Primary Research Article

Global Change Factors differentially impact Floral and Leaf Economic Traits

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Running Head: Floral and Leaf Economics in a Long-Term Climate Experiment

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Abstract

Background and Aims: Since the Industrial Revolution, rising atmospheric CO_2, warming, and more frequent droughts have significantly impacted ecosystems. While the response of leaf functional traits to these global change factors have been widely studied, reproductive traits remain relatively understudied, despite their key role in the diversification and distribution of flowering plants. Here, we investigated how elevated CO_2, warming, drought, and their interactions affect floral, leaf and seed traits in two model grassland species. We also examined how these factors influence trait coordination.

Methods: Two perennial herbs, *Lotus corniculatus* and *Crepis capillaris*, were sampled from a 10-year climate manipulation experiment. We measured resource economic traits related to organ size, construction cost, and dry matter content in both leaves and flowers, along with seed size and number. Univariate and multivariate analyses were used to assess trait responses, and rank-abundance curves were employed to visualize changes in trait coordination across treatments.

Key Results: Floral traits, like leaf traits, exhibit trade-offs among themselves but are largely independent of leaf traits. Trait responses to global change factors were inconsistent across species, with drought being the dominant factor affecting only leaf traits in *L. corniculatus* and all organ types in *C. capillaris*. Extreme global change conditions led to stronger trait coordination in *L. corniculatus*, while *C. capillaris* showed less coordination.

Conclusion: Our results show that floral economic traits, like leaf traits, are responsive to individual and combined effects of global change factors. This highlights their importance in shaping plant strategies under environmental stress and emphasizes the need to better integrate floral traits into the whole-plant economic framework.

Keywords: Floral Economic Spectrum, Plant Economic Spectrum, Functional Ecology, Ecological strategies, Reproductive success, Trade-off, *Lotus corniculatus*, *Crepis capillaris*.

Introduction

Human activities since the Industrial Revolution have significantly increased greenhouse gas emissions, leading to today's high levels of atmospheric CO_2, which is the main driver of the ongoing global change (Borghi *et al.*, 2019; IPCC, 2022). The direct and indirect effects of this change have resulted in rapid alternations of functioning of plants and entire natural ecosystems (Feehan, Harley and van Minnen, 2009). Plants are particularly important in natural ecosystems as they are the primary producers, forming the base of the food webs and supporting all other life forms. Due to the significant impact of global change on ecosystems, it becomes crucial to understand the effects of different global change factors such as CO_2, warming and drought on plants (Descamps, Quinet and Jacquemart, 2021). By studying the impact of global change factors on plants, we can better predict and mitigate the adverse effects of climate change on biodiversity and ecosystem services, ensuring the sustainability and resilience of natural ecosystems.

Plant functional traits have long been used by ecologists as useful proxies for plant ecological strategies (Wright *et al.*, 2004; Reich, 2014) to gain insights into species response to changing environmental conditions (Mortensen, 1987; Ackerly *et al.*, 1992). Recent major global change factors, particularly elevated CO_2, temperature, and drought, significantly impact plant traits and physiology across multiple scales, although to different extents. Drought, due to its ease of implementation in experimental studies, seems to be the most extensively studied of all the global change factors. It has significant negative effects on a range of plant functional traits, including vegetative traits related to competitive ability (plant height, leaf area and root diameter) (Lidon, 2012; Burkle and Runyon, 2016; Zhou *et al.*, 2018; Rodríguez-Alarcón, Tamme and Carmona, 2022), resource use strategy traits such as specific leaf area and specific root length (Jung *et al.*, 2014; Wellstein *et al.*, 2017;

Rodríguez-Alarcón, Tamme and Carmona, 2022) and reproductive traits such as flower size and number, floral rewards, and seed set (Kuppler *et al.*, 2021; Akter and Klečka, 2022; Höfer *et al.*, 2023).

Temperature has a more varied impact on plant traits. While it has been shown to have significant negative effects on both vegetative and reproductive traits (Niu *et al.*, 2000; Liang, 2016; Descamps, Quinet and Jacquemart, 2021), studies have revealed that traits such as leaf area, stem length, stem diameter, fine-root biomass and pollen germination are optimized at certain temperature (Nicotra *et al.*, 2008; Dostálek, Rokaya and Münzbergová, 2020; Wang *et al.*, 2021; Shin, Yeon and Kim, 2023; Kumarathunge *et al.*, 2024) and decline with both temperature increase and decrease. Due to the variability of temperature-optima across species, the effects of temperature on plants are much more species-specific compared to the more consistent effects of drought.

Elevated CO_2 generally enhances photosynthesis, leaf area, carbohydrate concentration, and boosts plant biomass when water is sufficient (Duan *et al.*, 2018; Temme *et al.*, 2019). Long-term Free-Air CO_2 Enrichment (FACE) experiments have further validated these findings, showing sustained increases in photosynthetic rates and biomass accumulation over several growing seasons (Ainsworth and Long, 2005; Leakey *et al.*, 2009). However, the effects of elevated CO_2 on plant reproductive traits are far less studied compared to its effects on vegetative traits (but see Wang, Taub and Jablonski, 2015; Glenny, Runyon and Burkle, 2018).

While many studies explored the effects of temperature, moisture and CO_2 separately, it has been suggested that these factors may strongly interact with each other and should thus be

studied in combination (e.g., Qaderi, Kurepin and Reid, 2006; Albert *et al.*, 2011; Mueller *et al.*, 2022). For example, Qaderi et al. (2006) suggested that elevated CO_2 mitigates the negative effects of drought on plant height, stem diameter, and leaf area. However, one another study has found that drought can limit the positive effect of elevated CO_2 on biomass production (Temme *et al.*, 2019). Temperature plays a dual role: it may enhance CO_2-driven photosynthesis (Long, 1991; Pastore *et al.*, 2020) but can also interact with drought to negatively affect stem and leaf traits (Qaderi, Kurepin and Reid, 2006).

As shown above, numerous studies have explored the effects of global change factors and their interactions on leaf and root traits. However, the interactive effects of these factors on reproductive traits, particularly in relation to resource allocation strategies, remain largely understudied. Examining the economic spectra of different plant organs enhances our understanding of their distinct resource allocation strategies, helping to explain global trade-offs and the biophysical constraints that shape plant form and function (Wright *et al.*, 2004; Violle *et al.*, 2007; Freschet *et al.*, 2010; Reich, 2014; Kramer-Walter *et al.*, 2016). Investigating the floral economic spectrum is especially valuable, as it provides insights into how plants optimize reproductive output under global change and might help understand how these changes would affect pollinator attraction and behaviour (E□Vojtkó *et al.*, 2020; Roddy *et al.*, 2021, 2023).

Most studies examining the response of plant traits to environmental factors focus on the variation of traits in individual plant organs (e.g. Nie *et al.*, 2013; Jung *et al.*, 2014; Bongers *et al.*, 2017; Hai *et al.*, 2023; Fenollosa *et al.*, 2024). However, different organs respond to environmental factors differently but the responses of different organs may also covary with each other. In an analysis of a wide range of leaf and root traits across 24 species, it was

found that leaf traits exhibited stronger and more homogenous response to drought while the response of root traits to drought was highly variable and species-specific (Lozano *et al.*, 2020). This study underscores the need to investigate the coordination of traits among different organs in response to stress factors. Additionally, given the decoupled nature of reproductive traits such as floral and seed traits from vegetative traits such as leaf traits due to the different selective forces acting on them (Salguero-Gómez *et al.*, 2016; E□Vojtkó *et al.*, 2022), their responses are highly likely to be multi-faceted.

The present study seeks to fill the above identified gaps in our knowledge by investigating how global change factors, namely CO_2, temperature and drought, affect floral, leaf and seed traits and the covariation between them in two model grassland species. Specifically, this study addresses the following questions:

Q1. How do floral, leaf and seed traits vary in response to elevated CO_2, warming and drought?

H1. Plant traits respond more strongly to drought than to CO_2 and temperature. Increased drought and temperature have more negative effects while increased CO_2 has more positive effects as a result of increased photosynthetic rate.

Q2. How do these global change factors interact to affect floral, leaf and seed traits?

H2. In the interaction between temperature and CO_2, CO_2 would negate the negative effects of warming. Increasing temperature exacerbates the negative effects of drought which are partially mitigated by elevated CO_2.

Q3. How do global change factors influence the covariation of flower, leaf and seed traits?

H3. Elevated global change factors exert a strong filtering action on the covariation of plant traits across different organs, leading to coordinated trait adjustments to adapt to stressful

conditions. We hypothesize that like leaf traits, floral traits would also undergo changes to adapt to the individual and interactive global change factors and show a strong coordinated response with traits of leaves and seeds.

