Title Shifting impacts of climate change: long-term patterns of plant response to elevated CO_2, drought and warming across ecosystems

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Abstract

Field experiments that expose terrestrial ecosystems to climate change factors by manipulations are expensive to maintain, and typically only last a few years. Plant biomass is commonly used to assess responses to climate treatments and to predict climate change impacts. However, response to the treatments might be considerably different between the early years and a decade later. The aim of this data analysis was to develop and apply a method for evaluating changes in plant biomass responses through time, in order to provide a firm basis for discussing how the ‘short-term’ response might differ from the ‘long-term’ response. Across 22 sites situated in the northern hemisphere, which covered three continents, and multiple ecosystems (grasslands, shrublands, moorlands, forests, deserts), we evaluated biomass datasets from long-term experiments with exposure to elevated CO_2 (eCO_2), warming or drought. We developed methods for assessing biomass response patterns to the manipulations using polynomial and linear (piecewise) model analysis, and linked the responses to site-specific variables such as temperature and rainfall. Polynomial patterns across sites indicated changes in response direction over time under eCO_2, warming, and drought. In addition, five distinct pattern types were confirmed within sites: ‘no response’, ‘delayed response’, ‘directional response’, ‘dampening response’, and ‘altered response’ patterns. We found that biomass response direction was as likely to change over time as it was to be consistent, and therefore suggest that climate manipulation experiments should be carried out over timescales covering both short and long-term responses, in order to realistically assess future impacts of climate change.

Keywords

Response curve, log response ratio, long-term field experiments, FACE, drought, warming, ClimMani, break point analysis

Introduction

Predicted and observed increases in temperature and CO_2 concentration and changes in precipitation patterns (IPCC 2013) have motivated experimental scientists to manipulate climate factors in-situ at the ecosystem scale over the last three decades. Warming, increased atmospheric CO_2 concentration and reduced rainfall became the main factors of global climate change research. Driven by research questions concerning ecosystem vulnerability and carbon sequestration, but limited by available funding and technical challenges, scientists attempt to use such experiments to determine climate change impact under future scenarios. Climate manipulation experiments can impose continuous and empirically comparable climatic impacts on both managed and natural ecosystems (Beier et al. 2004; Kröel-Dulay et al. 2015; Mikkelsen et al 2008). Based on findings from these experiments it is becoming increasingly evident, that the temporal patterns in responses of plant communities to climatic factors are not straight forward. In climate manipulation studies, the vegetation parameters such as individual density, standing biomass, or Annual Net Primary Production (ANPP) can show no response, or a delayed, dampened or intensified response to climate treatments (Estiarte et al. 2016; Körner 2006; Smith et al. 2015). Indeed, it has been reported that there were contrasting effects of the climate treatment over the duration of the experiment, i.e. early vs. late in the experiment (Mueller et al. 2016; Niu et al. 2010; Smith et al. 2015). The divergence within an experiment through time or between experiments could result in a criticism of the manipulation treatment technology or design. However, the development in the plant response can be attributable to evolutionary and ecological controls (Niu et al. 2008; Kröel-Dulay et al. 2015; Rütting and Andresen 2015; Bilton et al. 2016). To investigate this further, there is a need to assess how common the changing response patterns are.

Highest attention in climate change research has been directed to ecosystem carbon balance, where aboveground plant biomass is often the major response variable studied, due to its relative ease of measurement, role in carbon sequestration (Dieleman et al. 2012), and potential insertion into climate model predictions (IPCC 2013; Luo et al. 2015). Aboveground biomass also has multiple roles to play in forage quantity and quality in grazed ecosystems (Ruppert et al. 2015), and for many ecosystem services (Isbell et al. 2011), and therefore as an overall community parameter has often lead to its use as an indicator of community health, resistance/resilience (Ruppert et al. 2015) and/or general response of the community to climate change. This parameter does not give the full picture of community response to climate change, as root biomass (Arndal et al. 2013; Körner 2000), species plastic responses (Liancourt et al. 2015), and species identity/composition (Bilton et al. 2016) are important for interpretation, but will not be entirely captured. However, in general, aboveground biomass is a relatively well studied and consistent measure, which can be transferred across ecosystems and plant types (e.g. annuals, herbaceous perennials, and woody species) and will therefore be the focus of the current analysis.

In this regard, a general prediction for elevated CO_2 (eCO_2) was to increase biomass production in ecosystems, which has recently been observed across many long-term (7 to 11 years) FACE (Free-Air Carbon dioxide Enrichment) experiments (Feng et al. 2015). Similarly, a general positive biomass response across warming experiments has been shown in the short (Dieleman et al. 2012) and long-term (Kaarlejärvi et al. 2012). In contrast, the vegetative response to reduced precipitation (drought) has been predicted to result in a decrease in biomass (Sala et al. 2012) which has been shown in some manipulation experiments (Kröel-Dulay et al. 2015). However, it has been commonly acknowledged that changes of treatment related response patterns for long-term extended experiments are possible and must be investigated with caution, as effect size might change over time (Keuper et al. 2011; Körner 2016; Leuzinger et al. 2011; Mueller et al. 2016; Smith et al. 2015). Elevated CO_2, drought and warming impacts on the plant community are likely to be highly context dependent, and are therefore likely to affect any response patterns. For example, warming may have a positive impact on biomass in cooler regions, but cause reductions in biomass – due to increased aridity – in hot/dry regions.

Additionally, site climatic factors can define plant community composition and the plasticity of plant species inhabiting those regions through their adaptations to the specific climate e.g. the specific leaf type and anatomical adaptations, which leads to different responses of communities to the climate change drivers. Under this notion, plants can be adapted to warm, dry, or variable climates, which can result in greater resistance of the community to climate change in these regions (Tielbörger et al. 2014), and therefore impact upon response patterns. Altogether, climate variables have a large impact on the prominence of biomass response patterns that are observed across ecosystems. Therefore, in the current study, sites were categorized by climatic variables and tested for their response to the climatic change factors to differentiate response direction and pattern type for ecosystems where differences between short and long-term effects were most likely.

