



Higher sensitivity of gross primary productivity than ecosystem respiration to experimental drought and warming across six European shrubland ecosystems

Qiaoyan Li^{a,*}, Albert Tietema^b, Sabine Reinsch^c, Inger Kappel Schmidt^a, Giovanbattista de Dato^d, Gabriele Guidolotti^e, Eszter Lellei-Kovács^f, Gillian Kopittke^b, Klaus Steenberg Larsen^a

^a Department of Geosciences and Natural Resource Management, University of Copenhagen, Denmark

^b Institute for Biodiversity and Ecosystem Dynamics, University of Amsterdam, the Netherlands

^c UK Centre for Ecology & Hydrology, Environment Centre Wales, Bangor, United Kingdom

^d CREA Council for Agricultural Research and Economics, Research Centre for Forestry and Wood, Arezzo, Italy

^e Research Institute on Terrestrial Ecosystems (IRET), National Research Council (CNR), Porano, TR, Italy

^f Institute of Ecology and Botany, Centre for Ecological Research, Hungary

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ABSTRACT

Shrubland ecosystems across Europe face a range of threats including the potential impacts of climate change. Within the INCREASE project, six shrubland ecosystems along a European climatic gradient were exposed to ecosystem-level year-round experimental nighttime warming and long-term, repeated growing season droughts. We quantified the ecosystem level CO_2 fluxes, i.e. gross primary productivity (GPP), ecosystem respiration (R_{eco}) and net ecosystem exchange (NEE), in control and treatment plots and compared the treatment effects along the Gausson aridity index. In general, GPP exhibited higher sensitivity to drought and warming than R_{eco} and was found to be the dominant contributor to changes in overall NEE. Across the climate gradient, northern sites were more likely to have neutral to positive responses of NEE, i.e. increased CO_2 uptake, to drought and warming partly due to seasonal rewetting. While an earlier investigation across the same sites showed a good cross-site relationship between soil respiration responses to climate over the Gausson aridity index, the responses of GPP, R_{eco} and NEE showed a more complex response pattern suggesting that site-specific ecosystem traits, such as different growing season periods and plant species composition, affected the overall response pattern of the ecosystem-level CO_2 fluxes. We found that the observed response patterns of GPP and R_{eco} rates at the six sites could be explained well by the hypothesized position of each site on site-specific soil moisture response curves of GPP/ R_{eco} fluxes. Such relatively simple, site-specific analyses could help improve our ability to explain observed CO_2 flux patterns in larger meta-analyses as well as in larger-scale model upscaling exercises and thereby help improve our ability to project changes in ecosystem CO_2 fluxes in response to future climate change.

1. Introduction

Ecosystems around the world are now experiencing a much higher frequency and intensity of climate extremes than in the past (Ummenhofer and Meehl, 2017). Extreme climatic events, such as heatwaves, droughts, and floods have severe impacts on the carbon cycle and balance in ecosystems. However, forecasting of ecosystem carbon exchange responses to extreme events is complicated, by the highly nonlinear responses of many carbon cycling processes (Li et al.,

2021). In the past two decades, central and northern European countries have been stricken by major summer heat waves and droughts (Bastos et al., 2020) with severe impacts on the terrestrial ecosystems. Those impacts have been mostly explored on forests and grasslands (Du et al., 2020; Li et al., 2021), with little focus in shrubland ecosystems.

At the global scale, shrublands occupy about 14–17.6 % of the total land cover (Hansen et al., 2000; Broxton et al., 2014), yet little information is available on how shrubland ecosystem-level carbon dynamics respond to climate extremes and climate changes, such as long-term

* Corresponding author.

E-mail address: qli@ign.ku.dk (Q. Li).

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severe drought and warming (Wu et al., 2011; Liberati et al., 2021). Shrublands are widely recognized human-shaped habitats with high conservation and natural value in the European landscape varying from *Calluna vulgaris* heathlands to forest-steppe shrubland and Mediterranean maquis ecosystems (Beier et al., 2009; Wessel et al., 2004). As a result of high rates of loss and degradation, shrublands have become the focus of increasing conservation concerns (Newton et al., 2009). The observed decline in shrubland areas is generally due to the lack of management, overgrazing, excessive wildfires, polluting atmospheric deposition and fragmentation due to different land uses (Wessel et al., 2004; Fagúndez, 2013). In addition to these various threats, climate change may make these ecosystems even more vulnerable as climate affects plant diversity, community structure and ecosystem functions (Fagúndez, 2013).

Water availability and temperature are important climate drivers for ecosystem processes such as plant photosynthesis, soil microbial decomposition, and carbon translocation (Gorissen et al., 2004; Davidson and Janssens, 2006; Abbasi et al., 2020). Warming and drought may strongly impact carbon fluxes and carbon dynamics by altering both the overall structure and functioning of terrestrial ecosystems (Luo et al., 2001; Nemani et al., 2003; Walker et al., 2006; Doughty et al., 2015). Generally, drought is expected to negatively affect gross primary productivity (GPP), ecosystem respiration (R_{eco}) and their difference, i.e. net ecosystem exchange (NEE) (Sloat et al., 2015; Morgan et al., 2016), while warming on the other hand is expected to stimulate GPP and R_{eco} (Wu et al., 2011), as well as soil respiration (R_s) (Bond-Lamberty and Thomson, 2010; Reinsch et al., 2017). Even small changes in temperature and/or soil moisture therefore have the potential to affect ecosystem carbon dynamics (Gorissen et al., 2004; Llorens et al., 2004; García-Palacios et al., 2021). Considering that climate warming is a continuous process, while heatwaves and droughts are stressors imposed irregularly on ecosystems, the opposing effects of drought and warming on the flux components (GPP, R_{eco} and NEE), and their resulting net carbon balance under a changing climate remain highly uncertain.

In the past decades, eddy covariance has been widely used as a state-of-the-art method for carbon flux measurements at ecosystem, regional, and global scales (Lasslop et al., 2012; Lund et al., 2012). However, eddy covariance measurements are not applicable to plot sizes typical for in-situ climate change manipulation experiments. At the plot scale, chamber-based measurements of NEE and R_{eco} by using transparent and dark chambers have been widely used (Larsen et al., 2007; Selsted et al., 2011). Furthermore, the eddy covariance method is only able to measure NEE directly without precise divergence of the two important flux components: plant photosynthesis and respiration (Larsen et al., 2007), which could be measured directly with transparent and dark chamber measurements. Chamber-based measurements therefore remain very well-suited for observing changes in each flux component and overall carbon balance at the ecosystem level in field scale manipulation experiments.

