species subjected to elevated CO_2 concentrations are presented.

Trait	Species group	Effect sizes			Q_B tests		
		Mean	Lower 95% CI	Upper 95% CI	Q_B	df	*p*
Photosynthetic rate	Invasive	0.15	0.04	0.26	2.86	1	0.091
	Native	0.02	-0.09	0.13			
Stomatal conductance	Invasive	-0.20	-0.35	-0.05	2.69	1	0.101
	Native	-0.38	-0.53	-0.22			
Water use efficiency	Invasive	0.23	0.08	0.39	0.19	1	0.660
	Native	0.19	0.03	0.34			
Specific leaf area	Invasive	-0.04	-0.11	0.03	0.06	1	0.813
	Native	-0.03	-0.10	0.04			
Height	Invasive	0.15	0.06	0.25	0.24	1	0.622
	Native	0.12	0.02	0.21			
Shoot biomass	Invasive	0.52	0.45	0.59	11.43	1	0.001
	Native	0.31	0.22	0.41			
Root biomass	Invasive	0.27	0.11	0.43	2.24	1	0.135
	Native	0.12	-0.01	0.24			
Root-shoot ratio	Invasive	0.10	-0.01	0.21	0.20	1	0.653
	Native	0.16	-0.07	0.40			
Total biomass	Invasive	0.28	0.19	0.36	2.33	1	0.127
	Native	0.18	0.10	0.27			

Discussion

Responses of invasive and native plant species to drought stress

We predicted that both invasive and native plant species would show decreased performance in response to drought stress. Our meta-analysis indicated that the photosynthetic rate, stomatal conductance, shoot biomass and total biomass decline significantly in both groups of plants growing under reduced water availability. These results are consistent with numerous earlier studies showing that, when invasive and native plant species of various growth forms are subjected to simulated drought stress, they decrease their physiological functions, including photosynthetic carbon assimilation and stomatal conductance (Garcia-Serrano et al. 2009; Molina-Montenegro et al. 2011; Ding et al. 2021) and growth performance, including biomass production (Nernberg and Dale 1997; Huang et al. 2017; Valliere et al. 2019; Santamarina et al. 2022), in different ecosystems in arid, temperate and Mediterranean regions. In response to drought stress, plants often partially or completely close their stomata to limit water loss; this physiological response results in a decrease in net photosynthetic rates (Drenovsky et al. 2012b; Hatfield and Dold 2019; Ding et al. 2021). Over the long term, reduced photosynthetic rates in plants limit carbon gain and subsequently this results in decreased biomass production. Our findings, in combination with others, support the contention that both invasive and native plant species, irrespective of their origin, would suffer in water-limited environments because of downregulation of physiological processes and decreases in growth performance (Domenech and Vila 2008; Drenovsky et al. 2012b; Pan et al. 2017; Valliere et al. 2019).

We further hypothesised that the negative effects of drought stress will be greater for natives than for invasive species. Our results showed that, while invasive and native plant species were similar with respect to most traits under drought conditions, natives had significantly lower height growth and root biomass production when compared to their invasive counterparts. This indicates that invasive species were taller and invested more biomass into below-ground growth than did native species in environments with decreased water availability. For invasive species, modifications in biomass allocation could be beneficial under drought conditions. Increased allocation to the root system could be a key adaptation mechanism for the invasive species in decreased water availability, because roots can strongly affect water and nutrient acquisition in plants (Lopez-Iglesias et al. 2014; Larson and Funk 2016), especially in arid and semi-arid systems (Drenovsky et al. 2012b; Ding et al. 2021). As compared to the native species, greater allocation to roots by invasive species has previously been reported in a few large-scale experimental studies involving water constraint. For example, in a community-level comparison with 12 pairs of invasive and native plant species in California, Grotkopp and Rejmanek (2007) revealed that invasive species allocated more biomass to root tissue than did their co-occurring native species. Therefore, greater biomass allocation to the root system can have significant implications for the growth and survival of invasive species and, consequently, to the community dynamics and species distributions in water-limited conditions.