The first set of defined response types were presented by Körner (2006) for FACE experiments, however until now, response types for drought and warming systems have been less systematically addressed. Several types of plant response pattern to eCO_2 were suggested, and it was acknowledged that responses might change through time and across ecosystems. The first response pattern type suggested was a fixed positive or intensifying response. Körner (2006) predicted this would occur in FACE experiments situated in systems relatively unlimited by other resources (nutrients, space, water). The second response pattern type was a transient response. Here, an effect (positive) would be observed in biomass under eCO_2 in the early years, but would peak and return to the original state/level, which would be observed as no treatment effect at a later point in time. This transient response type was predicted to occur in systems where resource limitations constrain the positive CO_2 response (Körner 2006). Nitrogen (N) availability is one of the potentially limiting resources, however, a recent meta-analysis of FACE studies showed that at sites classified as nutrient poor, gross N mineralization increased, which directly increases plant availability of inorganic N (Rütting and Andresen 2015). Hence, sites with increased N mineralization, with N_2 fixation (Liang et al. 2016) or with ectomycorrhiza status (Terrer et al. 2016) would not return to a ‘no response’ due to N limitation. The progressive N limitation (Luo et al. 2004) would rather be avoided and a positive plant biomass response would be sustained. However, other patterns, such as transient responses, may emerge by regarding ecosystem specific data in connection with resource limitations which may develop over time and thus preventing positive response to eCO_2 in the long-term. Directly connected to resource limitations, climatic differences between sites, especially related to water availability (precipitation amount and timing) and temperature might cause variability in biomass response patterns. Elevated CO_2, and also warming and drought, exert controls on access to the nutrients, and control mineralization (Sardans et al. 2008; Williams et al. 2012), the consequences of which will be explored in the current analysis.

Smith et al. (2015) suggested three types of response patterns (besides the ‘no-response’ pattern) as general concepts for climate manipulation factors (specifically for N addition and water manipulations across the USA), where the first two types overlap with Körner’s (2006) definitions; 1) continuous directional response (being positive or negative), 2) a transient response, and 3) a stepped response type. They proposed a series of mechanisms which cascade in a hierarchical fashion leading to ecosystem responses, ranging from initial and relatively rapid responses of individuals (physiological plasticity), to changes in community composition, and finally species immigration and loss (Smith et al. 2009; see also Grime et al. 2007). The authors suggested that such step-wise acclimations and adaptations, typically expressed by individuals in the next growing season or the next generation, could show up as a step in the response curve (and a stabilisation at the new level). Indeed, a number of drought and warming manipulation studies have reported species composition changes over the course of an experiment, showing shifts in abundances and dominance of particular species and functional groups (Andresen et al. submitted; Bilton et al. 2016; Harte and Shaw 1995; Kröel-Dulay et al. 2015; Niu et al. 2008; Prieto et al. 2009). In our data analysis, we have no means to distinguish individual, community composition or species level changes, however we still expect to see fingerprints of these compositional changes observed while analysing the commonly used parameter ‘aboveground biomass’.

Although manipulation experiments may show clear impacts on the plant community by changing species composition, this can lead to a no net effect at the total biomass level, as seen in a drought manipulation experiment in Israel (Bilton et al. 2016). There, it was shown that reduced precipitation gradually selected for dry associated species and reduced the presence of wet associated species, but had no overall impact on total biomass. Similar conclusions were drawn using the classical passive warming chambers within the international tundra experiment (ITEX) network (Elmendorf et al. 2016). There the authors found a change in the plant community which they termed “thermophilization”, which revealed that the warming treatments selected for species from warmer niche distributions. This was despite the fact that there was no observed change in total biomass or productivity between treatments. Furthermore, species composition change may also account for transient patterns, where an initial impact of the climate manipulation either decreases or increases the presence of some species. This change triggers the emergence (or disappearance) of other species over time, forming a polynomial response shape for total aboveground biomass (Liu et al. *personal communication*). Furthermore, the biomass patterns may not return to the previous state, but continue to be polar (opposite treatment effect late compared to early) in the experiment. Next to no response, the stepwise response was the most frequent among sites within the Smith et al. (2015) meta-analysis, and therefore we also expected the stepwise pattern to be frequent response type among climate manipulation sites in this study. However, also the polynomial (transient) type is likely to be an important and frequent response pattern in long-term experiments (Leuzinger et al. 2011).

The terminology of transient, directional and stepwise response types are applicable for our research questions, however here we apply our own specific definitions to allow for generalizations across FACE, drought and warming biomass response patterns (Figure 1).

Following a hierarchy in responses, we expect to find i) 'no response' will be common (Smith et al 2015); ii) a 'delayed response' i.e. no early response will be followed by an increase or a decrease in biomass; iii) the 'directional' (linear) response is similar to those of Körner (2006) and Smith et al. (2015); iv) a 'dampening response' i.e. an initial response followed by a lesser slope (sometimes flat) of the early response direction (Figure 1) may be similar to the stepwise type of Smith et al. (2015); and finally, v) an 'altered response' i.e. a response which goes in one direction in early years then changes direction for later years is similar in principle to the transient response of Körner (2006) and Smith et al. (2015). However, the 'altered response' may continue beyond the original level, or may not reach the original level again (Figure 1).

The overall goal of our data analysis method was to determine if response patterns of plant biomass to climate manipulations show any distinct trends through time, providing a mechanism for advancing our understanding of climate change response patterns. Furthermore, by acknowledging that a response trend can change from short to long-term, we aimed to define whether responses are similar or contrasting under different climatic conditions. Ultimately we aimed to answer the question: ***Can we identify 'short' versus 'long-term' responses of aboveground biomass to climate change manipulations?***

Methods for data analysis

Field site experiments

The data for this analysis was collected from 22 field sites across the northern hemisphere, (Figure 2), from a wide variety of terrestrial ecosystems including grassland, shrubland, moorland, forests and deserts. Most sites had continuous long-term single treatment and control designs, but a number of sites also had combined treatments with up to four factors. We therefore studied 13 sites with drought, 9 sites with elevated atmospheric CO_2 concentration, and 11 sites with warming experiments (Table 1, S1 and S2).

Warming manipulations were implemented using: i) warming by passive night-time warming done with retractable curtains (Beier et al. 2004; Mikkelsen et al. 2008), ii) infrared heater lamp installations (Dukes et al. 2005; Niu et al. 2010; Zelikova et al 2014), and iii) thermocouples installed on the soil surface (Fridley et al. 2011).

Rainfall removal during the growing season was implemented using different types of coverage such as: i) drought by retractable curtains (Beier et al. 2004; Mikkelsen et al. 2008), ii) partial rain exclusion by PVC strips (Barbeta et al. 2015; Tielbörger et al. 2014) or by removable transparent shelters (Fridley et al. 2011; Reich et al. 2014), or iii) drought by stable transparent roofs (Jentsch et al. 2007). Finally, experiments elevating atmospheric CO_2 concentration used the FACE technique (Hendrey and Miglietta 2006).