Between 1999 and 2006, six European shrubland sites with experimental night-time warming and growing season drought were gradually established along a precipitation and temperature gradient within the INCREASE network (Beier et al., 2004; Lellei-Kovács et al., 2016). Most of the sites have been kept running for about 10 years. Changes in the soil, vegetation, nutrients, biomass and R_s have been reported (Emmett et al., 2004; Gorissen et al., 2004; Schmidt et al., 2004; Peñuelas et al., 2007; Reinsch et al., 2017; Kröel-Dulay et al., 2015). However, the responsiveness of NEE, GPP, and R_{eco} to climate change in these shrublands has not previously been reported in a coordinated way across all six sites. Here, we explore the responsiveness of ecosystem-level carbon fluxes to the long-term growing season drought and nighttime warming manipulations across six European shrubland ecosystems. Sites were located along temperature (Mediterranean to temperate/humid oceanic) and precipitation gradients (xeric to mesic/hydric). Across the environmental gradients, we tested the following hypotheses: (1) long-term progressive and cumulative drought leads to a decline in GPP,

R_{eco} and NEE (i.e. less net carbon uptake), while warming increases GPP, R_{eco} and NEE (i.e. higher net carbon uptake). (2) The pattern of ecosystem carbon fluxes across the environmental gradients is expected to follow the same pattern as previously reported for plant biomass and R_s rates, i.e. hydric ecosystems being more affected by drought and warming than mesic ecosystems (Reinsch et al., 2017).

2. Materials and methods

2.1. Site descriptions

The experimental manipulations of growing season drought and warming were carried out at six different European shrubland sites (Fig. 1): Brandbjerg (Denmark; DK_B); Mols (Denmark; DK_M); Clocaenog (United Kingdom; UK) and Oldebroek (The Netherlands; NL) are heathlands (Beier et al., 2004), while Kiskunsag (Hungary; HU) is a continental forest-steppe, and Capo Caccia (Italy; IT) is a Mediterranean shrubland (de Dato et al., 2008). Most of the sites have a temperate oceanic or continental climate with the growing season around April–September, while IT, the warmest site, has a Mediterranean climate and a different growing season in the periods of October–May (de Dato et al., 2008). Similar climate types result in analogous dominant species in the DK_B, DK_M, UK, and NL, which are *Calluna* and *Deschampsia flexuosa* to various degrees (Table 1), whereas in HU and IT, the dominant species are shrub-sized *Populus alba* and *Cistus monspeliensis*, respectively (Peñuelas et al., 2007; Kröel-Dulay et al., 2015; Mojzes et al., 2017).

At each site, field-scale untreated control plots ($n = 3$), passive night-time warming plots ($n = 3$) and drought treatment plots ($n = 3$) were replicated in a randomized block design ($n = 6$ at DK_B site). Mean annual precipitation (MAP) and mean annual air temperature (MAT) were recorded at the site level. The warming treatment was achieved by using extractable curtains from dusk till dawn reflecting 97 % and 96 % of direct and diffuse infrared radiation, respectively, to prevent heat loss at night (Beier et al., 2004; Beier et al., 2008). Another set of transparent waterproof extractable curtains was used to remove the precipitation during rain events for about two months during the growing season for most of the sites. At the IT site, an additional drought period was established during the autumn growing season (Beier et al., 2004; Beier et al., 2008). To avoid effects of the warming treatment on the hydrology, rain sensors triggered the warming curtains to automatically retract during nocturnal rain events (Peñuelas et al., 2007). When the wind speed was over 10 m s^{-1} , the curtains were also automatically retracted. Growing season drought and night-time warming manipulations were started in 1999 at DK_M, UK and NL sites, in 2001 at HU and IT sites, and in 2006 at DK_B sites (Mikkelsen et al., 2008; Peñuelas et al., 2007; Reinsch et al., 2017). All the setup details are described in previous literature by Beier et al. (2004), Beier et al. (2008) and Mikkelsen et al. (2008).

2.2. Ecosystem-level CO_2 flux measurements

All CO_2 flux measurements were conducted in each experimental plot ($4 \text{ m} \times 5 \text{ m}$) with pre-installed soil collars ($60 \text{ cm} \times 60 \text{ cm}$) on a biweekly or monthly basis at each site for at least one year between 2011 and 2013, aiming to cover all seasons except during snow cover periods (see mean fluxes measured in Suppl. Fig. S1). As described in previous studies (Beier et al., 2009; Lellei-Kovács et al., 2011; Lellei-Kovács et al., 2016; Guidolotti et al., 2017), the CO_2 fluxes were measured by infrared gas exchange systems LI-6400XT (LICOR Biosciences, Lincoln, NE, USA) at the NL, DK_B and DK_M sites and LI-8100 (LICOR Biosciences, Lincoln, NE, USA) at the UK and IT sites attached to a 216 L transparent chamber. The chamber was equipped with a fan as well as a PAR sensor (LI-COR quantum sensor). At the HU site, an ADC Leaf Chamber Analyzer 4 (ADC BioScientific, Hoddesdon, UK) was used with a similar transparent chamber (288 L).