Materials and Methods

Study Site and Experimental Setup

This study was conducted within the framework of a long-term multifactorial global change experiment (named ClimGrass) at the Agricultural Research and Education Centre (AREC) in Raumberg – Gumpenstein (Meeran *et al.*, 2021; Reinthaler *et al.*, 2021; Radolinski *et al.*, 2025). This study site is located in Styria, Austria (47°29′37″N, 14°06′0″E), 710m above sea level and was established in 2012 in a managed sub-montane C3 grassland. The soil is classified as Cambisol with loamy texture. Aboveground biomass is mown and removed three times a year and plots are regularly bolstered with mineral fertilizer with a total load of 90 kg N $ha^{-1}y^{-1}$, 65 kg P $ha^{-1}y^{-1}$ and 170 kg K $ha^{-1}y^{-1}$. This is done to compensate for the macronutrients lost due to harvests (Pötsch *et al.*, 2019). The experimental design comprises of a total of 54 plots (4 × 4m each) representing individual and combined effects of three levels of temperature (ambient, +1.5°C, +3°C), atmospheric CO_2 concentration (ambient, +150ppm, +300ppm) and drought (Piepho *et al.*, 2017; Pötsch *et al.*, 2019). The CO_2 and temperature treatments started in May 2014 while the drought treatments started in May 2017. The different temperature and CO_2 levels were established based on potential future climate scenarios and were simulated through a combination of infrared heating systems to increase air temperature and a mini-FACE (Free Air CO_2 Enrichment) approach for fumigation with CO_2 (Piepho *et al.*, 2017; Pötsch *et al.*, 2019). The plots which acted as control were not heated or fumigated and were equipped with non-functional heaters and/or mini-FACE rings of same shape and size which blew ambient air to account for potential disturbances (Piepho *et al.*, 2017; Pötsch *et al.*, 2019). Dynamic rainout shelters controlled by

rain sensors were deployed on 12 plots to generate water stress in combination with ambient and future climate change. Half of these plots were maintained at ambient conditions with the remaining half being exposed to the extremes of CO_2 (+300ppm) and temperature(+3°C) (Radolinski *et al.*, 2025; Tissink *et al.*, 2025).

Plant Sampling and Trait Measurements

For this study, we selected a set of plots representing six treatments: Control (C0T0D0), elevated CO_2 concentration (+300ppm)(C1T0D0), increased temperature/warming (+3°C)(C0T1D0), drought (C0T0D1), combination of elevated CO_2 and warming (C1T1D0) and finally combination of elevated CO_2, warming and drought (C1T1D1). The plots were additionally narrowed down based on the presence of either of two model grassland species, *Lotus corniculatus* L. and *Crepis capillaris* (L.) Wallr (see below). These two species are the two most common insect pollinated species occurring in the experimental plots and have the same flowering period.

Lotus corniculatus L. (Fabaceae) is a polycarpic perennial non-clonal herb widely distributed across Europe (Chytrý *et al.*, 2021). It usually flowers between June and August in a umbel inflorescence type (Chytrý *et al.*, 2021). The corolla is zygomorphic, yellow and consists of five petals each: the upstanding ‘standard’, the lateral two wings and the final two lower petals uniting to form the ‘keel’ with the overall shape of the corolla being butterfly-like (*Nature Gate*, 2011). The plant is primarily insect pollinated.

Crepis capillaris (L.) Wallr. (Asteraceae) is an annual herb and is native in Europe being widespread as far north as Denmark and southern Sweden (Stace, 2010; Govaerts, 2024). It usually flowers between May and June in a synflorescence corymbiform inflorescence type. Each flower head contains 50-70 flowers. The corolla is ligulate, 6.0-15.0 mm long, and

yellow with a ligule tinged red (Kilian, 2024). It is pollinated by insects but is also capable of selfing (Chytrý *et al.*, 2021).

The sampling was conducted on 22nd and 23rd of July 2023. For *L. corniculatus*, a total of 45 samples were collected from 21 plots across the 6 treatments, with 6 to 10 samples per treatment. For *C. capillaris*, 39 samples were taken from a total of 27 plots with 5 to 11 samples per treatment. Within each plot, samples were collected at least 10 cm apart with maximum 2 samples per plot and wrapped in water-saturated paper towels and stored in the refrigerator until further processing (approximately 48 hours). Alongside flowers and leaves of both species, seeds of *C. capillaris* were also sampled, dried in paper bags and stored.

To estimate Leaf Area (LA), Specific Leaf Area (SLA) and Leaf Dry Matter Content (LDMC), each leaf which was previously wrapped in wet tissue paper (during sampling) was weighed to determine its saturated mass and then subsequently scanned in a flatbed scanner to determine the LA. The leaves were dried at 70°C for 72 hours and after which their dry mass was also taken. Leaf area was estimated using ImageJ software. SLA was calculated as LA divided by leaf dry mass and LDMC was estimated as the ratio of leaf dry mass to saturated mass (Pérez-Harguindeguy *et al.*, 2013).

The flowers of the two species were processed differently due to variation in their morphology. The petals of *L. corniculatus* were dissected out from the flowers and weighed to obtain their saturated mass. Afterwards, they were separated out into their individual petal types: one standard petal, two wings and one keel. The separated petals were then flattened and scanned, dried similarly to leaves and then weighed again using a Mettler Toledo Microbalance (d = 0.5µg) to get their dry mass. The scanned petals were processed through ImageJ to obtain their individual petal area. As the keel is composed of 2 fused petals, its area was multiplied by 2. The total petal area of all the petals was taken as the Display Area (DA). The total SPA of the whole corolla of each flower was calculated (DA / Dry Mass). Petal Dry

Matter Content (PDMC) was calculated by dividing the total dry mass of the petals by their saturated mass.

For *C. capillaris*, 5 individual ray florets were dissected out and then weighed, flattened and scanned to get their fresh mass and petal area. They were then dried and weighed to get their dry mass. Due to the homogeneity of ray florets, the florets were processed together, and their SPA was calculated as the total area of 5 ray florets divided by their total dry mass. Here, DA was calculated as an average of the 5 individual ray florets. PDMC was also obtained. The number of seeds in each flowerhead was counted. Seeds number per flower head (SN) was calculated by dividing the total number of seeds taken from a plant by the number of flower heads. The total weight of the seeds in a flower head were weighed using the microbalance mentioned above. The Seed Mass (SM) was then calculated by dividing the weight of all the seeds in a flower head by the number of seeds.

Statistical Analyses

All statistical analyses were carried out in R software version 4.3.1. All analyses have been done for each species separately. AI assistance was used to generate initial R code for certain analytical approaches.

Correlations between traits were analyzed using Pearson's correlation test. Correlograms were created using the "corrplots" package (v 0.95) (Wei and Simko, 2024) while the "ggplot2" package (v 3.5.1)(Wickham, 2016) was used for creating all the other plots.

Shapiro-Wilk test was performed to evaluate normality of the trait values. Based on the p-values obtained, the normality of the original trait value was compared with its logarithmic and square-root transformations. The form of the trait value with the highest p-value was selected for inclusion in the linear models, as it indicated the closest approximation to a normal distribution. In *L. corniculatus*, SPA and LDMC were square-root and log-

transformed respectively while all other variables were used in their original form. In *C. capillaris*, only DA was kept in its original form with SPA, PDMC, LDMC and SN being square-root transformed, and LA, SLA and SM being log-transformed.

Linear models were utilized to analyse the effect of CO_2 (C), temperature (T), drought (D) and the interactions between CO_2 and temperature (C×T) and the interaction of (CO_2 + temperature) with drought (CT×D) on leaf and reproductive traits of both species separately. This approach was necessary due to the experimental design, which included drought conditions in only two scenarios: drought alone and with increased CO_2 and temperature.

All traits were standardized prior to multivariate analyses exploring all traits together. All multivariate analyses were carried out with untransformed trait value data using the Vegan package in R (v 2.6.10)(Oksanen *et al.*, 2025). Principal Component Analysis (PCA) was carried out to get an understanding of the joint changes in all the plant traits measured followed by redundancy Analysis (RDA) to test for the effects of climate. Permutational Analysis of Variance (PERMANOVA) was conducted (with 9999 permutations) to determine the significance of the global change factors in the RDA.