An aboveground biomass parameter was estimated for each year using various methods across the sites. Typically tree stands were assessed using dimensional measures of the trunk and litterfall. Another non-destructive measurement was the ‘point-intercept’ method, where a pin is lowered into the vegetation and plant hits on the pin in a fixed grid are recorded. Plant pin hits were correlated to pin hits of plots where biomass was harvested as reference (Kröel-Dulay et al. 2015). Other sites, typically grasslands, harvested biomass above defoliation height as part of the management type and hereby directly assessed the agriculturally relevant forage production (Schneider et al. 2004). We have aligned these measures as equally valid estimates of annual biomass production in this analysis.

Groupings of sites into types of climatic categories (Table S3; Table S4) was done using the field site geographic coordinates to access site climate data from the ‘WorldClim’ database (Hijmans et al. 2005). For each site we extracted the temperature and rainfall parameters: mean annual temperature (MAT), mean diurnal temperature range (mean of monthly (max. temp. – min. temp.)), temperature seasonality, maximum temperature of warmest and minimum temperature of the coldest month, annual precipitation, precipitation of wettest (PWM) and driest month, and precipitation seasonality. For each manipulation factor, sites were put into one of three groups, based on their site climatic values (e.g. coldest MAT; intermediate MAT; warmest MAT sites; Table S3; Table S4).

Treatment effect size and certainty

The data analysis mainly compared single treatment responses in comparison to responses in the control. In addition, for combined manipulations, the treatment combinations of interest were compared to the single factor treatment (e.g. to test the warming factor, we compared; warming + nitrogen combination versus nitrogen as control), to get a single factor response (Table S1, S2). To compare different manipulation effects, the effect sizes were presented as a log ratio response (LRR equation 1) (Hedges et al. 1999).

$$\mathrm{LRR} = \ln(\mathrm{treated}) - \ln(\mathrm{control}) \quad (1)$$

Log ratios have a number of strengths for the presented comparisons. Firstly, a log ratio is a relative response, in theory allowing for relative impacts of the manipulation to be observed. Secondly, an LRR is also symmetric, therefore making no prior assumptions as to the direction of the response to a manipulation e.g. a doubling of biomass is expressed by the same value as a halving. Lastly, since biomass often has a log-normal distribution, we calculated a difference in treatment effect based on the statistically correct (logarithmic) scale.

For all sites where a pre-treatment year was provided, we estimated the starting effect size at year 0 by taking the intercept value of a simple regression from year 0 to years 2 or 3. Using this method, in experiments where a clear treatment effect in early years was occurring, the intercept was very similar to the taking the year 0 value (therefore not hiding any patterns we were interested in). However, it was deemed a more suitable method than simply taking the year 0 data to provide an unbiased starting point that is independent of natural year-to-year variation (i.e. if effect sizes showed large fluctuations naturally, a year 0 value would be an inappropriate estimate of initial treatment plot differences). The starting effect size was subtracted from the other yearly values to normalize the dataset. Plot-wise data was not always available, therefore, for each year, treatment means and standard deviations of the means were calculated on the normal (untransformed) scale, and then converted to log value. Certainty of the mean LRR values were then estimated on the normal scale by coefficient of variance of the standard error (CVse), adjusted for sample size (equation 2; Sokal and Rohlf 1995). The reciprocal of the CVse's were then used to weight yearly mean LRR values throughout the analysis as follows:

$$\mathrm{CVse} = (\mathrm{sd}/\mathrm{mean}) * (1+ (1/4*n)) * (\mathrm{sqrt}(n))^{-1} \qquad (2)$$

$$\mathrm{Weight} = (\mathrm{CVse}_c + \mathrm{CVse}_t)^{-1} \qquad (3)$$

Data analysis

We used two approaches to identify response patterns: i) an accumulated approach to analyse multiple studies simultaneously within a group of treatment type or category of climatic zone and vegetation type, and ii) a segmented piecewise regression (break point analysis) to analyse individual experimental responses.

All statistical analyses were carried out in R version 3.1.1 (R Core Team, 2008), using statistical packages "lme4" (Bates et al. 2015) for the accumulated approach, and package "segmented" (Muggeo 2008) for the piecewise regression approach.

Accumulated approach across sites

For the accumulated approach, within the main treatment factors drought, warming and eCO_2, a mixed model was applied to the experimental mean LRR values (equation 1) weighted using the weight values (equation 3), with site as a random factor nested within a categorical factor year. To estimate and display yearly mean values across all sites included in our analysis, the categorical fixed factor year was tested, and the coefficients used as mean estimates. To test response over time, the continuous fixed factor year was fitted as both a linear model (LRR =

a + b*Year) and a polynomial model (LRR = a + b*Year + c*Year^2). Model comparison for goodness of fit was made between the linear and polynomial models using log-likelihood estimation tested against the Chi^2 distribution to obtain p-values (indicated in the text as significant ($P < 0.05$) differences or differences by tendency ($0.05 < P < 0.1$)).

A linear model as best fit, may indicate no response or a directional change. Whereas a significantly improved model using the polynomial equation, provided evidence that the relationship is unlikely to be linear. While more mechanistic approaches may provide better estimates for the exact relationship, our method was deemed sufficient to allow us to assume that with a polynomial curve as a better explanation, response directions were different at the start and end of the experiments (e.g. show a ‘delayed’, ‘dampening’ or ‘altered’ response).

Piecewise approach within sites

Mean responses have the potential to lead to inaccurate or misleading conclusions, so to confirm any trends we therefore analysed all individual experiments using segmented piecewise regression. Here, models of different degrees of complexity were tested: Model 1, simple linear regression, using weighted LRR as response (equation 1 and 3), and the continuous variable year as an explanatory factor; Models 2 to 4 were then fitted to each dataset, as either 2-line, 3-line, or 4-line models. The best model was identified using model comparison with log-likelihood estimation on the F-distribution. If a more complex model provided a better fit (p value<0.1), we assumed that there was a strong tendency for different response patterns within the experiments. Segmented regression uses maximum likelihood to minimise the differences between lines to form an *almost* continuous line (albeit with different slopes), returning estimates for individual line slopes (and associated t-values) and breakpoints of the connecting lines (useful for determining the point of change within the experiment). Multiple simulations were run to avoid false convergence of the breakpoint estimate, and visual estimates were used to confirm the accuracy of the automated findings.