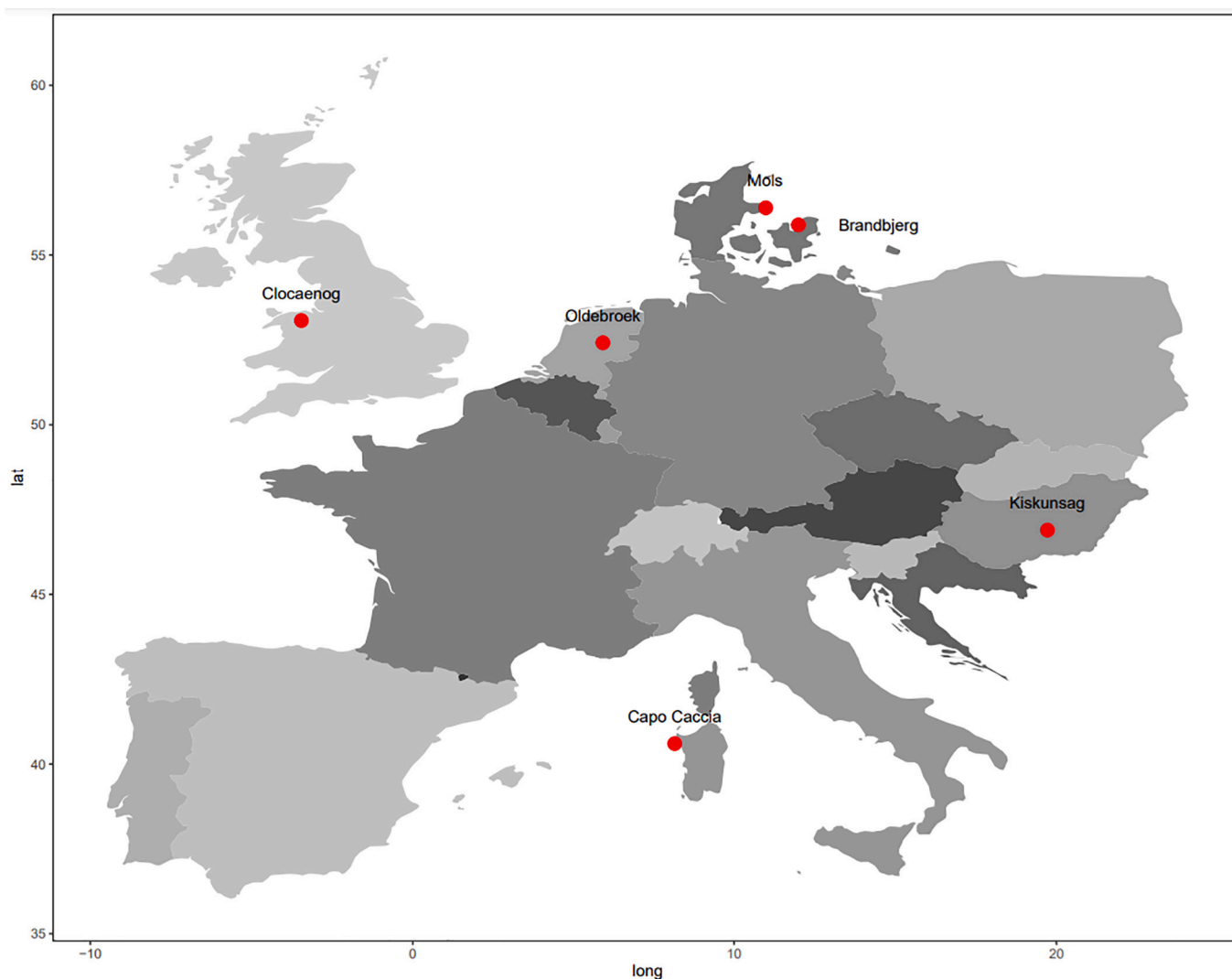


Fig. 1. Map of the six European sites where the drought and warming manipulations were set up and the CO₂ fluxes were measured. See site details in Table 1.

Table 1

Experimental site information and drought/warming treatment effects. MAP = mean annual precipitation, MAT = mean annual temperature, MAP_{red} = percentage reduction in precipitation (drought treatment), MAT_{inc} = mean annual temperature increase (warming treatment). GI = Gausson index of aridity. GI-D = Gausson index of aridity calculated by decreased mean annual precipitation. GI-W = Gausson index of aridity calculated by increased mean annual temperature. IT = Italy, HU = Hungary, DK_M = Denmark Mols, DK_B = Denmark Brandbjerg, NL = The Netherlands, UK = United Kingdom.

	Clocaenog, UK	Oldebroek, NL	Brandbjerg, DK_B	Mols, DK_M	Kiskunság, HU	Capo Caccia, IT
MAP (mm)	1263	1005	757	669	558	544
MAT (°C)	7.4	8.9	9.4	8.7	10.5	16.1
MAP _{red} (%)	25	19	8	18	22	16
MAT _{inc} (°C)	0.2	0.3	0.2	0.9	0.4	0.4
GI	85.34	56.46	40.27	38.45	26.57	16.89
GI-D	64.00	45.73	37.04	31.53	20.73	14.19
GI-W	83.09	54.62	39.43	34.84	25.60	16.48
Period	2011.1–2011.12	2011.2–2011.12	2011.7–2013.1	2011.1–2012.7	2011.3–2011.10	2010.2–2010.11
Dominant species	<i>Calluna vulgaris</i>	<i>Deschampsia flexuosa</i> <i>Calluna vulgaris</i>	<i>Deschampsia flexuosa</i> <i>Calluna vulgaris</i>	<i>Deschampsia flexuosa</i> <i>Calluna vulgaris</i>	<i>Festuca vaginata</i> <i>Populus alba</i>	<i>Cistus monspeliensis</i> <i>Helichrysum italicum</i>
Soil type (FAO)	Peaty Podzol	Haplic Arenosol	Sandy Podzol	Sandy Podzol	Calcaric Arenosol	Luvisol and Leptosol

NEE and R_{eco} fluxes were measured using the same chambers but under transparent and dark modes, respectively (Selsted et al., 2011). In most cases, NEE was measured over a short duration ranging from 90 s to four minutes after the transparent chamber was placed on the soil collars. Chambers were then lifted and vented thoroughly before R_{eco} was measured with the chamber darkened over a similar time interval. About 20 s of data were removed from the calculation (deadband) of the

NEE flux while the deadband was sometimes longer for R_{eco} in order to be sure that active CO₂ uptake by the plant leaves had seized. For the data quality assurance, both linear and non-linear methods (Hutchinson and Mosier, 1981; Larsen et al., 2007) were applied to the chamber CO₂ concentration change over time during chamber deployments to calculate the NEE and R_{eco} fluxes, and then the best fitted fluxes were selected based on R². GPP fluxes were calculated as the difference between NEE

(transparent chamber) and R_{eco} (darkened chamber).

2.3. Data analysis and statistics

To quantify and compare the drought and warming effects on the GPP, R_{eco} and NEE rates ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) across the European climate gradient of the six study sites, we calculated mean differences \pm standard error between the treatments (Drought, Warming) and the controls across all campaigns for each site.