Contrary to our expectation, significant performance differences between invasive and native plant species existed only in height growth and root biomass production amongst the eight physiological and growth traits we analysed in response to drought stress. Therefore, strong evidence for invasive plant species differing substantially from native species in water-limited environments was lacking. We argue that, if the variation exists in only two traits, as was found in this global meta-analysis in height and root biomass between invasive and native plant species, it is unlikely that invasives will outcompete natives based solely as a result of these response differences in drought conditions. Our findings are consistent with those of earlier studies (e.g. Funk et al. (2016); El-Barougy et al. (2020); Westerband et al. (2021)) and support the argument that trait differences between invasives and natives should be weak or even absent under stressful conditions. Recently, Lau and Funk (2023) suggested that, in stressful conditions where resources are in constraint, invasive and native plant species compete for the same pool of limiting resources; therefore, these two groups of species should not be so different in terms of their performance since the maladaptation to extreme conditions prevents them from becoming established. Accordingly, a broad-scale comparison of performance differences between invasive and native plant species across contrasting climatic conditions including decreased water availability revealed that environmental filtering has led to similar trait values in native and invasive herbaceous plants (Tecco et al. 2010). Likewise, El-Barougy et al. (2020) also revealed that invasive and native plant species have overlapping trait values for specific leaf area, height and above-ground biomass under limited soil water or nutrient availability. These findings provide a support to the long-held notion that invasive and native plant species should be similar in most traits because of strong abiotic filters in stressful environments.

Responses of invasive and native plant species to CO_2 enrichment

Fitting with our expectation, CO_2 enrichment promoted physiological processes and growth changes in both invasive and native plant species. We found that, irrespective of species origin, plants grown in environments with a high CO_2 concentration had considerably higher water-use efficiency, shoot biomass and total biomass. Our results also demonstrate that stomatal conductance decreased significantly in both species groups subjected to elevated CO_2 concentrations. Reduced stomatal conductance may have contributed to the increased instantaneous water-use efficiency under elevated CO_2 concentrations, as observed previously in many species, including invasives and natives grown at high CO_2 concentrations (Ainsworth and Long 2005; Guerrieri et al. 2019; Hatfield and Dold 2019; Mathias and Thomas 2021). Moreover, in response to CO_2 enrichment, there were significant increases in the photosynthetic rate, height and root biomass, but only in invasive plant species. The increased photosynthetic rate in invasive species could explain their increased growth under an elevated CO_2 concentration as compared with that of plants grown in ambient conditions (Song et al. 2010; Lei et al. 2011; Blumenthal et al. 2013). Overall, our results are largely consistent with many earlier studies showing that raising atmospheric CO_2 concentration generally improves physiological functions and increases biomass accumulation in plants regardless of their origin in many ecosystems (Anderson and Cipollini 2013; Hager et al. 2016; He et al. 2018), although the effect can vary, based on the plant growth form and competitive ability of species (Sasek and Strain 1991; Vilà et al. 2007; Gufu et al. 2019).

Many earlier studies underlined the success of invasive species as a function of invasive-native performance differences across various conditions, such as environments with high CO_2 concentrations, high soil nutrients or ample water availability (e.g. Vilà et al. (2007); Funk et al. (2016); Sardans et al. (2017); Valliere et al. (2019); Musso et al. (2021)). Accordingly, in this study, we predicted that invasive plant species would respond more strongly than native species to elevated CO_2 concentrations because they generally possess growth and allocation traits that allow rapid carbon capture. Our comparison between the responses of invasive and native plant species to CO_2 enrichment showed that the only significant difference was in shoot biomass. The greater increment in above-ground biomass production under an elevated CO_2 concentration in invasive species than in their native competitors may enhance their competitive abilities and this could potentially be a mechanism promoting the success of invasion with ongoing increases in CO_2 concentration. Although some earlier studies have yielded contradictory results (e.g. Bradford et al. (2007); He et al. (2018)), our findings are in line with several other studies which also assessed a higher allocation of biomass to above-ground tissues in invasives species of different growth forms over their native counterparts at high CO_2 concentrations in various experimental conditions. As an example, Hager et al. (2016) found that an elevated CO_2 concentration stimulated shoot biomass in invasive grasses much more than that of their native competitors in a greenhouse experiment, even though the two species groups had similar responses in specific leaf area and conductance. Similarly, a FACE study also reported a greater increase in above-ground biomass production in an invasive forb as compared to a dominant native grass in response to CO_2 enrichment (Blumenthal et al. 2013).

Our findings are surprising considering that invasive plant species are presumably more successful than their native counterparts on a global scale and in high resource environments. Numerous empirical studies previously found a divergence in responses between invasive and native plant species to elevated CO_2 concentrations in a long suite of traits including photosynthetic rate, stomatal conductance, specific leaf area, height, root biomass, total biomass and reproduction (Smith et al. 2000; Huxman and Smith 2001; Hättenschwiler and Körner 2003; Baruch and Jackson 2005; Song et al. 2009; Manea and Leishman 2011; Ibrahim et al. 2021) and these physiological and morphological traits play a significant role in invasion success in novel environments. While we detected a significant difference between native and invasive species in shoot biomass and a marginally significant difference in the photosynthetic rate, other traits did not vary with species origin. Here, a significant performance difference between these two species groups in only one of the nine assessed traits lends only weak support to our hypothesis. It has been reported that responses of plant traits to elevated CO_2 concentrations are species-specific and vary significantly amongst invasive species and amongst native species (Poorter 1993; Vilà et al. 2007; Rogers et al. 2008; Song et al. 2009; Sullivan et al. 2010; Lei et al. 2011; Tooth and Leishman 2013). Therefore, in this study, the difference between invasive and native species might not have been detected in most traits because of high interspecific variability within each species group. These results suggest that many invasive species are unlikely to dominate in environments with high CO_2 concentrations; however, both invasive and native species are likely to grow vigorously.