To assess the covariation of traits in response to global change factors, separate PCAs were conducted for each treatment. Prior to this, the number of values from the plots were adjusted such that there was equal number of samples and plots from all treatments. This included removing values from treatments which had considerably number to prevent the skewing of response to one treatment. The variance explained by each principal component was extracted for each treatment and adjusted for compatibility. These results were visualised as rank abundance curves using ggplot2 package in R.

Results

The results are presented in three sub-sections. The first section details the responses of plant traits in both species to the individual and interactive effects of global change factors. For each species, we first report findings from the multivariate analysis, followed by results from the univariate analysis. The second section examines the covariation among plant traits, while the final section presents how trait covariation is influenced by global change factors.

Response of Plant Functional Traits to Global Change Factors

Lotus corniculatus

The three global change factors and their interactions collectively explained 29% of the trait variation in the multivariate redundancy analysis (RDA) ($p = 0.002$ for the overall model). When tested individually, drought (D) and warming (T) had significant effects, CT×D had marginally significant effects (Fig. 1) while elevated CO_2 and C×T did not have any significant effect. Among the significant predictors, drought accounted for the highest variance (10.2 %), followed by warming (6.3%) and then CT×D (4.8%) (Table 1 in Supplementary Information).

The significant global change variables, drought and temperature, formed a gradient on the first RDA axis (19.03%). DA and leaf traits (LA, SLA, and LDMC) varied along this gradient, with increasing drought being associated with an increase in LA and LDMC alongside a decrease in SLA. Temperature was diametrically opposite to DA, indicating that increasing temperature levels would lead to a reduction in DA. The second RDA axis accounted for 4.7% of trait variation and was related to CT×D. DA was well-represented on this axis, indicating that the most extreme condition, CTD, would lead to a decrease in DA. The remaining three RDA axes represented 3.5% of the variation.

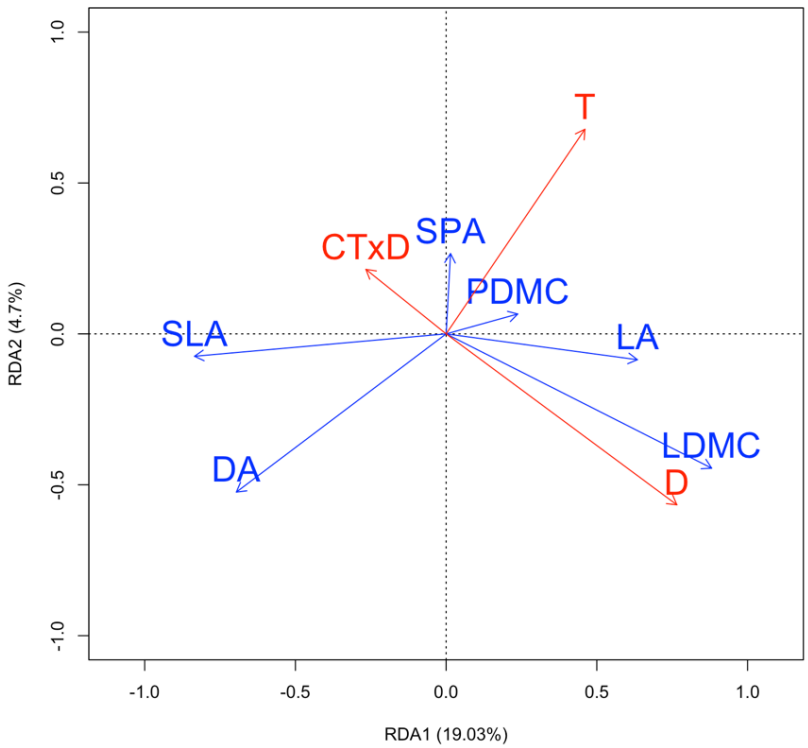

Fig. 1. RDA plot of *L. corniculatus*. Significant global change factors have been shown in red while plant traits have been shown in blue. DA – Display Area, SPA – Specific Petal Area, PDMC – Petal Dry Matter Content, LA, Leaf Area, SLA – Specific Leaf Area LDMC – Leaf Dry Matter Content, T – Warming (+3°C), D – Drought, CT×D – Elevated CO_2, warming and drought.

The univariate analyses of *L. corniculatus* traits revealed that drought had the most consistent and significant effects (Fig. 2), increasing LA, LDMC while decreasing SLA (Fig. 3d, 3e and 3f). CO_2 induced variation in two out of the three leaf traits, reducing SLA and increasing LDMC (Fig. 3a and 3b). The temperature effect was more trait specific as it had a significant effect only on DA (Fig. 3c), causing a substantial decrease in DA under higher temperature. In terms of interactions, C×T overall caused a decrease in DA, as warming negated and reversed the positive effect of CO_2 (Fig. 3g). In the case of SLA, the decrease caused by CO_2 became stagnant with increasing temperature (Fig. 3h). In the most extreme treatment

(CT×D), drought had a buffering effect on increase of LDMC by CO_2 and temperature (Fig. 3i).

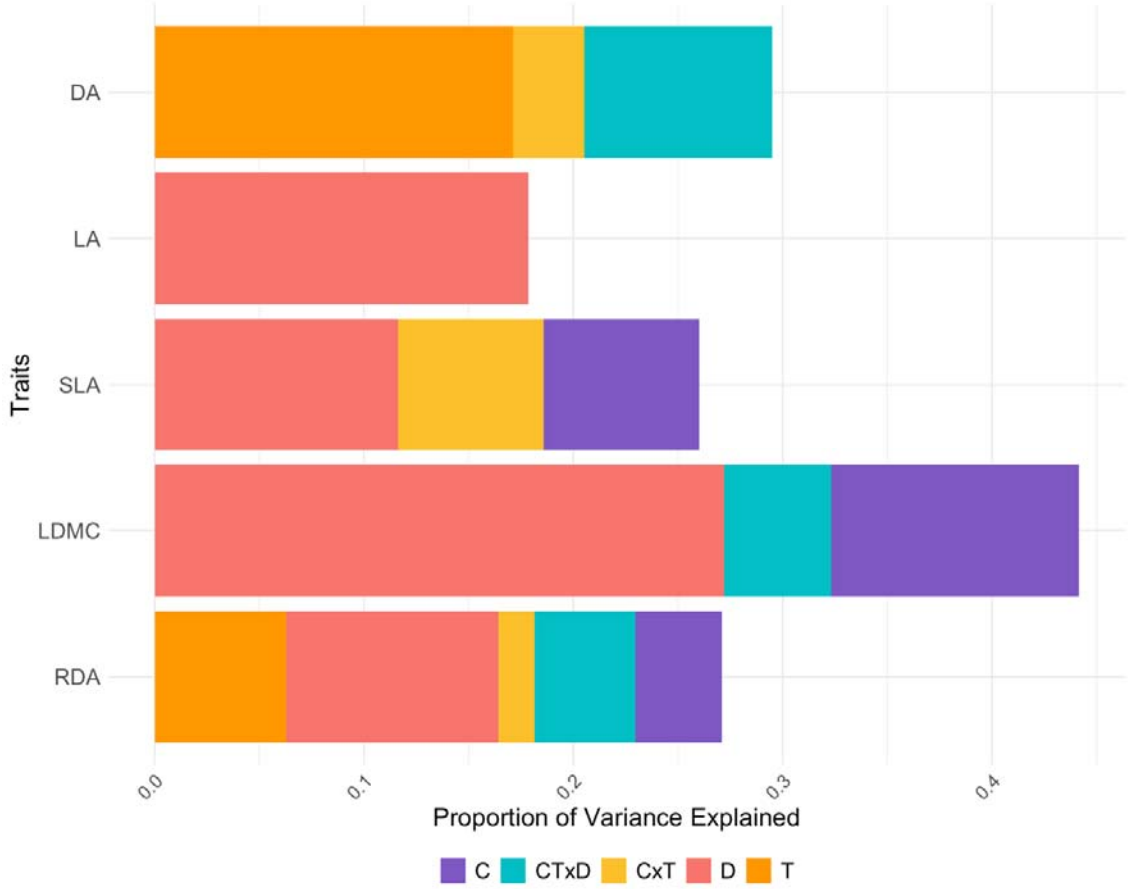

Fig. 2. Variance partitioning plot for *L. corniculatus* showing magnitude of variation explained by the different global change factors. DA – Display Area; LA – Leaf Area; SLA – Specific Leaf Area; LDMC – Leaf Dry Matter Content; C – Elevated CO_2 (+300ppm), T – Warming (+3°C), D – Drought, C×T – Elevated CO_2 combined with warming, CT×D – Elevated CO_2, warming and drought. RDA results are of multivariate analysis. Only the significant variables of $p < 0.05$ are shown. SPA and PDMC do not have any significant predictors and are thus not shown.