We compared the responses of GPP, R_{eco} and NEE to the long-term drought and warming along an aridity gradient, calculated as a modified Gausson Index (GI) (Peñuelas et al., 2007):

$$GI = \frac{MAP}{2 * MAT} \tag{1}$$

MAP (mm) and MAT ($^{\circ}\text{C}$) (Table 1) at each site were adjusted for the site-specific reductions in MAP (MAP_{red}) induced by the drought treatment and the increase in MAT (MAT_{inc}) induced by night-time warming, respectively.

The statistical effects of drought and warming on the CO_2 fluxes data (GPP, R_{eco} and NEE) were tested for each site separately using a non-parametric Kruskal-Wallis test (Kruskal and Wallis, 1952). We further used linear regression to analyse the relationship between NEE and GPP and NEE and R_{eco} , respectively. All the data processing and statistical

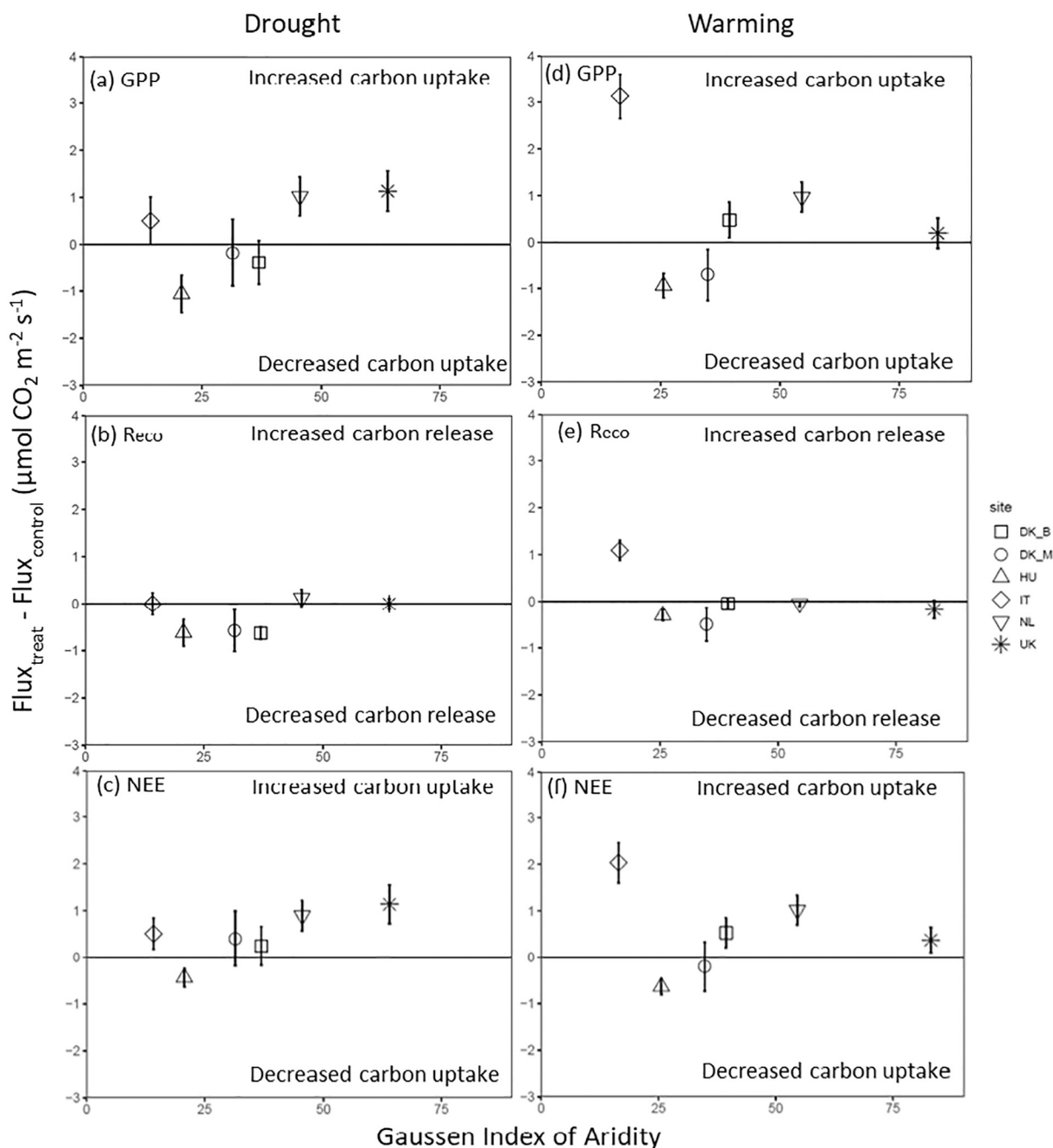


Fig. 2. Mean changes ($Flux_{treat} - Flux_{control}$) in rates of gross primary productivity (GPP), ecosystem respiration (R_{eco}) and net ecosystem exchange (NEE) in response to drought (a, b, c) and warming (d, e, f) across the Gausson Index of Aridity (GI) of the six study sites. Data represent mean differences \pm standard error between treated plots and controls across all measurement campaigns at each site. Mean annual precipitation (MAP) and mean annual temperature (MAT) (see Table 1) that were used for the calculations of GI were adjusted for site-specific reductions in MAP induced by drought treatment and additions in MAT increased by warming treatment respectively. IT = Italy, HU = Hungary, DK_M = Denmark Mols, DK_B = Denmark Brandbjerg, NL = The Netherlands, UK = United Kingdom.

analysis were done in R (Version 4.12, R Development Core Team, 2020).

3. Results

Across the sites, experimental drought reduced MAP by 8–22 %, while warming increased the MAT by 0.9–1.2 °C at the plot scale (Table 1, Reinsch et al., 2017). Based on the Gaussem index (Table 1), the most xeric site was IT followed by HU < DK_M < DK_B < NL, with the most hydric site located in the UK, where the soil is waterlogged during periods of the year. The general seasonal pattern of GPP, R_{eco} , and NEE rates in control plots reflect the respective growing and non-growing season patterns across all sites (Suppl. Fig. S1).