Results

Accumulated patterns across sites

When grouping information from all sites using the accumulated approach, response patterns of above-ground biomass to all three main climate manipulation factors (drought, warming and eCO_2) showed indications of a differing response over time (Figure 3). By the mid-way point in recordings (ca. 8-10 years) on average the drought manipulations decreased aboveground biomass, with a lowest yearly mean value in year 10 with ~1.14 times less biomass on average under drought than control. Contrastingly, warming and eCO_2 generally increased biomass, with highest yearly values in year 8 for warming (~1.19 times more biomass under warming than control) and in year 10 for eCO_2 (~1.26 times more biomass under eCO_2 than control) (Figure 3).

Importantly, taking all sites into consideration, these response directions changed during the course of the experiments. Under drought, the polynomial fit showed a tendency to provide a better fit than a linear model ($p = 0.075$ Chi2 = 3.1767); whereas under warming ($p = 0.039$, $Chi^2=4.24$) and eCO_2 ($p = 0.014$, $Chi^2=6.06$) polynomial fits were clearly the better descriptor of response over time. Under all manipulation factors, it seems that at the midpoint in recordings, the treatment response slope dampened and reversed in direction, sometimes resulting in mean values that indicated opposing effects in the later years compared to in the early time-points (see Figure 3 drought and eCO_2). Some care must be taken in interpreting these accumulated responses, because at later time-points variations in yearly effect size differed, depending on which experiments were included in the analysis e.g. negative effect in year 13 in eCO_2, but highly positive in years 17 and 18 (Figure 3). This suggests that not all experiments show these altering response patterns over time, but certainly that the majority of sites have opposing or no effects at the later time points.

Sites grouped by climate parameters

To disentangle the response patterns by their climatic characteristics, sites were grouped according to temperature or rainfall categories (see Methods for details; Tables S3 and S4).

Looking at the biomass responses to drought, using mean annual temperature (MAT; Figure 4) to group sites, the 'coldest MAT' and 'intermediate MAT' sites showed decreasing negative responses to the drought treatment, indicating a directional response type. Contrastingly, the 'warmest MAT' sites showed no response to the drought treatment over time ($P>0.05$). In contrast, a division of the sites into three groups by 'precipitation of wettest month' (PWM) (Figure 5) and annual precipitation (not shown), showed little in terms of consistent hierarchical responses across the site groupings. For PWM, it was the driest sites which showed a directional negative response ($t=-2.04$, $p =0.04$), with neither wetter groups showing a response over time. However, for annual precipitation, the only directional response was found in the intermediate group (strongly decreasing), with a no response pattern in the driest and wettest site groups.

Different long-term biomass response patterns for the warming treatments were visible by dividing sites into three MAT groups (Figure 4). The 'warmest' and 'intermediate MAT' sites had the most positive biomass responses in early years, and had polynomial fits different from the linear fit ($P=0.042$ and 0.088, respectively), suggesting that the response pattern altered from increasing to decreasing. Contrastingly, the coldest group showed persistently no response. Furthermore, the driest group of the PWM (Figure 5), and of the AP (not shown), both had a polynomial model as best fit (in both $P < 0.001$), suggesting a change in response direction, reaching into negative effects, while the 'wetter' sites had simple constant positive response patterns.

The eCO_2 experiments showed the largest average biomass effect sizes across the three addressed climate factors. The climatic site division by PWM (Figure 5) revealed two different pattern types, with a directional positive response type revealed at the driest sites. Contrastingly, a polynomial pattern expressing a maximum effect size in intermediate years, proved to be a better description of the response pattern for sites with intermediate precipitation (P=0.039) and at tendency in those sites with high precipitation (P=0.051). These two response pattern types start out with the same direction (positive), but at the 'wetter' sites, the direction changes to be dampening and negative over time. The same pattern for wetter and drier groups was found classifying sites using annual precipitation (not shown).

Piecewise regression within sites

In order to gain an understanding of within-experiment response patterns for the main treatment factors CO_2, drought and warming, the biomass response patterns were analysed by break point analysis using segmented piecewise linear regression. This technique revealed five distinct common response patterns over time (Figure 1), and the number of experiments within each category (Table 2). These results confirmed some of the findings from the accumulated approach, and in addition add extra detail and accuracy to our interpretations.

In total, out of 68 experimental comparisons, we found that a great proportion of experiments (roughly half for all three main factors) showed a change in response over time (Table 2). Similar to the findings of Smith et al (2015), the most dominant response pattern observed across all experiments was that of 'no response'. 'Delayed responses' were rare, and only noted under drought and warming, and not under eCO_2 (Table 2). Perhaps surprisingly rare also was the consistent 'directional response', which occurred at similar frequencies within experiments as the 'dampening' type (a change in the strength of slope over time).

Finally, and noteworthy, was the number and degree by which some of the biomass response patterns shifted over time to become 'altered' in their direction. In most examples of altered response types, the reversal of the biomass response direction was in correspondence with the patterns found in the accumulated analysis: increasing then decreasing under eCO_2 (7 out of 10) and warming (9 out of 9); decreasing then increasing under drought (2 out of 3, and by far the strongest two in terms of effect magnitude and direction switch). This confirmed that these patterns are far from rare, and what we saw in the accumulated analysis was a fair reflection of what may be observed within a climate manipulation experiment. Interestingly, in some cases, the later directional responses continued so that the climate treatment effect switched from positive (or negative) in early stages to negative (or positive) in later years, establishing an entirely different, and opposing, interpretation of biomass response depending on which treatment year is taken as being conclusive.

Discussion

With the two implemented forms of analysis (accumulative across sites, piecewise within sites), our study highlights that response direction of plant aboveground biomass often changes over the course of long-term climate manipulation experiments. Under all three manipulation treatments, a polynomial curve described vegetation change over time better than a simple linear relationship. This was highly supported by our piecewise regressions, whereby five distinct response pattern types were identified, and confirmed that i) a differing response direction is as likely to occur in long-term experiments as a consistent response direction, and ii) altered directional patterns more commonly switched in direction similar to that noted in the accumulative analysis, and that sometimes effect sizes showed an opposite response early compared to later in the experiment. These findings emphasise that great care must be taken when interpreting climate change impacts on aboveground biomass from short-term experiments. The potential mechanisms involved in these response pattern types are discussed with relevance to climatic regions, adaptations and the specific inference under the different treatment factors. Furthermore, we suggest caveats of the current analyses and areas of further investigation applicable for ultimately determining long-term consequences of climate change on plant communities around the world.