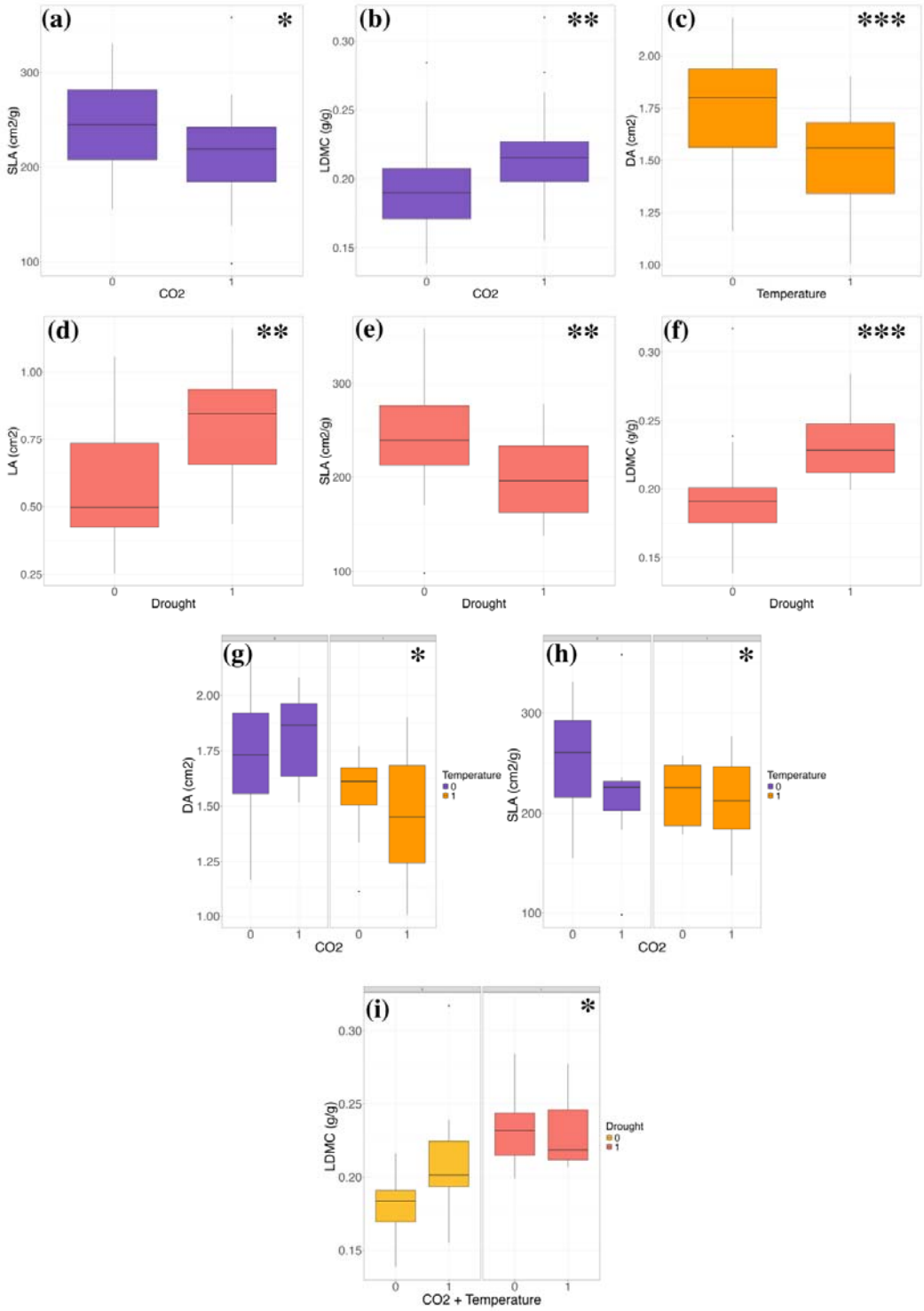

Fig. 3. Boxplots illustrating the individual and combined effects of global change factors on plant traits of *L. corniculatus*. Significance level is indicated in the top right corner (* = 0.05;

** = 0.01; *** = < 0.001). Functional trait studied denoted in the Y-axis while treatment is denoted in the X-axis. For legend of plant traits see Fig. 2.

Crepis capillaris

The RDA analysis of *C. capillaris* showed that the global change factors accounted for 20% of the total trait variation ($p = 0.003$ for the overall model) and drought (7.7%) and C×T (4.5%) having significant effect on the plant traits (Fig. 4).

These two global change factors were highly correlated in the first RDA axis (13%), with drought being the primary and C×T the secondary contributor to variation along this axis. The constrained variation in floral traits (DA, SPA, and PDMC), leaf traits (SLA and LDMC), and SN was chiefly represented along this axis. The patterns indicated that drought had a positive relationship with the Dry Matter Content traits (LDMC and PDMC) while having a negative relationship with all other traits. Among these traits, SN showed the strongest inverse relationship with drought. The second RDA axis accounted for 4% of the total variation, with temperature as the dominant factor. LA was best represented along this axis, possibly indicating that increasing temperature would cause a decrease in LA, although this relationship was not significant. The remaining three RDA axes explained 3% of the variation.

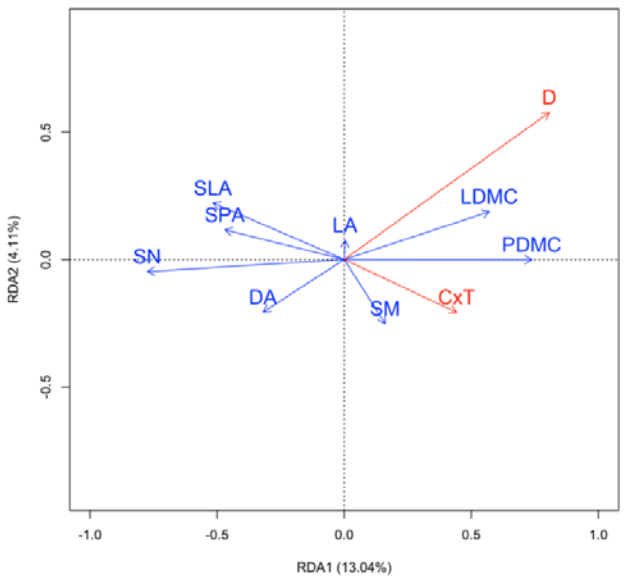

Fig. 4. RDA plot of *C. capillaris*. Significant global change factors have been shown in red while plant traits have been shown in blue. DA – Display Area, SPA – Specific Petal Area, PDMC – Petal Dry Matter Content, LA – Leaf Area, SLA – Specific Leaf Area, LDMC – Leaf Dry Matter Content, SN – Seed Number, SM – Seed Mass, D – Drought, C×T – Elevated CO_2 combined with warming.

The findings in the univariate analysis reflected the general patterns observed in the RDA. Similar to *L. corniculatus*, trait variation in *C. capillaris* was primarily dictated by drought, which was the only climatic variable having a significant effect on the majority of plant traits. Its magnitude of variation was highest in SN, followed by PDMC and then the other traits (SPA, LDMC, and DA) (Fig. 5). An increase in drought levels caused a significant decrease in DA, SPA, and SN while leading to an increase in PDMC and LDMC (Fig. 6a – 6e).