Compared to the control plots, the mean changes of GPP, R_{eco} , and NEE to drought varied across sites (Fig. 2, Suppl. Table S1). While we expected overall a negative effect of drought on GPP rates, drought only tended to decrease or did not affect GPP rates at the HU, DK_M and DK_B sites (Fig. 2a, Table 2). In contrast, GPP rates significantly increased at UK ($P = 0.013$) and tended to increase also at IT and NL. R_{eco} rates responded more as expected with significantly lower rates at DK_B ($P < 0.001$) and HU ($P = 0.015$) but showed neutral responses at the remaining sites (Fig. 2b). Resulting NEE flux rates at the sites (Fig. 2c) exhibited overall neutral to positive responses to drought, i.e. with significant increased carbon uptake at both DK_B ($P = 0.031$) and UK ($P = 0.013$). Only the HU site showed a non-significant tendency to a decreased carbon uptake in response to drought (Fig. 2c).

The responses to warming showed similar trends as observed for drought, with mean changes of GPP, R_{eco} , and NEE rates varying a lot across sites (Fig. 2, Suppl. Table S1). Warming significantly increased GPP rates at IT ($P = 0.028$) and DK_B ($P = 0.018$) and tended to increase GPP at NL and UK sites, while decreasing tendencies were observed at the HU and DK_M sites (Fig. 2d, Table 2). In contrast, R_{eco} showed neutral responses to warming across all sites (Fig. 2e) except for IT, where it tended to increase ($P = 0.053$). The responses of NEE consequently mimicked the GPP responses, with significantly increased carbon uptake at DK_B ($P = 0.038$), and a tendency to increased uptake at IT ($P = 0.087$), while the remaining sites spanned from weaker decreasing (HU, DK_M) to increasing trends (NL, UK). The performed linear regressions of the change in NEE as functions of either changes in GPP or R_{eco} in response to drought and warming showed similar trends across all sites (Fig. 3). The explained variance (R^2) of the linear regression between observed changes in GPP and NEE rates, including both the responses to drought and warming, was very high ($R^2 = 0.926$) and the relationship was highly significant ($P < 0.001$). This pattern was consistent across all measurement campaigns at each individual site, where GPP was highly correlated to NEE with a range of R^2 between 0.68 and 0.77 (Suppl. Table S2). In comparison, the relationship between changes in R_{eco} and NEE was still significant ($P = 0.047$) but explained a much lower fraction of the observed variance ($R^2 = 0.338$).

Table 2

Non-parametric Kruskal-Wallis test results of CO₂ flux rates (gross primary productivity (GPP), ecosystem respiration (R_{eco}) and net ecosystem exchange (NEE)) across sites. Asterisks denote significant differences between control and drought/warming treatments within each site (p values < 0.1^(*); p values < 0.05^(*); p values < 0.01^(**)).

Site	<i>p</i> values of non-parametric Kruskal-Wallis test					
	Drought			Warming		
	GPP	R_{eco}	NEE	GPP	R_{eco}	NEE
UK	0.034*	0.713	0.013*	0.515	0.640	0.891
NL	0.669	0.932	0.601	0.304	0.844	0.180
IT	0.373	0.356	0.534	0.028*	0.053 ^(*)	0.087 ^(*)
DK_B	0.550	<0.001**	0.031*	0.018*	0.679	0.038*
DK_M	0.983	0.641	0.747	0.785	0.865	0.772
HU	0.078 ^(*)	0.015*	0.447	0.706	0.784	0.482

Based on the observed differences in responses of GPP and R_{eco} to drought and warming across the six experimental sites distributed across a European climate gradient, a conceptual framework is proposed (Fig. 4). The presented concept complements the previously reported conceptual framework for soil respiration rates across the same sites (Reinsch et al., 2017). Fig. 4a shows the expected GPP and R_{eco} flux responses of the six shrubland sites based on the Gaussem aridity index. The black solid line indicates the generalized level of GPP/ R_{eco} rates in response to position on the Gaussem aridity index with the six study sites superimposed. The black arrows indicate the directional change in response to drought treatments in different sections of the curve, i.e. response can be either positive, negative or neutral depending on position. The red broken line indicates how the flux rates are modulated by warming, and the red arrows indicate how flux rates change from ambient to warming at different positions of the Gaussem aridity index.

For five out of the six sites, the observed responses of GPP and R_{eco} followed the expected pattern (Fig. 4). However, IT was expected to be on the far left-hand side of the solid curve based on its position on the Gaussem aridity index. Yet, the observed lack of GPP and R_{eco} flux responses to drought indicate that it should be positioned more in the centre of the response curve. This site-specific position is further confirmed by the observed positive response of IT to warming for both GPP and R_{eco} rates. This suggests that the growing season, site-specific soil moisture level is more suitable for explaining the observed patterns across all sites than the annual-based Gaussem aridity index, because the growing season at IT is more during the colder and wetter spring and autumn rather than during the warm and dry summer. This would explain why fluxes at this site respond positively to warming and neutrally to drought. Fig. 4b and c therefore show the actual, observed patterns for mean responsiveness of GPP and R_{eco} , respectively, along the growing season, site-specific soil moisture curve with IT now positioned more to the centre. In this way, panels 4b and 4c fit with all observed flux responses across the six study sites.

Furthermore, based on the observations across all sites, we found that warming modulated the soil moisture response curves of GPP and R_{eco} rates differently than expected, i.e. by narrowing the curvature causing a smaller “window” for potentially positive effects on both GPP and R_{eco} flux rates in the centre of the soil moisture response curves. While we expected positive warming modulation both in the centre and on the right-hand shoulder of the response curve (Fig. 4a), we observed a pattern across the sites suggesting a negative warming modulation on both shoulders of the GPP/ R_{eco} response curves (Fig. 4b, c).

4. Discussion

Across the European climate gradient covered in this study, we found that GPP, R_{eco} and resulting NEE fluxes showed different sensitivities to the imposed drought and warming manipulations (Fig. 2) with site-specific variation beyond what could be explained directly by the Gaussem aridity index (Fig. 4). As the soil conditions (structure, pH, carbon and nitrogen content, etc.) as well as the plant communities across the sites were quite variable (Beier et al., 2008; Lellei-Kovács et al., 2016; Reinsch et al., 2017), the asymmetrical biogeochemical cycling of both carbon and nitrogen against climate change (i.e. warming or drought) may also lead to various degrees of progressive nitrogen limitation (see Luo et al., 2004) across sites and thereby influence the site-specific plant production. Different plant strategies to adapt to their local environments may also play an essential role in hampering cross-site generalizations. Finally, the different start times of drought and warming treatments across the six study sites may have affected the observed CO₂ flux patterns as well (Sippel et al., 2018). Despite these potential biases when comparing flux rates across the sites, we did observe a clear pattern of larger GPP than R_{eco} responses to the treatments (Fig. 2), as also previously reported (Jaksic et al., 2006). This may be expected as GPP is also the main source of carbon for R_{eco} (Law et al., 2002; Yu et al., 2013).