Response Pattern Types

Our piecewise regression analysis identified five distinct response pattern types occurring within the long-term climate manipulation experiments, which suggests that different mechanisms are associated with vegetation response under climate change. 'No response' was our most common finding, and is similar to the pattern analysis results of Smith et al. (2015). A no response pattern is indicative of some form of resistance of the community to climate change (Grime et al. 2008; Tielböreger et al. 2014). In terms of maintaining a community of similar aboveground biomass - generally considered important for carbon sequestration (Dieleman et al. 2012), forage production in grazed systems (Golodets et al. 2013; Ruppert et al. 2015), and a large array of ecosystem services (Isbell et al. 2011) - for many of the long-term experiments included in our analysis, we show how little these communities may react with regard to climate change. This could be due to a non-significant response with respect to the climate treatment increment which was not strong enough to impose a change in community. However, even though the total community biomass seems to be highly resistant to climate change or the manipulation imposed, a number of studies have shown that even with no-net response, the individuals and species represented within these communities may be changing considerably (Bilton et al. 2016; Elmendorf et al. 2016; Soussana et al. 2007). Indeed, species composition change is a factor which can not be accounted for in our analysis, and it seems likely that under all these climate manipulation factors, ongoing selection will be occurring over time, gradually selecting for adaptations initially with respect to plastic responses, genotypes, and ultimately species (Grime et al. 2007; Ňuelas et al. 2013; Smith et al. 2009). This hierarchical order of community response to climate change is likely to manifest itself in all the different response pattern types identified in the current study, and the rates at which these occur are likely to be associated with the treatment factor, and the adaptations inherent in the community. Delayed responses, for example, are potentially mediated by the resistance of the plant community to climate change, but over time, the accumulated impacts start to affect the plant community, whether overcoming the inherent plastic adaptations of the individuals, or as the community changes considerably to affect overall biomass.

The ‘dampening response’ type suggests a mechanism which reduces the impact of the climate treatment on the plant biomass, which could be due to a limitation of nutrient resources or environmental constraints (Körner 2006), or the community reaching a new stable state at a different level of resources, through a new community or adaptations (acclimation) (Herbert et al 1999).

And finally, the altered directional response could have multiple interpretations and mechanisms. These could be accounted for by species composition changes as some species initially increase/decrease and others then decrease/increase later on once the community interactions have changed (Niklaus et al. 2001). It also seems likely that any initial responses may be due to plastic responses of the individuals, and that later as selection processes continue, they respond by acclimation or from those responses of a new community.

Responses to Drought

Ecosystems have been shown to differ in the sensitivity of their productivity (Annual Net Primary Productivity ANPP) to between-year precipitation variability: where the driest ecosystems tended to be more sensitive than the mesic (Huxmann et al. 2004). However, such relationships may not be strong in the long-term, as no supporting evidence was found in a review of eleven drought experiments (Estiarte et al. 2016). This is possibly due to high variation of rainfall/precipitation conditions from year-to-year to which the communities are often exposed. This variation is often considerably greater than the variation in temperature and CO_2 levels, for which the plants have been selected (Jentsch et al. 2007). However, this is controversially discussed, with some studies showing or hypothesising that there should be stronger community responses to reduced precipitation in wetter regions (Bilton et al. 2016), whereas others suggest dry regions should be most affected (Golodets 2015; Huxmann et al.

2004). In our study, it seems that precipitation quantity at a site (or at least for the parameters tested) is not a consistent measure for determining community resistance to long-term reductions in precipitation. Although we identified changing pattern types using piecewise regressions, - e.g. in one example an altered response pattern occurred, with an initial decrease in biomass to a midpoint but then greater biomass by the end of the recordings - there was no consistency in which precipitation regions these site patterns belonged.

Indeed, classifying the sites by temperature seemed to show the most consistent patterns. These findings suggest that MAT manages to group our particular sites well in terms of aridity, with the warmest sites being most resistant to climate change manipulations, as previously suggested (Tielbörger et al. 2014, Bilton et al. 2016). It is possible that plants growing at warmer sites are better adapted to aridity due to more regular exposure in their evolutionary history.

In natural systems, the evolutionary restrictions of the occurrence of plants in defined climatic zones are also likely to define the magnitude and direction of biomass responses to drought. But whether the investigated plant communities are resistant to drought or vulnerable and responding with composition changes cannot be resolved with this data analysis. However, it is likely that drought tolerant species gain biomass at the cost of drought sensitive species (Bilton et al. 2016; Kröel-Dulay et al. 2015; Lui et al. *personal communication*), which is potentially hidden from our analysis but could partly explain the 'no response to small positive response' seen at sites in warm and wet climates in our study in the long term.

Responses to Warming

In general, increased temperatures (warming), has a dual effect on ecosystems by increasing nutrient mobilisation and extending the growing season in temperate regions (Ehrenfeld et al. 2005), the benefits of which may be negated by increases in water loss through evapotranspiration from a system (Luo 2007). Altogether, in the accumulative analysis of our study, sites with indications of dry and warm climates were prone to changing the biomass response direction, from an increasing positive response over to a decreasing and negative biomass response midway through. Also, all altered response patterns identified using piecewise regression within sites were in this direction. The altered directional patterns experienced at the drier and warmer of our analysed sites, may be due to the increased mobilisation of nutrients in the early phases of an experiment, which follows the principles of nutrient limitation later in the experiment as predicted under eCO_2 (Körner 2006; Luo et al. 2004). Moreover, effects on community composition may also be occurring, whereby those species which are generally more adapted to increased temperature also grow larger during the initial phases, and then outcompete other less adapted species.

Contrastingly, the coldest MAT sites showed persistently no response, refuting our hypothesis that colder regions would have the largest positive responses to warming. These observations were markedly different than results gleaned from provenance trial transfer functions, where trees from coldest origins benefitted most with enhanced growth by transfer to slightly warmer sites (Reich and Oleksyn 2008). Indeed, we expected that at the warmest sites, due to increased aridity, the warming treatment would decrease biomass. The groupings of ‘maximum temperature of the warmest months’ (not shown), supported the MAT findings for the warming induced biomass response, and both suggest that site selection may account for no biomass decrease in warmer sites. This highlights that more climate warming manipulation experiments should be performed in the driest regions to identify clear trends.