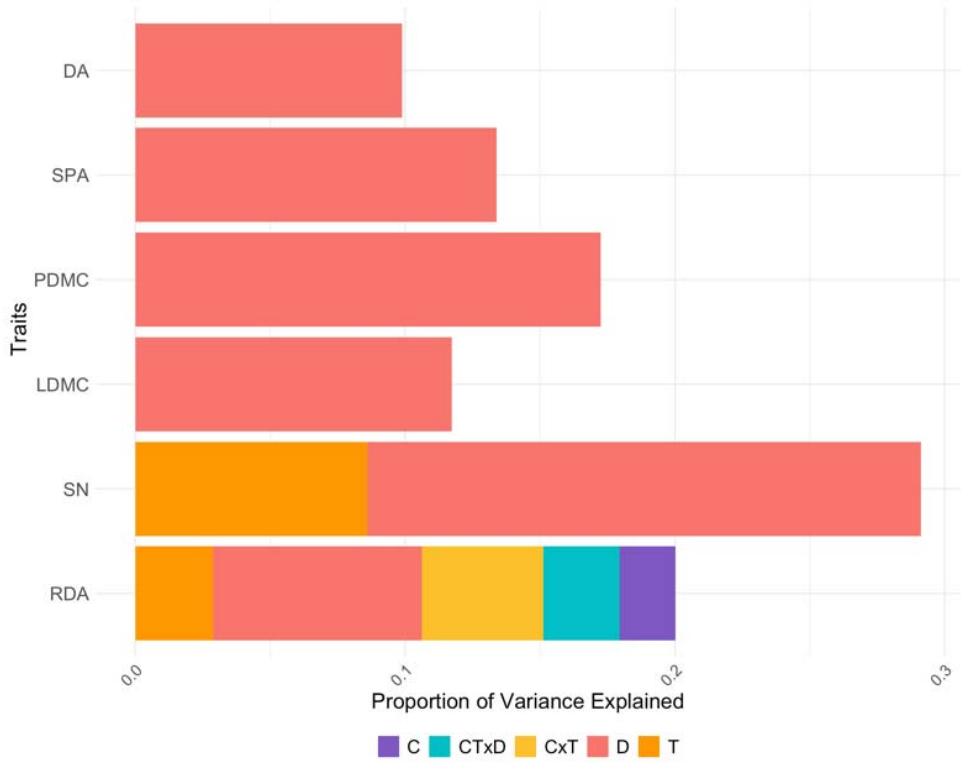

Fig. 5. Variance partitioning plot for *C. capillaris* explaining magnitude of variation in relation to the three global change factors and their interactions. C – Elevated CO_2 (+300ppm), T – Warming (+3°C), D – Drought, C×T – Elevated CO_2 combined with warming, CT×D – Elevated CO_2, warming and drought, DA – Display Area, SPA – Specific Petal Area, PDMC – Petal Dry Matter Content, LA – Leaf Area, LDMC – Leaf Dry Matter Content, SN – Seed Number. RDA results are of multivariate analysis. Only the significant variables of $p < 0.05$ are shown. SLA does not have significant predictors.

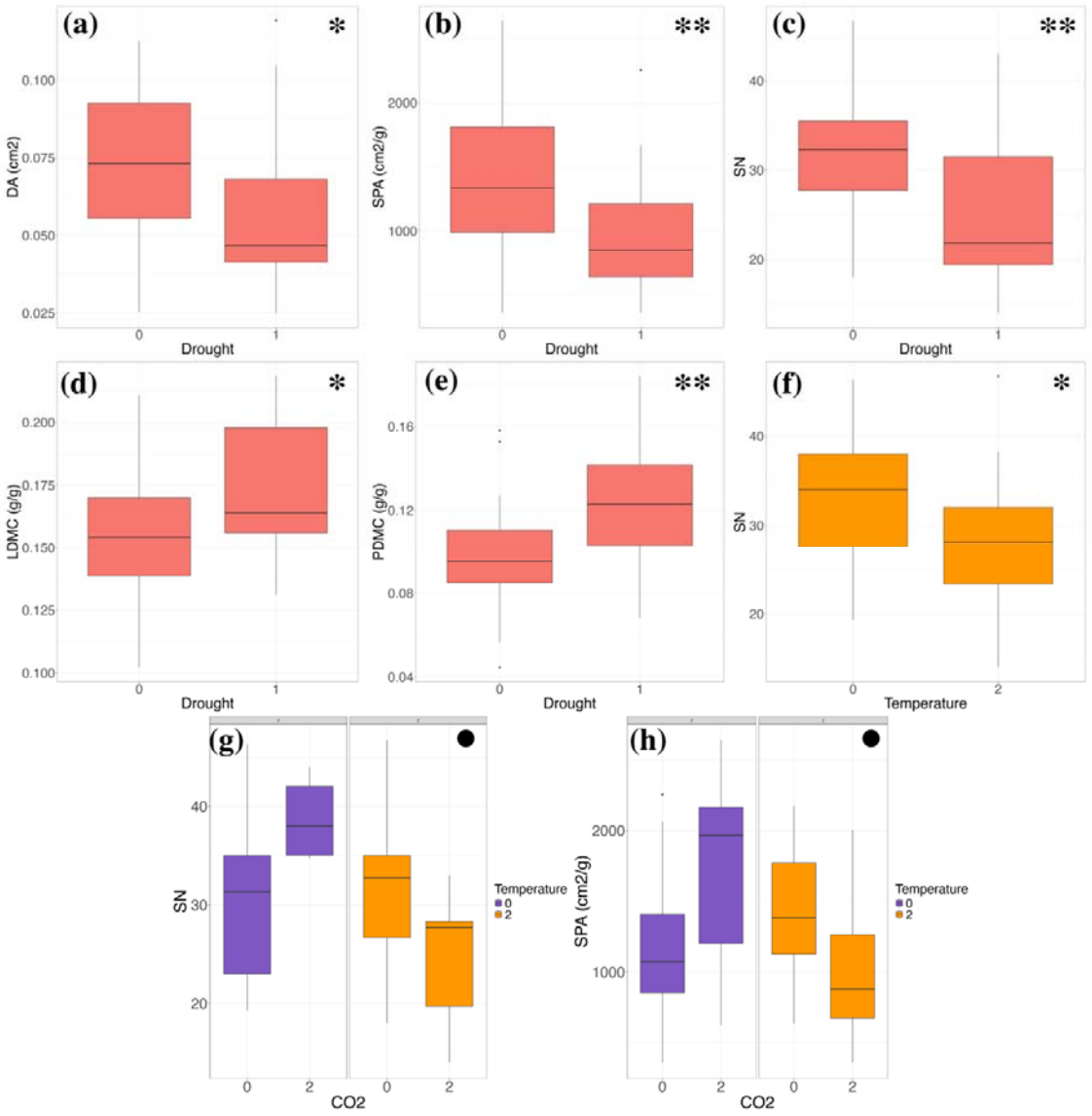

Fig. 6. Boxplots illustrating the effects of global change factors on plant traits of *C. capillaris*. Significance level is indicated in the top right corner (· = <0.1; * = 0.05; ** = 0.01). Functional trait studied denoted in the Y-axis while treatment is denoted in the X-axis. For legend of plant traits see Fig. 5.

Similar to *L. corniculatus*, effect of temperature in *C. capillaris* is also trait-specific and caused a significant effect only for Seed Number (SN), which was negatively related to warming (Fig. 6f). In terms of interactions, although under ambient temperature conditions,

increase in CO_2 intensity causes increase in SPA, warming is shown to negate the positive effect of CO_2 with CT showing slight reduction in SPA despite the positive effect of CO_2 (Fig. 6g). This pattern is mirrored in the effect of CO_2 and temperature on SN (Fig. 6h).

Covariation Between Plant Traits

The initial Principal Component Analysis (PCA) of both species revealed two independent axes of variation among leaf and floral traits. In *L. corniculatus*, the first two axes accounted for 64% of the variation (Fig. 7a). The first axis accounted for 35.2% of the variation and was primarily associated with leaf traits (SLA and LDMC). The second axis accounted for 28.8% of the variation and was linked to floral traits (SPA and PDMC). Specific area traits (SLA and SPA) were negatively correlated with their dry matter counterparts (LDMC and PDMC). Regarding floral traits, DA occurred closely with SPA, and together they were orthogonal to the leaf traits, where LA occurred closely with LDMC.

In *C. capillaris*, the first two principal components accounted for 55.2% of the total trait variation (when analyzed without seed traits) (Fig. 7b). The first axis was dominated by floral traits (DA, SPA, and PDMC) (33.6%), while the second axis was dominated by leaf traits (LA, SLA, and LDMC). Similar to DA in *L. corniculatus*, DA in *C. capillaris* occurred closely with SPA and was orthogonal to leaf traits (SLA and LDMC). SLA and LDMC were also negatively correlated.

When seed traits (SN and SM) were added to the PCA (Fig. 7c), the overall patterns of dominance remained the same. Seed Number (SN) was negatively correlated with the Dry Matter Content traits (PDMC and LDMC). The loadings for SM consistently had low

absolute values across all principal components, with a maximum of -0.3 on PC3. This implied that SM played a negligible role in defining the principal components.