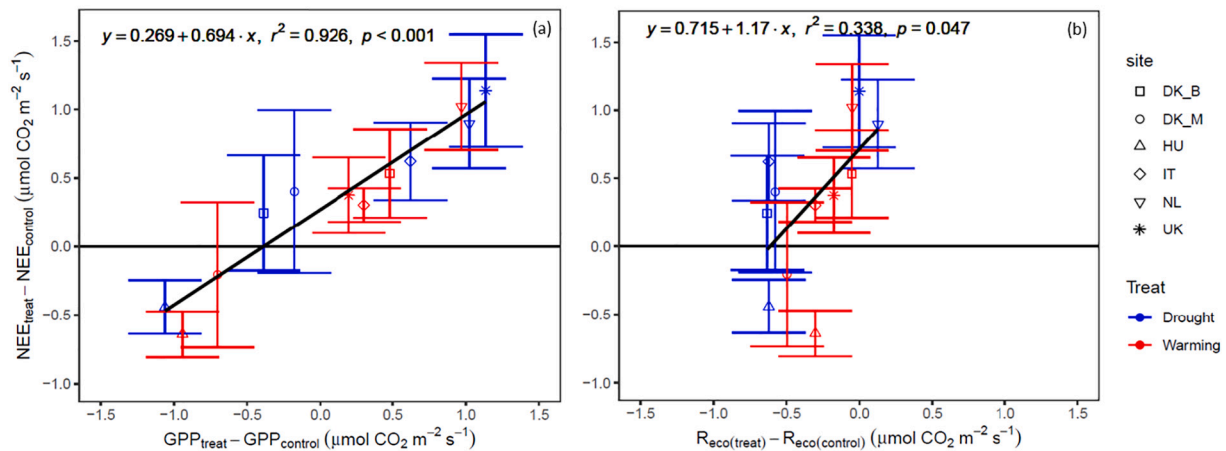


Fig. 3. Linear regressions of the relationships between changes ($\text{Flux}_{\text{treat}} - \text{Flux}_{\text{control}}$) in (a) net ecosystem exchange (NEE) and gross primary productivity (GPP) and, (b) NEE and ecosystem respiration (R_{eco}) across the six study sites. Data represent mean differences \pm standard error between treated plots and controls across all measurement campaigns at each site. Regressions include both effects of drought and warming. The linear equation, R^2 and adjusted P -value of the regression are indicated in both panels. IT = Italy, HU = Hungary, DK_M = Denmark Mols, DK_B = Denmark Brandbjerg, NL = The Netherlands, UK = United Kingdom.

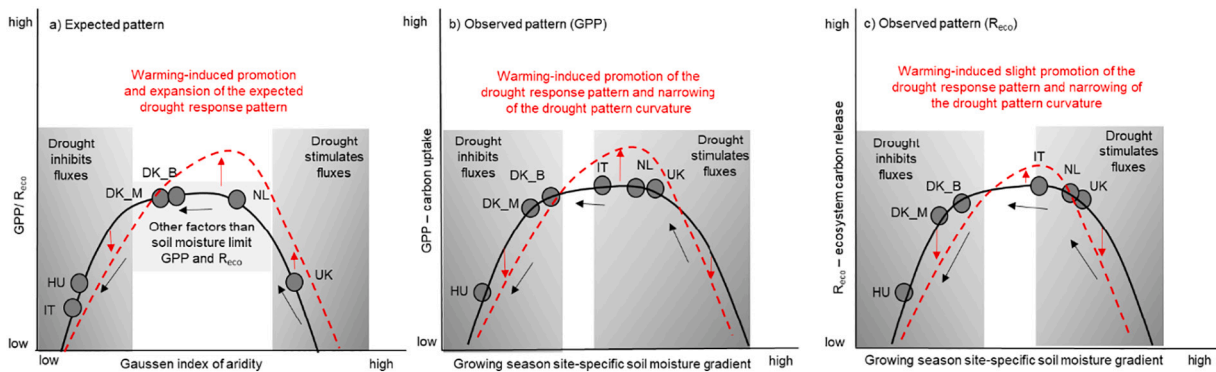


Fig. 4. Conceptual framework of gross primary productivity (GPP) and ecosystem respiration (R_{eco}) responses to drought and warming. (a) The expected response pattern for both GPP and R_{eco} is based on the calculated Gaussen index of aridity. (b) The observed pattern for GPP responsiveness. (c) The observed pattern for R_{eco} responsiveness. The black solid line in each panel represents the ambient distributions of each site and black arrows indicate how site responsiveness moves on the curve in response to drought. The red broken line indicates how warming changes the curvature of the GPP and R_{eco} relationship with soil moisture and the red arrows indicate how the site moves in response to warming. The vertical difference between the solid black and the red broken lines represents the effect of warming at any given level of soil moisture. The vertical difference of the amplitude between (b) and (c) indicates the different GPP and R_{eco} response magnitude. IT = Italy, HU = Hungary, DK_M = Denmark Mols, DK_B = Denmark Brandbjerg, NL = The Netherlands, UK = United Kingdom.

The xeric site HU was the only place where GPP tended to decrease significantly ($P = 0.078$) in response to drought. Drought stress may be intensified due to synergistic effects of decreased precipitation rates in the drought treatment with other factors at this site, such as the extremely low soil organic carbon content (Lellei-Kovács et al., 2011, 2016), which causes both low soil water retention capacity as well as low plant nutrient availability. The observed trend of increase in GPP rates rather than decrease at the remaining study sites are in contrast to observations showing a decrease in aboveground net primary productivity (aNP) at most of our sites (Reinsch et al., 2017) as well as reports of declining GPP rates from other drought experiments (Zhang et al., 2012). However, we found that the dominant species at four of the six investigated sites, *Calluna* (common heather), was not negatively affected by the imposed growing season droughts as there was still enough precipitation to maintain ecosystem functionality (Kopittke et al., 2014). At the hydric site (UK), the potential alleviation of water logging may also explain our observed positive GPP responses to drought here. Furthermore, the UK site has a high soil organic matter content compared to the other sites (Lellei-Kovács et al., 2016), which could provide sufficient soil nutrients to support additional plant

growth. In addition, Lorens et al. (2004) found that the leaf net photosynthetic rates changed along a geographical gradient in water availability, where plants exposed to drought, were able to maintain higher leaf photosynthetic rates than control plants in relation to the accumulated rainfall over the months before the drought. The non-significant increased GPP rates, or rather lack of a negative effect on the GPP rates, in response to drought at the IT site might be because of the high resistance to drought. At this Mediterranean site, summer drought takes place naturally every year leading to a plant community highly adapted to a dry summer environment. However, the IT site as mentioned before also differentiates from the other sites in having the major growing season during spring and autumn, thereby relying much less on growth during the hot and dry summer.