Responses to elevated CO_2

The factor eCO_2 showed the largest magnitudes of effect sizes in biomass response of all three treatment factors tested. All climate manipulation experiments have an instantly imposed treatment effect that changes the climate parameter relative to ambient. Thereafter, the treatments are constant throughout the long-term experiment, compared to the ‘natural’ slower background increase in CO_2 concentration and temperature over decades. The initial step increase may impose an unrealistic response, particularly in the short-term. However, the intense experimental treatments are needed in order to predict the community response to future climate change, which cannot be obtained by a simple monitoring of natural changes. Thus, biomass response during the first years of a CO_2 experiment have to be treated with caution as compared to biomass increase under a slowly developing change in climatic conditions (Rastetter et al. 1997). However, by deploying the climate treatments for many years in long-term experiments (beyond this initial phase), realistic acclimation responses to future climatic conditions are likely (Mueller et al. 2016; Schneider et al. 2004). Still, it is surprising that manipulations of eCO_2 commonly alter the direction of the biomass response over time. Sometimes these even manifest themselves as decreases in biomass at the end of the experimental duration, which contradicts many predictions of the effects of rising CO_2 levels on plant communities, and those values are often used to predict the effect of climate change in ecosystem models (IPCC 2013).

For eCO_2 manipulations, there is little literature to our knowledge that links community composition change to other gradients of climatic factors, an area which would be of high relevance in future studies. Undoubtedly there are a number of ecophysiological adaptations possessed by plants (e.g. stomatal closure) which are useful under drought conditions, but could also affect response under eCO_2. A connection between regional climatic adaptations and CO_2 elevation should therefore be possible. Our results, when categorising sites by precipitation (PWM), at least suggested some connection, showing that consistent increasing responses were generally found in the drier sites, whereas an altered direction was more likely to occur in wetter sites.

The hypothesis about soil nutrient availability as a controlling factor for plant biomass response was not addressed by our investigation, but could be used as a means to categorize sites and searching for long or short-term patterns in parallel to what has been described here.

While applicable to all climate manipulation factors, it is often hypothesized that nutrient availability will change over time particularly within eCO_2 experiments (Körner 2006; Luo et al. 2004). However, there is growing evidence that warming and drought may also play a role in nutrient mineralization (Luo et al. 2007). Linking the original state of nutrient availability to the changes in availability over time under treatments, may lead to improved interpretations of altered response pattern types seen in experimental studies, making results more applicable to future climate change predictions.

Biomass as a response parameter

Plant biomass is a popular measure for biotic carbon sequestration, and is often a parameter in Earth System models (IPCC 2013; Luo et al. 2015), in the form of a carbon pool that can increase in response to elevated atmospheric carbon dioxide. With our results, we suggest that modellers that use plant biomass as a factor for carbon sequestration, seek to use responses of long-term, and not only short-term data series, because the response directions and patterns may change through time. One could argue that we only see half of the reality (or the 'tip of the iceberg') by looking at only above ground biomass but not below ground biomass. Indeed, research has shown that belowground responses are important (Arndal et al. 2007; Körner 2000), and especially in cases where aboveground responses were sparse, below ground responses might show different response patterns; we can only urge for more research of plant root biomass response in future work.

It is also worth noting that for ecosystems with annuals, biomass is reset annually and is equivalent to ANPP whereas for perennial ecosystems differences in biomass arise because of accumulation of differences in ANPP. Therefore ecosystems showing positive ANPP-precipitation relationships under control treatment are more likely to accumulate differences in biomass under drought (Estiarte et al. 2016). This expectation would also be applicable for other climate change/manipulation factors, and highlights that care must be taken when interpreting responses seen in standing above-ground biomass compared to an ANPP response, particularly for plants of different life history. To account for this, an early attempt was made in the current analysis to group some of these sites by their plant type characteristics (e.g. annuals, grasslands, shrublands, moorlands, and forests), whereby the rate and magnitude of response, especially with regard to overall biomass, was hypothesized to occur at different times. However, this broad scale categorization did not provide a clear indication, arguably either due to lack of replication, or multiple interacting effects with climate adaptations. With a greater number of studies included in a similar analysis, and greater accuracy of life-span estimates, we beleive that interpretation by expected life-time of an individual may prove to add significant understanding as to how plants may respond in the long-term to climate change manipulations and climate change itself.

Conclusions

A large number of field long-term manipulation studies exist, and our survey is far from complete. The number of experiments are also growing as more are being conducted and being funded for longer time periods. However, it is noticeable that all of the sites for which we obtained data are from the northern hemisphere. Future research should include more long-term data series and rainfall addition experiments – a common prediction of climate change. Perhaps even more importantly, experiments should be set-up in climatic regions currently not covered, to build up the global picture. In particular, sites in the southern hemisphere, warming at sites in arid zones, and manipulations in tropical regions are particularly sparse.

Despite these limitation we can draw overall conclusions for a given climatic driver, and show that a response pattern is as likely to vary through time as it is to be persistent. These findings highlight that care must be taken when interpreting climate change impacts on overall biomass from short-term experiments. We suggest that plant physiological changes and individual plastic responses, enforced by climate manipulations in the early years, is only one possible mechanism behind the response of the current community. However, longer-term experiments with multiple climate change factors are more likely to reveal how a new community may develop and how it will respond as climate change persists. Furthermore, long-term experiments are essential to provide input parameters for ecosystems models which are used to predict ecosystem dynamics under future climate change scenarios.

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Table 1. The field sites in the meta-analysis, with locations indicated in the map (Figure 2). The treatments with drought indicate percentage of rainfall removal, with irrigation the percentage addition of water; warming treatment type is indicated as being: thermocouples installed at the soil, retractable curtains giving passive night time warming, or infrared heating lamps installed over the vegetation; N indicates a combination with nitrogen fertilization. Combined treatments of the treatment factors, clipping of vegetation or plant species (+comb.). For years measured, number in brackets indicates number of sampling years.