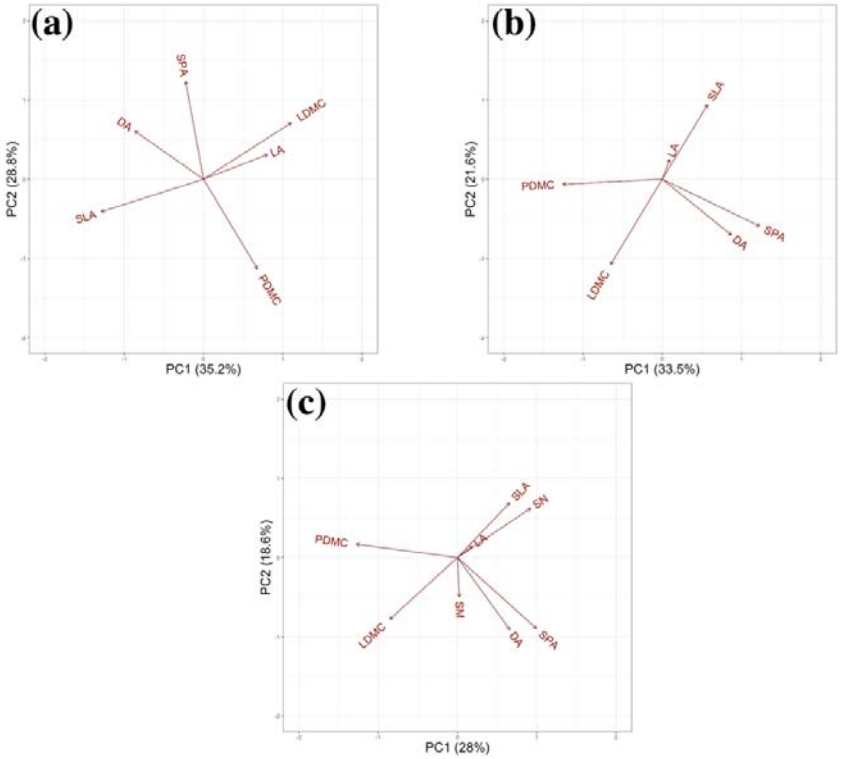

Fig. 7. PCA plot of (a) *L. corniculatus* (b) *C. capillaris* (without seed traits) and (c) *C. capillaris* (with seed traits). DA, Display Area; SPA, Specific Petal Area; PDMC, Petal Dry Matter Content; LA, Leaf Area; SLA, Specific Leaf Area; LDMC, Leaf Dry Matter Content; SN, Seed Number; SM, Seed Mass.

Coordinated Changes in Traits in Response to Global Change Factors

When analyzing the covariation of plant traits under each climatic regime separately, we found that different treatments led to coordinated adjustments in traits; however, the coordinated responses were not similar across species. In *L. corniculatus*, the most extreme treatment (C1T1D1) caused a major coordinated adjustment in traits, with the variation explained along the first axis alone increasing by around 40% compared to the control treatment (C0T0D0), which induced the lowest coordination (Fig. 8a). Overall, treatments

representing combined elevated global change factors (CT×D and C×T) tended to induce a higher degree of coordination than treatments with individual global change factors (C, T, and D).

By investigating the PCA plots of the individual treatments (Supplementary Information Fig. 2 and 3), we revealed that coordination was dictated by either one of the dry matter content traits (LDMC and PDMC) in the control (C0T0D0), elevated CO2 (C1T0D0), and elevated temperature (C0T1D0) treatments, while size-related (LA) and tissue-concentration-related (SLA and SPA) traits dominated in the drought (C0T0D1) and elevated CO2 and temperature (C1T1D0) treatments. Both LDMC and SPA dominated in the most extreme treatment (C1T1D1).

These patterns were partially mirrored in *C. capillaris* (Fig. 8b). The control treatment (C0T0D0) showed the least trait coordination. The C1T1D0 treatment induced the highest coordinated response, followed by the elevated CO2 treatment (C1T0D0). The coordination induced by the other global change factor treatments was less clearly defined. The lack of clear patterns of coordinated response to global change factors was shown even more clearly when seed traits were included (Fig. 8c). When investigating the PCA plots of the individual treatments, all treatments were dominated by a highly varying mix of traits along the first and second axes, with no clear dominance by traits of different organs (floral vs. leaf traits) or traits representing differing growth strategies (dry matter traits vs. size-related traits).

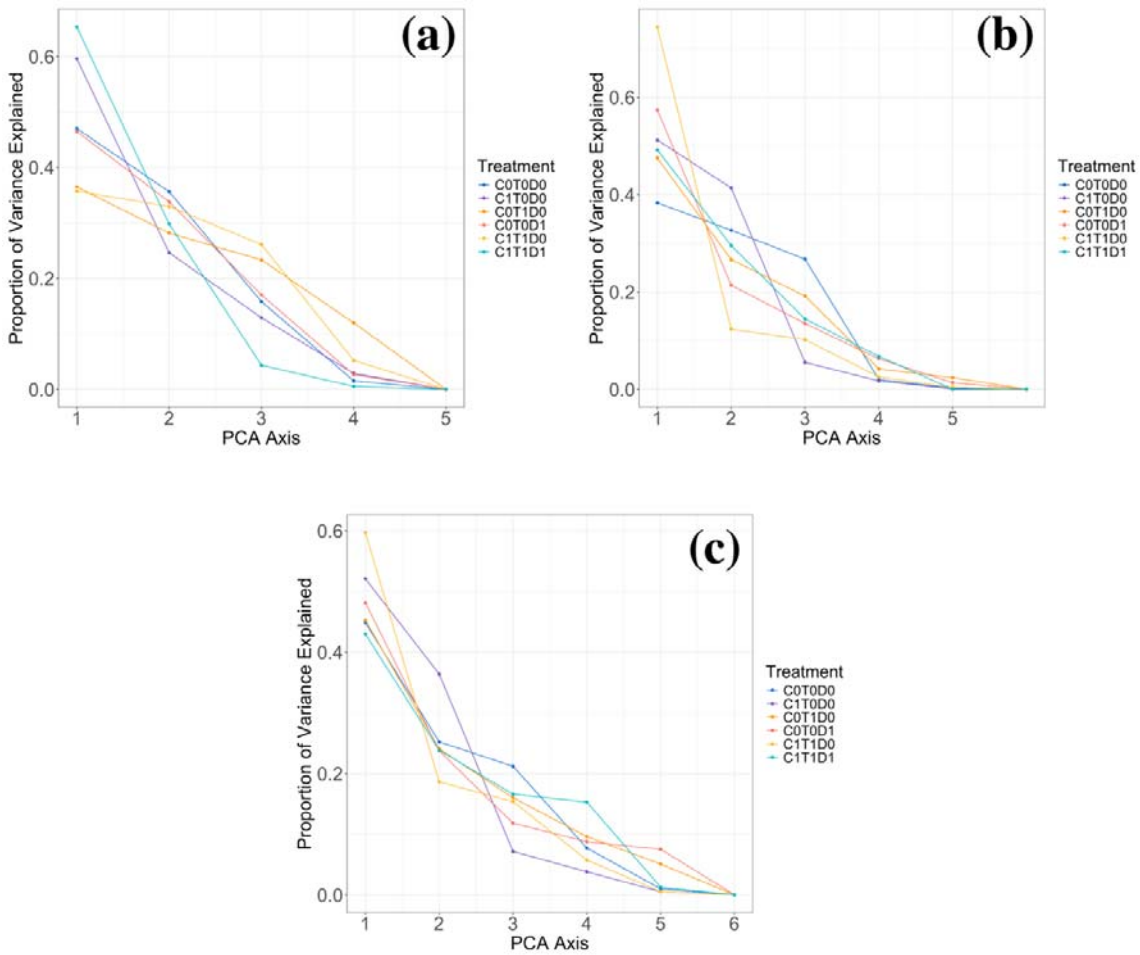

Fig. 8. Variation explained in the traits by each of the PCA axes under different treatments in (a) *L. corniculatus*, (b) *C. capillaris* (without Seed Traits) and (c) *C. capillaris* (with Seed Traits). C0T0D0 - Ambient Control, C1T0D0 – Elevated CO_2 (+300ppm), C0T1D0 – Warming (+3°C), C0T0D1 – Drought, C1T1D0 – Elevated CO_2 combined with warming, C1T1D1 – Elevated CO_2, warming and drought.

Discussion

The results of this study show that global change simulated for multiple years significantly impacts not only vegetative traits but also reproductive traits such as floral and seed traits although responses vary between species. Our study supported (H1) indicating that plant traits respond more to drought than to elevated CO_2 and warming. Contrary to (H2), the

negative effects of temperature were not mitigated by elevated CO_2 conditions. Finally, in line with (H3) global change factors and their interactions exerted a strong filtering on covariation of plant traits, albeit this phenomenon is species specific.