The significant negative responses of R_{eco} rates to drought observed at HU and DK_B as well as the tendency to a decline at DK_M site (Table 2) were expected as a similar decline in R_s rates was reported across the sites (Emmett et al., 2004; Reinsch et al., 2017). Gorissen et al. (2004) previously suggested this to be due to persistently reduced plant carbon flow from the roots to the soil compartments, including the microbial biomass, causing a decrease in heterotrophic respiration. In

contrast to the previously reported decrease in R_s rates (Reinsch et al., 2017), the IT site did not follow the expected pattern along the Gaussen aridity index and showed no effect of drought on R_{eco} rates (Fig. 2b). Compared to the GPP rates, the lack of effect of drought on R_{eco} rates at the IT site could be explained by the high natural resistance to drought at the Mediterranean site. Additionally, it has been suggested that plant productivity and ecosystem carbon fluxes generally have a higher sensitivity to increased precipitation than to decreased precipitation (Wu et al., 2011), which means that decreased productivity during drought stress can be compensated or even over-compensated by increased productivity during the following re-wetting. At the hydric UK site, the potential alleviation of water logging caused by the drought treatment affected R_{eco} rates much less than GPP rates indicating that a more oxygenated soil environment has led to a stronger response of plant activity compared to soil microbial activity. At the NL site, the increasing trend of R_{eco} rates in response to drought was more likely due to soil acidification in the control plots, which has led to a decreased survival of *Calluna* plants in control plots compared to drought plots (Lawson et al., 2004; Kopittke et al., 2014).

Based on the decline of R_s and aNPP in response to drought across all sites, except for the UK site (Reinsch et al., 2017), and since R_{eco} rates in the current study overall responded more negatively to drought than GPP rates (Fig. 2a & b), we hypothesize that the drought treatment at all sites, except for HU, promoted the belowground plant carbon allocation primarily to the deeper roots in order to better access available water and nutrients. Furthermore, the larger decline of R_s than R_{eco} rates with drought at IT and NL indicate that the belowground microbial activity may suffer more from drought stress than the aboveground autotrophic respiration. Davidson et al. (2006) suggested that soil moisture influences R_s rates indirectly by affecting substrate availability and especially under drought conditions. Strong edaphic water limitation coupled with the resource dynamics (Maestre et al., 2013) would inhibit both belowground soil microbial activity as well as aboveground plant growth. At the HU site, R_{eco} rates tended to decrease more than the previously reported R_s rates demonstrating a decline in both aboveground and belowground respiration after the experimental long-term drought because the plant community overall was more severely drought stressed here compared to other sites. In contrast, the increased R_s rates observed previously in drought plots at the hydric UK site indicate that ambient soil water content generally limited soil aeration (Reinsch et al., 2017) and microbial activity, while the unchanged R_{eco} rates in response to drought at the same time indicate that the aboveground plant respiration may have decreased. A potential explanation could be that the plants allocate more carbon belowground to deeper roots when water stress is alleviated, in order to provide better nutrient uptake for the support of enhanced plant growth.

In most experiments, warming has been reported to enhance ecosystem-level photosynthesis rates (Sullivan et al., 2008) and stimulate overall plant productivity (Welker et al., 2004; Peñuelas et al., 2007). According to our observations, similar significant positive responses were found at IT and DK_B as well as tendencies to positive responses at NL and UK (Fig. 2d, Table 2). However, part of the previous studies showed that experimental warming led to a decrease in plant biomass and GPP rates due to warming-induced drought stress (de Valpine and Harte, 2001; De Boeck et al., 2007; De Boeck et al., 2008; Lellei-Kovács et al., 2008). In our experiments, the passive night-time warming effects on soil drying were expected to be minimal (with the exception of HU, see Lellei-Kovács et al., 2008; Lellei-Kovács et al., 2011), although reduced air humidity and dew formation was reported for the warming plots at night (Bruhn et al., 2013; Lellei-Kovács et al., 2008). A tendency to a decline in GPP rates was observed at DK_M, but an even more obvious decline in GPP rates was noticed in the summer season at the HU site (Fig. S1), which may be due to warming-induced drought, especially as this site also has low MAP compared to the other sites. However, the low level of soil organic carbon (Lellei-Kovács et al., 2011, 2016) may again also be a dominant co-limiting factor

intensifying the negative effects of warming and observed decline in GPP at the HU site. At the IT site, higher nitrogen mineralization rates (de Dato, 2004) and leaf nitrogen content (de Dato et al., 2010) were observed in the warming plots, which may account for the significantly increased GPP rates in response to warming. At the hydric UK site, we note that GPP rates were much less susceptible to changes in temperature than to changes in soil water availability. From our results, we found that the wet soil also moderately buffered the warming by the conductive heat flux in the soil as the soil temperature differences among control plots (7.95 °C), drought plots (8.02 °C) and warming plots (8.25 °C) were fairly small compared to the other sites.

When considering the effects of warming on R_{eco} rates in the long term, the net outcome will mainly depend on how warming influences the plant community and its allocation to the belowground (Bardgett et al., 2008). In contrast to previously reported results of increased GPP and R_{eco} rates in response to warming (Wu et al., 2011), our results showed that warming either had no effect or decreased R_{eco} rates compared to control plots at all sites, except for IT (Fig. 2e). The overall lack of responses of R_{eco} rates in our study may be due to the different seasons cancelling out high and low fluxes during growing and non-growing seasons, respectively. For the IT site, Liberati et al. (2021) suggested that R_{eco} was affected by changes in vegetation structure and composition as the total plant cover was found to be higher under the warming treatment. In contrast to the highly positive coupling between GPP and R_{eco} suggested by Law et al. (2002), the responses of R_{eco} across the DK_M, NL, and UK sites did not follow the increasing trend as seen for GPP. The different magnitudes of GPP and R_{eco} responses can likely be accredited primarily to belowground processes rather than to changes in aboveground autotrophic respiration at NL and DK_M, as the long-term changes in R_s rates in response to warming were also generally negative (Reinsch et al., 2017). However, the UK site has high Q_{10} values (Emmett et al., 2004) and R_s was observed to be promoted by warming (Reinsch et al., 2017), indicating that the autotrophic respiration might be limited more than the soil microbial activity.