Site name	**country**	**treatments**	**years measured**	**vegetation**	**references**
Buxton	England, UK	drought (20%), warming (thermoc.) irrigation (20%) +comb.	1994-2009 (13)	grassland	Fridley 2011
Clocaenog	Wales, UK	drought (25%), warming (curtains)	1998-2012 (12)	shrubland	Kröel-Dulay 2015
Oldebroeck	Netherlands	drought (19%), warming (curtains)	1998-2011 (11)	shrubland	Kopittke 2013
Mols	Denmark	drought (18%), warming (curtains)	1998-2012 (10)	shrubland	Kröel-Dulay 2015
Brandbjerg	Denmark	CO_2, drought (8%), warming (curtains) + comb. (3 factor)	2004-2012 (8)	shrubland	Kröel-Dulay 2015
GiFACE	Germany	CO_2	1997-2014 (18)	grassland	Andresen 2016
EVENT I	Germany	drought	2004-2010 (7)	grassland	Jentsch 2007
SwissFACE	Switzerland	CO_2, N, clipping	1993-2002 (10)	grassland	Schneider 2004
Garraf	Catalonia, Spain	drought (49%), warming (curtains)	1998-2015 (d=18) (w=9)	shrubland	Kröel-Dulay 2015
Prades	Catalonia, Spain	drought (30%)	1999-2014 (17)	forest	Barbeta 2015
Porto Conte	Italy	drought (16%), warming (curtains)	2002-2012 (6)	shrubland	Kröel-Dulay 2015
Kiskunsag	Hungary	drought (22%), warming (curtains)	2001-2012 (12)	grassland	Kröel-Dulay 2015
Matta	Israel	drought (30%)	2002-2014 (12)	shrubland/an.	Tielbörger 2014
Lahav	Israel	drought (30%)	2002-2014 (12)	shrubland/an.	Sternberg 2011
Great plains	Oklahoma, USA	warming (infrared lamp), clipping	2000-2008 (9)	grassland	Niu 2010
Oak Ridge	Tennessee, USA	CO_2	1998-2008 (11)	forest trees	cdiac.ornl.gov
Duke FACE	N. Carolina, USA	CO_2	1996-2002 (7)	forest trees	Norby 2005
Rhinelander	Wisconsin, USA	CO_2 in Aspen, +comb. Maple, Birch	1998-2008 (11)	forest trees	Talhelm 2014
Jasper Ridge	California, USA	CO_2, N, warming (infrared lamp), irrigation (50%), +comb. (4 factor)	1998-2014 (17)	grassland	Dukes 2005

PHACE	Wyoming, USA	CO_2, warming (infrared lamp) +comb.	2005-2013 (9)	grassland	Mueller 2016
BioCON	Minnesota, USA	drought (45%)	2006-2015 (10)	grassland	Reich 2014
BioCON	Minnesota, USA	CO_2, NCO_2	1998-2015 (18)	grassland	Reich 2001; 2014

Table 2. Response pattern trends in the logratio time series, the main factor results counted for elevated CO_2, drought and warming. The response categories defined were: i) No response; ii) Delayed response (early years no response then increase or decrease), iii) Directional response (linear increase or decrease), iv) Dampening response (an early response, followed by a less steep or flat response) and v) Altered responses (initial shift to positive or negative followed by a response in opposing direction, possibly with stabilising afterwards). The types are illustrated in Figure 1.

Category	**Short to long-term**	**CO_2**	**drought**	**warming**
No response	Same	12	5	10
Delayed response	Differ	0	3	2
Directional response	Same	1	3	3
Dampening response	Differ	3	3	1
Altered response	Differ	10	3	9

Figure captions

Figure 1. Conceptual diagram of the types of response categories defined were: i) No response; ii) Delayed response (early years no response then increase or decrease), iii) Directional response (linear increase or decrease), iv) Dampening response (an early response, followed by a less steep or flat response), and v) Altered response (initial shift to positive or negative followed by a response in opposing direction, possibly with stabilising afterwards).

Figure 2. Presentation of the field sites by circle, the colour indicating the main treatment factor. National boundaries were generated using rworldmap (South 2011).

Figure 3. Accumulated analysis from a total of 22 sites (68 experimental comparisons) showing response of total above ground biomass to long-term climate manipulations. Three main climate manipulation factors were analysed comparing with log response ratios (LRR) control treatments to: Drought (reduced precipitation), warming (increased temperature), and elevated CO_2. Points indicate mean estimates of yearly LRR given by categorical mixed model analyses, corrected for starting year. Error bars are standard errors given by the mixed models, and point size is the reciprocal of this SE (indicating variance and number of sites compared). Superimposed are both linear and polynomial continuous mixed model fits.

Figure 4. Long-term experimental sites divided into three site groups defined by Mean Annual Temperature (MAT); showing above-ground biomass responses (expressed as log response ratio, LRR) to climate manipulations. Points indicate mean estimates of yearly LRR given by categorical mixed model analyses, corrected for starting year. Error bars are standard errors given by the mixed models, and point size is the reciprocal of this SE (indicating variance and number of sites compared). Superimposed are both linear continuous mixed model fits and polynomial fits, when model comparison ($P<0.1$).

Figure 5. Long-term experimental sites divided into three site groups defined by Precipitation in the Wettest Month (PWM); showing above-ground biomass responses (expressed as log response ratio, LRR) to climate manipulations. Points indicate mean estimates of yearly LRR given by categorical mixed model analyses, corrected for starting year. Error bars are standard errors given by the mixed models, and point size is the reciprocal of this SE (indicating variance and number of sites compared). Superimposed are both linear continuous mixed model fits and polynomial fits, when model comparison ($P<0.1$).

Supplementary Material

Supplementary Table S1. Details of the database, at each treatment year (0 is pre-treatment year) the count of experiments within all sites, and in brackets the count of individual plots.

Year	total	drought	eCO_2	warming
0	49 (686)	14 (252)	16 (208)	19 (226)
1	65 (1017)	17 (278)	23 (453)	25 (286)
2	66 (1023)	16 (272)	26 (471)	24 (280)
3	66 (973)	15 (216)	26 (471)	25 (286)
4	64 (1011)	15 (266)	26 (471)	23 (274)
5	68 (1059)	17 (278)	26 (495)	25 (286)
6	62 (1023)	14 (260)	26 (495)	22 (268)
7	62 (1019)	14 (256)	25 (489)	23 (274)
8	50 (875)	10 (208)	21 (441)	19 (226)
9	47 (841)	11 (214)	19 (421)	17 (206)
10	42 (709)	9 (112)	19 (421)	14 (176)
11	40 (673)	10 (118)	15 (373)	15 (182)
12	30 (594)	6 (86)	14 (368)	10 (140)
13	30 (566)	6 (46)	11 (350)	13 (170)
14	25 (516)	4 (26)	11 (350)	10 (140)
15	21 (492)	2 (14)	11 (350)	8 (128)
16	26 (542)	4 (34)	11 (350)	11 (158)
17	4 (228)	1 (6)	3 (222)	0
18	2 (216)	0	2 (216)	0

Supplementary Table S2. Details of the database, ‘years’ is duration of experiments and the count is number of experiments, and in brackets the number of sites.

Years	total	drought	eCO_2	warming
6	2 (2)	1 (1)	1 (1)	0
7	12 (1)	4 (1)	4 (1)	4 (1)
8	5 (2)	0	2 (1)	3 (2)
9	3 (2)	1 (1)	0	2 (1)
10	6 (2)	1 (1)	4 (1)	1 (1)
11	5 (3)	2 (2)	1 (1)	2 (2)
12	5 (3)	2 (2)	3 (1)	0
14	4 (2)	2 (2)	0	2 (2)
16	22 (3)	3 (2)	8 (1)	11 (2)
17	2 (2)	1 (1)	1 (1)	0
18	2 (1)	0	2 (1)	0

Supplementary Table S3. Site details of long-term manipulation experiments, showing climatic parameters as given by WorldClim online database (average 50 year estimates between 1950-2000). Indicated are whether site contained (#) drought, warming and/or elevated CO^2 manipulations.