Response of Plant Functional Traits to Individual Global Change Factors

Global change factors significantly influenced the functional traits of both *L. corniculatus* and *C. capillaris*, though the responses varied across traits and species. In *L. corniculatus*, drought was the dominant factor, but other global change factors also affected two of the three leaf traits (SLA and LDMC) and one floral trait (DA). In contrast, *C. capillaris* was primarily influenced by drought, which had a significant impact on all floral traits (DA, SPA, and PDMC), as well as one leaf trait (LDMC) and one seed trait (SN). Temperature was the only other significant factor, affecting only seed number (SN). Species-specific responses have been reported in many previous studies (Ainsworth and Long, 2005; Descamps *et al.*, 2020; Kuppler and Kotowska, 2021; Bernauer *et al.*, 2024). The key reasons for this could be their unique evolutionary history, differing life histories and differences in their functional strategies.

The finding that drought is the dominant factor affecting plant traits of both species aligns with our first hypothesis (H1). Drought stress has been consistently been shown to reduce traits such as leaf area, specific leaf area (SLA), flower size, and seed number (Lidon, 2012; Wellstein *et al.*, 2017; Descamps, Quinet and Jacquemart, 2021; Höfer *et al.*, 2023), while increasing leaf dry matter content (LDMC) (Jung *et al.*, 2014). A notable exception in our study is the response of leaf area. In *L. corniculatus*, leaf area increased under drought, contrary to what was found by most prior studies (e.g., Westoby *et al.*, 2002; McDonald *et al.*, 2003; Yates *et al.*, 2010; Bjorkman *et al.*, 2018; Zhou *et al.*, 2020). Our finding is

supported by a study of *Limonium* species, where larger leaves were associated with higher growth capacity and higher water use efficiency (Conesa, Mus and Galmés, 2019). Our study demonstrated a conservative strategy in which plants increased dry matter content traits (such as LDMC and PDMC) while reducing tissue construction cost-related traits (such as SLA and SPA). This shift suggests a higher investment in structural tissues, aligning with the plant's adaptive response to environmental stress (Poorter *et al.*, 2009). Smaller plant parts with smaller and more densely packed cells require less water to maintain cell turgor, thereby improving plant water status during drought stress (Galen, Sherry and Carroll, 1999; CHAVES *et al.*, 2002). Although this strategy is cost-effective for temporary survival, the reduction in flower size, a crucial visual cue for pollinators, could potentially decrease pollinator visitation rates and thereby reducing population growth rates (Descamps, Quinet and Jacquemart, 2021). However, a decrease in SPA may also suggest increased floral longevity due to reduced flower maintenance costs (Spigler and Woodard, 2019). This could mitigate the potential negative effects of smaller flower size. While no general patterns of decreasing visitation rates by pollinators under water deficit conditions have been identified (reviewed in Kuppler and Kotowska, 2021), the potential impact of floral trait variation on pollinator behaviour requires further attention.

Warming only induced response in two plant traits, decreasing display area of *L. corniculatus* and seed number of *C. capillaris*. Although there are many previous studies which predicted a significant linear relationship between leaf traits (LA, SLA and LDMC) and temperature (Eg. Atkin *et al.*, 2006; Poorter *et al.*, 2010; Fontana *et al.*, 2017; Dostálek, Rokaya and Münzbergová, 2020), our findings on leaf traits were more in line with a study conducted in the Bavarian Alps consisting of 223 species (Rosbakh, Römermann and Poschlod, 2015) where a significant relationship between SLA and temperature was found only at the

community level with no response at either the species or population level. This could be because of the predominant effect of drought on vegetative traits as water availability is a greater limiting factor than warming in temperate climates (Fahad *et al.*, 2017; Zhou *et al.*, 2017). In regards to floral traits, although warming did not alter the per area structural investment in either species, it led to reduced display area in one of the them and this species-specific response in flower size has been replicated in other studies (Liang, 2016; Descamps *et al.*, 2021; Wiszniewski *et al.*, 2022). The stability of leaf traits alongside flower size reduction suggests that plants may prioritize biomass allocation over sexual reproduction under warming conditions. However, this could also reflect resource allocation towards increased competition in warmer climates. Temperature regulation plays a crucial role in the development and functioning of flowers (van der Kooi, Kevan and Koski, 2019) with different species requiring differing optimal temperatures to achieve maximum flower size (Pearson *et al.*, 1995; Zhang, Ampatzidis and Whiting, 2015). Species which can maintain and possibly increase flower size at higher temperatures have a greater probability of surviving in future climate scenarios over species which cannot. Given that in our study, specific petal area and display area were positively correlated in both species, this would indicate flowers of these species achieve a greater flower diameter with the same amount of carbon allocation. Similar to the plant's response to drought, while this would be a beneficial strategy in the short term, it is important to consider the trade-offs between longevity and construction costs based on plant economics (Reich, 2014). Larger flowers with lower construction costs (or high SPA) are generally expected to have shorter lifespans and tend to flower much more rapidly (Zhang *et al.*, 2017; Spigler and Woodard, 2019). Plants that can adjust their display size and flowering rate can enhance pollinator attraction when pollinators are rare and limit self-pollination when pollinators are common.

(Harder and Johnson, 2005).

In our experiment, elevated CO_2 levels resulted in a decrease in SLA an increase in LDMC in only one species (*L. corniculatus*). While several studies confirm our findings of decrease in SLA and increase in LDMC under elevated CO_2 (e.g., Centritto, Lee and Jarvis, 1999; Stiling and Cornelissen, 2007; Robinson, Ryan and Newman, 2012; Poorter *et al.*, 2022), others partially contradict them, showing increased SLA under elevated CO_2 (Duan *et al.*, 2018; Temme *et al.*, 2019). This variation may be due to differences in resource-use strategies among plants with different growth forms. Perennials like *L. corniculatus* often have thicker leaves with higher Leaf Mass per Area (lower SLA) and higher LDMC, leading to slower growth rates and lower resource acquisition compared to faster-growing annuals (Poorter *et al.*, 2009; Reich, 2014). When exposed to favourable conditions (such as elevated CO_2), perennials may not exhibit the same growth responses as annuals because their strategies prioritize survival and maintenance over rapid growth. In our study, elevated CO_2 level had no effect on floral traits. This is in line with (Bernauer *et al.*, 2024) while other studies have reported both increase and decrease of flower size under elevated CO_2 (Niu *et al.*, 2000; Hoover *et al.*, 2012; Maia *et al.*, 2023). These mixed findings highlight the complexity of plant responses to elevated CO2, emphasizing the need for further research to understand how different traits and growth strategies influence adaptation to changing environmental conditions.

Interactive Effects of Global Change Factors on Plant Traits

Regarding the combined effects of global change factors on plant traits, we hypothesized (H2) that the negative effects of either warming or drought would be partially mitigated by elevated CO_2. This hypothesis was not supported by our observations. The effects of interaction between elevated CO_2 and warming (C×T) were more negative for floral and seed

traits than effects of warming alone. Some studies have reported the induction of thermotolerance in plants under elevated CO_2 conditions (AbdElgawad *et al.*, 2016; Lee *et al.*, 2020) while others have reported CO_2 has little effect on the negative effects of temperature increase (Niu *et al.*, 2000). Although the experimental conditions for elevated CO_2 and warming which were in our study were comparable to those of Lee *et al.*, (2020); our results differ. In their study on growth and photosynthesis of potato crops, elevated CO_2 mitigated the negative effects of temperature, whereas in our study, it resulted in more pronounced negative effects. Considering these nuances, we conclude that while the positive effects of elevated CO_2 are well-documented, its interaction with temperature is complex, and the outcomes are highly species-specific.

The combination of elevated CO_2, warming and drought (CT×D) significantly affected only one trait in only one species, i.e. LDMC in *L. corniculatus*. While plants exposed to elevated CO□ and temperature exhibited higher LDMC than those in ambient conditions, drought-stressed plants showed a significantly greater LDMC than both ambient and elevated CO□ + temperature. Increased LDMC might be attributed to improved water-use efficiency, driven by reduced SLA (Wellstein *et al.*, 2017) and increased investment in non-structural carbohydrates (Blumenthal *et al.*, 2020; Rodríguez-Alarcón, Tamme and Carmona, 2022). Additionally, the observed reduction of SLA and increase of LDMC may be associated with changes in the composition of palisade parenchyma cells, which have been shown to increase in both number and size under water limitation (Peña-Rojas *et al.*, 2024).

Trait Covariation Patterns and Effect of Global Change Factors on Covariations

Our findings on trait covariation patterns indicating orthogonality of floral traits from leaf traits is in-line with (E□Vojtkó *et al.*, 2022). They explain this pattern by differing selective

forces acting on them alongside the increased evolvability of vegetative traits (E Vojtkó *et al.*, 2022). In regard to the effects of global change factors on trait covariation, we hypothesized (H3) that environmental extremes exert a strong coordinated response in plant functional traits. This phenomenon was found to be true for only one of our two species. This differential coordinated response of plant functional traits may reveal interesting insights into the adaptability and distribution of plant species across different habitats.