We were surprised to find that NEE at five sites out of six either remained unchanged or increased in terms of net carbon uptake in response to drought. Only at the HU site, the carbon uptake decreased in response to drought. The plant communities across the study sites therefore generally showed a high drought tolerance, often driven by neutral or even positive responses of GPP. The counterintuitive positive response of GPP and net carbon uptake to drought may originate from seasonal rewetting patterns, as seen especially at IT, DK_M, and DK_B. Here, the winter season is likely to have more precipitation than the growing season, which leads to a rewetting stimulation of plant growth and high resistance in terms of annual carbon balance. The observed acidification in the control plots caused the NL site to break the observed pattern across the European climate gradient (Kopittke et al., 2014) and, as mentioned, the low soil carbon content at the HU site (Lellei-Kovács et al., 2016) may explain why this site responded much more negatively to the drought treatment.

In response to warming, NEE and GPP rates showed very similar trends, indicating that also for warming, the effects on GPP rates were driving the observed changes of NEE responses from negative to positive along the Gaussen index of aridity with most sites showing a positive or neutral response to warming, except again for HU (Fig. 2f). From our results, we found that the neutral and positive responses are more likely among the northern sites where lower temperature is more likely to limit plant growth. While this was not expected at the IT site, the observed positive response of the plant community strongly suggests that the major growing season is outside the warmest and driest periods of the year, i.e. during periods of lower temperatures (spring and autumn) allowing for a positive response to increased temperatures. In contrast, the strong nutrient limitation at the HU site may have led to an intensification of the drought and warming effects leading to a more pronounced reduction in carbon uptake.

The suggested conceptual framework summarises the expected and

observed position of each site on the hypothesized site-specific soil moisture curve of CO₂ flux responses for each site (Fig. 3). Compared to the expected pattern based on the position of each site along the Gausson index of aridity, we found that only the IT site did not fit well with the expected position on the CO₂ flux response/soil moisture curve. Instead, because of the site-specific adaptation of the vegetation to the dry period, the site is actually responding to drought in a more neutral way, i.e., to climate conditions during the wetter and colder part of the year where soil moisture currently is not a limiting factor, indicating that it should have a position much more in the centre of the curve for both GPP and R_{eco} rates. The remaining sites fit well with the expected position based on their position on the Gausson index of aridity although especially UK appeared to be closer than expected towards the flatter part of the curve in the centre based on its observed relatively low sensitivity of R_{eco} rates to drought. The xeric HU site, being on the steeper part of the CO₂ flux response/soil moisture curve, was as expected more sensitive to drought than the moderate (DK_M & DK_B) and humid (NL) sites. While warming was expected to have a more negative impact on rates of GPP and R_{eco} at drier sites along the Gausson index of aridity and a positive effect when soil moisture is non-limiting for plant activity, the observed CO₂ flux responses indicate that warming overall narrows the CO₂ flux response/soil moisture curvatures, thereby leaving a more narrow “window” of soil moisture contents where warming may lead to higher rates of GPP and R_{eco} rates.

5. Conclusion

Despite the potential influence of different start times of the drought and warming treatments at the different study sites, we found that GPP was overall more sensitive than R_{eco} in responses to both drought and warming across sites and therefore also contributed more than R_{eco} to the observed changes in NEE (Fig. 3). The northern sites (DK_B, DK_M, NL and UK) were more likely to have neutral to enhanced carbon uptake in response to drought or warming. As expected, the UK site was more responsive to drought than warming compared to the other sites. The IT site also exhibited increased carbon uptake in response to warming and drought, which is associated with its site-specific Mediterranean climate characteristics and special plant community growing season pattern. Except for drought and warming effects, the HU site was more likely colimited by its low soil organic carbon content, which led to continuous negative responses. Overall, we found that the investigated shrubland ecosystems exhibited high resistance to drought and warming effects in terms of net carbon uptake, turnover and balance. The Gausson index of aridity is a useful tool for exploring broad trends of ecosystem responses to climate change. However, knowledge about site-specific ecosystem traits, such as plant community adaptations to local climate and timing of the growing season, soil texture, soil nutrient status etc., is still critical for predicting the actual effects of climate change at specific ecosystems and locations. Rather than using simple indices alone, such as the Gausson index of aridity, we here show that investigating and properly estimating the current site-specific position on a simple CO₂ flux response/soil moisture curve for each site improved our ability to explain the observed responses across sites. Such a site-specific analysis could potentially and relatively easily be taken into account in larger meta-analyses and models integrating responses to climate change over larger spatial scales and thereby improving our ability to predict responses to climate change more accurately.

CRedit authorship contribution statement

Qiaoyan Li: Conceptualization, final data analysis, investigation and visualization, writing draft and editing.

Albert Tietema: Funding acquisition, field investigation in the Netherlands, writing review and editing.

Sabine Reinsch: Field investigation in the United Kingdom, writing review and editing.

Inger Kappel Schmidt: Funding acquisition, field investigation in Denmark, writing review and editing.

Giovanbattista de Dato: Funding acquisition, field investigation in Italy, writing review and editing.

Gabriele Guidolotti: Funding acquisition, field investigation in Italy, writing review and editing.

Gillian Kopittke: Field investigation in the Netherlands, writing review and editing.

Eszter Lellei-Kovács: Funding acquisition, field investigation in Hungary, writing review and editing.

Klaus Steenberg Larsen: Funding acquisition, conceptualization, final data analysis, field investigation in Denmark, writing review and editing.

Declaration of competing interest

The present work has not been submitted elsewhere for publication, in whole or in part, and all the authors listed have approved the submission of the manuscript.

There is no interest conflict regarding this paper.

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Data availability

Data will be made available on request.

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Appendix A. Supplementary data

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