Site	Country	Latitude	Longitude	Mean Annual Temp. (°C)	Max Temp. of Warmest Month (°C)	Temp. Seasonality (Standard Dev. x 100)	Annual Precip. (mm)	Precip. of Wettest Month (mm)	Precip. Seasonality (Coeff. of Variation)	Drought	Warming	eCO^2
Buxton	England, UK	53.2	-1.92	8.0	19.1	469.1	1156	130	18	#	#	-
Clocaenog	Wales, UK	53.03	-3.28	7.4	17.7	452.1	1103	126	20	#	#	-
Oldebroeck	Netherlands	52.24	5.55	9.2	21.2	535.9	786	76	16	#	#	-
Mols	Denmark	56.23	10.57	7.5	19.9	586.6	592	62	21	#	#	-
Brandbjerg	Denmark	55.53	11.58	8.2	19.3	605.5	600	63	20	#	#	#
GiFACE	Germany	50.32	8.41	8.3	22.1	625.6	745	72	12	-	-	#
EVENT I	Germany	49.92	11.59	8.3	22.9	652.7	643	75	21	#	-	-
SwissFACE	Switzerland	47.27	8.41	9.4	23.6	635.2	1091	137	29	-	-	#
Garraf	Spain	41.18	1.49	16.4	27.6	507.1	561	80	34	#	#	-
Prades	Spain	41.21	1.2	15.7	27.5	522.4	555	74	34	#	-	-
Porto Conte	Italy	40.36	8.9	11.5	25.6	586.0	958	142	53	#	#	-
Kiskunsag	Hungary	46.53	19.23	11.1	27.3	777.3	554	70	23	#	#	-
Matta	Israel	31.42	35.03	17.8	31.1	520.9	326	74	105	#	-	-
Lahav	Israel	31.23	34.54	19.7	31.5	475	204	46	102	#	-	-
Great plains	Oklahoma, USA	34.59	-97.31	16.3	34.8	838.6	908	139	38	-	#	-
Oak Ridge	Tennessee, USA	35.54	-84.2	14.2	30.9	764.6	1396	150	15	-	-	#
Duke forest FACE	N. Carolina, USA	35.58	-79.05	15.5	31.8	752.5	1148	125	15	-	-	#
Rhinelander	Wisconsin, USA	45.4	-89.37	4.4	26.0	1103.6	816	112	43	-	-	#
Jasper Ridge	California, USA	37.24	-122.14	13.2	25.7	372.3	907	185	88	-	#	#
PHACE	Wyoming, USA	41.11	-104.54	7.8	29.8	845.5	381	65	62	-	#	#
BioCON	Minnesota, USA	45.24	-93.12	6.8	28.4	1156.4	757	113	50	#	-	-
BioCON-FACE	Minnesota, USA	45.24	-93.12	6.8	28.4	1156.4	757	113	50	-	-	#

Supplementary Tables S4 a,b,c. Site groupings as classified by site specific climatic parameters (See Supplementary Table 3). Groups rank from lowest values to highest for all parameters e.g. for Mean Annual Temperature group 1 are the coldest sites, whereas group 3 are the warmest sites; for Annual Precipitation group 1 are the direst sites, whereas group 3 are the wettest.

Table S4a. Drought (reduced precipitation) manipulation sites

Site	Country	Mean Annual Temp. (°C)	Max Temp. of Warmest Month (°C)	Temp. Seasonality (Standard Dev. x 100)	Annual Precip. (mm)	Precip. of Wettest Month (mm)	Precip. Seasonality (Coeff. of Variation)
Buxton	England, UK	1	1	1	3	3	1
Clocaenog	Wales, UK	1	1	1	3	3	1
Oldebroeck	Netherlands	2	1	2	3	2	1
Mols	Denmark	1	1	3	2	1	1
Brandbjerg	Denmark	1	1	3	2	1	1
EVENT I	Germany	2	2	3	2	2	1
Garraf	Spain	3	3	1	1	2	2
Prades	Spain	3	3	2	1	1	2
Porto Conte	Italy	3	2	2	3	3	3
Kiskunsag	Hungary	2	2	3	1	1	2
Matta	Israel	3	3	1	1	1	3
Lahav	Palestine	3	3	1	1	1	3
BioCON	Minnesota, USA	1	3	3	3	3	3

Table S4b. Warming (increased temperature) manipulation sites

Site	Country	Mean Annual Temp. (°C)	Max Temp. of Warmest Month (°C)	Temp. Seasonality (Standard Dev. x 100)	Annual Precip. (mm)	Precip. of Wettest Month (mm)	Precip. Seasonality (Coeff. of Variation)
Buxton	England, UK	1	1	1	3	3	1
Clocaenog	Wales, UK	1	1	1	3	2	1
Oldebroeck	Netherlands	2	2	2	2	2	1
Mols	Denmark	1	1	2	1	1	2
Brandbjerg	Denmark	2	1	3	2	1	1
Garraf	Spain	3	3	1	1	2	2
Porto Conte	Italy	3	2	2	3	3	3
Kiskunsag	Hungary	2	3	3	1	1	2
Great plains	Oklahoma, USA	3	3	3	3	3	3
Jasper Ridge	California, USA	3	2	1	2	3	3
PHACE	Wyoming, USA	1	3	3	1	1	3

Table S4c. Elevated CO_2 manipulation sites

Site	**Country**	**Mean Annual Temp. (°C)**	**Max Temp. of Warmest Month (°C)**	**Temp. Seasonality (Standard Dev. x 100)**	**Annual Precip. (mm)**	**Precip. of Wettest Month (mm)**	**Precip. Seasonality (Coeff. of Variation)**
Brandbjerg	Denmark	2	1	1	1	1	2
GiFACE	Germany	2	1	1	1	1	1
SwissFACE	Switzerland	2	1	2	3	3	2
Oak Ridge	Tennessee, USA	3	3	2	3	3	1
Duke forest FACE	N. Carolina, USA	3	3	2	3	2	1
Rhinelander	Wisconsin, USA	1	2	3	2	2	2
Jasper Ridge	California, USA	3	2	1	2	3	3
PHACE	Wyoming, USA	1	3	3	1	1	3
BioCON-FACE	Minnesota, USA	1	2	3	2	2	3