In *L. corniculatus*, Dry Matter Content traits (LDMC and PDMC) play a dominant role in the variation in three out of the six treatments (C0T0D0, C1T0D0 and C0T1D0). This is in line with studies showing that plants exposed to stressful conditions or elevated CO_2 have been found to pivot towards conservative strategies such as increased dry matter content (Centritto, Lee and Jarvis, 1999; Jung *et al.*, 2014; Bongers *et al.*, 2017; Mueller *et al.*, 2022). This prioritization of 'slow' traits in advent of stress allows plant species to survive in stressful climates (Bongers *et al.*, 2017; Mueller *et al.*, 2022). Additionally, functional traits of *L. corniculatus* showed the most coordinated response in the most extreme conditions (C1T1D1). This is in-line with previous studies (Lozano *et al.*, 2020; Mueller, Kray and Blumenthal, 2024). Drier, warmer habitats have been found to exert stronger selection pressures on plant traits to enhance water-use efficiency, heat tolerance and resource conservation which eventually leads to a stronger selection for trait coordination (Blumenthal *et al.*, 2020; Mueller, Kray and Blumenthal, 2024). Prioritization of slow traits and increased coordinated response to climatic stress would be the key contributing factors for the climatic adaptability of *L. corniculatus*. This species is widely distributed, thriving in parts of Mediterranean, semi-arid and even parts of South-Asian climates. This is in stark contrast to the adaptability of *C. capillaris* which is restricted to temperate European Climates ('Plants of the world online', 2024).

When examining the trade-offs between tissue concentration cost-related traits (SLA and SPA) and dry matter content traits (LDMC and PDMC) across different treatments, the coordination between these traits fluctuates frequently. For instance, in *L. corniculatus* under warming, the expected trade-off between SLA and LDMC is absent. Moreover, under elevated stresses—such as the C1T1D0 and C1T1D1 treatment, the well-established orthogonal relationship between floral and leaf traits is disrupted. In the most extreme treatment (C1T1D1) in both species, floral traits (DA or SPA) align within the same dimension as leaf traits (SLA, LDMC), diverging from patterns observed under less stressful conditions.

Global change factors have been known to alter plant trait coordination. For example, the significant linear relationship between nitrogen concentration per unit mass (N_{mass}) and SLA (Wright *et al.*, 2004; Díaz *et al.*, 2016), observed under ambient and moderate warming conditions, has been found to weaken under severe warming (Yu *et al.*, 2022). Given the strong filtering effects of global change factors such as drought on plant trait coordination (Lozano *et al.*, 2020; Mueller, Kray and Blumenthal, 2024), species may have reduced flexibility to maintain independent trait relationships across different organs. Instead, they may exhibit trait convergence as a survival strategy, leading to a breakdown of the typical orthogonal relationships observed under milder conditions. This highlights the profound impact of environmental stressors on plant functional trait dynamics.

Conclusions

Our study highlights the significant impact of individual and interactive effects of global change factors, including CO_2, temperature, and drought, on the floral economic traits of *L. corniculatus* and *C. capillaris*. Drought emerged as the dominant factor influencing most

plant traits, with species-specific variations in response intensity. The interactive effects of these global change factors also led to varied responses in floral economic traits. Notably, climatic extremes exerted a strong filtering effect on the trait coordination of *L. corniculatus*. To gain a comprehensive understanding of resource allocation strategies (trade-offs among traits) in plants under environmental stresses, larger studies encompassing a broader range of functional traits and larger species set are essential. Investigating the floral economic spectrum and its integration into the whole plant economic spectrum can provide valuable insights into the effects of divergent selective forces on different plant tissues and the potential consequences of shifts in these selective forces as a result of global change.

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Conflict of Interest

The authors declare no conflict of interest.

Authors Contributions

MM and DT conceived the idea and conceptualized the study under the supervision of ZM. MB and AS facilitated the provision of the experimental site for sampling. MM and DT performed the sampling and processed the floral, leaf and seed traits. MM analyzed the data and performed all statistical analyses with input from DT and ZM. MM drafted the manuscript, with substantial suggestions, input, and revisions from ZM and DT. MB and AS also provided feedback on the manuscript.

AI Assistance

AI assistants, including ChatGPT and Copilot, were utilized to aid in literature gathering, assist with statistical analysis, and refine the tone of the Introduction and Discussion sections. All outputs were meticulously cross-checked by the authors to ensure accuracy and prevent the inclusion of false information in the manuscript.

Availability of Data and Materials

The data that supports the findings of this study will be made openly available in a Zenodo repository upon acceptance along with the relevant software scripts being attached in GitHub.

Supplementary Information

Supplementary information has been included in a separate file and detail the following. **Fig. S1.** Correlogram representing all significant pairwise trait correlations in (a) *L. corniculatus* and (b)*C. capillaris*. **Fig. S2.** PCA plots showing trait coordination patterns of *L. corniculatus* under different treatments. **Fig. S3.** PCA plots showing trait coordination patterns of *C. capillaris* under different treatments (Without Seed Traits). **Fig. S4.** PCA plots showing trait coordination patterns of *C. capillaris* under different treatments (With Seed Traits). **Table S1.** The effect of climate on trait composition tested using RDA on *L. corniculatus* and *C. capillaris*. **Table S2.** Trait loadings and percentage of trait variation explained by successive principal components (PC) in *L. corniculatus*. **Table S3.** Trait loadings and percentage of trait variation explained by successive principal components (PC) in *C. capillaris*.

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			L. corniculatus					*C. capillaris*				
			C	T	D	CT	CTD	C	T	D	CT	CTD
Flower	DA	F	2.29	**21.49**	0.12	**4.26**	**11.25**	1.91	0.01	**5.05**	0.02	0.07
		P	0.134	**< 0.001**	0.729	**0.042**	**0.001**	0.174	0.942	**0.030**	0.900	0.788
	SPA	F	0.06	0.67	3.24	0.52	0.21	0.27	0.35	**8.06**	*3.05*	1.22
		P	0.808	0.414	*0.075*	0.474	0.647	0.607	0.560	**0.007**	*0.088*	0.275
	PDMC	F	0.01	1.30	1.08	0.05	0.29	0.17	0.19	**9.76**	*3.19*	2.64
		P	0.931	0.257	0.301	0.815	0.594	0.679	0.667	**0.003**	*0.081*	0.111
Leaf	LA	F	1.08	3.31	**10.86**	0.29	0.34	0.00	0.00	0.22	0.25	0.60
		P	0.305	*0.076*	**0.002**	0.596	0.561	0.948	0.980	0.644	0.619	0.445
	SLA	F	**4.96**	2.23	**7.76**	**4.63**	2.14	0.00	0.00	0.22	0.25	0.60
		P	**0.031**	0.143	**0.008**	**0.037**	0.151	0.948	0.980	0.644	0.619	0.445
	LDMC	F	**9.76**	0.05	**22.44**	1.00	4.21	0.10	0.06	**5.89**	1.17	2.98
		P	**0.003**	0.816	**< 0.001**	0.322	**0.046**	0.751	0.813	**0.020**	0.287	0.092
Seed	SN	F						0.92	**5.31**	**12.66**	*3.52*	0.30
		P						0.344	**0.027**	**0.001**	*0.068*	0.588
	SM	F						0.51	1.51	0.42	2.08	0.01
		P						0.478	0.227	0.520	0.157	0.939

Table 1. Effect of global change factors (CO_2, temperature and drought) on plant traits of *L. corniculatus* and *C. capillaris.* Significant effects (p-values < 0.05) are marked in bold while marginally significant effects (p-values between 0.05 and 0.1) are marked in italics

List of Figure Legends

Figure 1: RDA plot of *L. corniculatus* 13
Figure 2: Variance partitioning plot for *L. corniculatus*..... 14
Figure 3: Boxplots illustratiiong the effects of global change factors on plant traits of *L. corniculatus* 15
Figure 4: RDA plot of *C. capillaris* 16
Figure 5: Variance partitioning plot for *C. capillaris*..... 17
Figure 6: Boxplots illustratiiong the effects of global change factors on plant traits of *C. capillaris* 18
Figure 7: PCA plot of *L. corniculatus* and *C. capillaris*..... 20
Figure 8: Variation explained in the traits by each of the PCA axes under different treatments in *L. corniculatus* and *C. capillaris.*..... 22