Study constraints

Our findings do not provide a clear indication whether invasive plant species will dominate over natives in drought stress or elevated CO_2 concentrations. We acknowledge some limitations associated with this synthesis. First, most of the plant species included in this study were herbaceous (86%) (Suppl. material 1: table S1). Previously, Tecco et al. (2010) and Westerband et al. (2021) compared trait differences between invasive and native plant species across a broad range of species and climatic conditions in several ecosystems and suggested that herbaceous invasive and native species growing in the same conditions do not exhibit trait differences. However, this was not the case for woody invasive species, in which functional attributes differed from those of woody natives in all ecosystems and conditions (Tecco et al. 2010). Therefore, marginal trait differences between invasive and native species in this meta-analysis could be driven by the dominance of herbaceous species. Here, we did not attempt to analyse our data separately based on plant life forms owing to the small sample sizes. Additional empirical studies that compare the physiological and morphological trait differences between woody invasive and native plant species growing in drought stress or CO_2 enrichment conditions could lead to more precise predictions.

Moreover, the majority of the studies included in this meta-analysis were short-term, mostly lasting one growing season (90%) (Suppl. material 1: table S1). However, responses of plant species to drought stress or CO_2 concentration gradients could vary over long time periods, especially at different life stages in biannual and perennial plants (Leadley et al. 1999; Stöcklin and Körner 1999; Laube et al. 2015); hence, the differences in plant attributes between invasive and native species can become more apparent over time. For example, long-term analyses have suggested that invasive species are far better able to respond to altered environmental conditions by adjusting their phenology than those of native plant species and this property facilitates invasion at the community level (Willis et al. 2010). Further, in this synthesis, we only retrieved data from monocultures since only a few studies examined experimental plants grown in competition. However, in introduced communities, invasive plant species commonly occur together with their native counterparts and grow in competition with each other. Thus, our results should be interpreted with caution when considering the real world, because we only evaluated the main effects of drought stress and elevated CO_2 and excluded the interacting effects of competition and a focal treatment (see Vila et al. 2021 for interaction effects).

Finally, we did not evaluate various traits, such as reproduction, survivorship, allelopathy and susceptibility to herbivory, owing to limited data availability and these traits may differ between invasive and native plant species in environments with decreased water availability or high CO_2 concentrations (Horton and Clark 2001; Anderson and Cipollini 2013; Duell et al. 2021) and may also play a role in invasion success in such altered conditions. Hence, including a broader spectrum of traits, beyond those related to physiological processes and growth, can be helpful for robust predictions of the relative success of invasives and natives under drought and elevated CO_2 concentrations.

Conclusions

The findings of this meta-analysis indicate that drought stress suppresses the performance of both invasive and native plant species, while an elevated CO_2 concentration stimulates physiological processes, except stomatal conductance and growth traits in both plant groups. Our results also indicate that, compared with native plant species, invasive species had a significantly greater height growth and invested more biomass to below-ground root system in drought conditions and had a greater allocation to above-ground biomass production in elevated CO_2 concentrations. These differential responses of invasive plant species in growth traits may provide them with an advantage in adaptation over native species under decreased water availability and CO_2 enrichment. However, the magnitude of responses in most traits did not differ substantially between invasive and native plant species, indicating that invasive species are unlikely to outcompete natives in these altered environmental conditions. This certainly does not mean that invasive species will not be pervasive in the future, as they are capable of greater allocation to below-ground and above-ground biomass production compared with that of native counterparts under variable environments. Still, we need to be careful when predicting a bleak future regarding intensive dominance of invasive plants across different environmental conditions.

Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

NS and CB conceptualised and designed the study; NS extracted and analysed the data and developed graphs and tables; NS wrote the first draft of the original manuscript; KS and CB reviewed and edited the manuscript. All authors approved the submission to the journal.

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Data availability

Datasets were shared in the open access file directories of Figshare https://doi.org/10.6084/m9.figshare.27924888.

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Supplementary material 1

Additional information

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Data type: docx

Explanation note: **table S1.** Overview of the experimental studies included in the meta-analysis. **fig. S1.** Funnel plot representing the relationship between effect size (lnR) and the inverse of the standard error (SE) in drought stress. **fig. S2.** Funnel plot representing the relationship between effect size (lnR) and the inverse of the standard error (SE) in elevated CO2 concentration.

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