North Atlantic Oscillation Modulates Long-Term ANPP Dynamics via Precipitation or Temperature, Depending on Soil Nutrient Levels

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Abstract

Precipitation and temperature are major controls of the inter-annual dynamics of Aboveground Net Primary Production (ANPP). However, the effect of humans, through fertilization, acts on ANPP in combination with environmental variations. This raises two questions that drive our research: (1) How do seasonal variations of global atmospheric patterns, such as the North Atlantic Oscillation (NAO), affect precipitation and temperature, and ultimately influence ANPP? (2) Does long-term fertilization modify the potential pathway from the NAO, through precipitation and temperature, to ANPP? We addressed these questions using data from plots with either ‘high’ or ‘low’ nutrient addition from the world longest ecological experiment (period used for this analysis: 1950 to 2018), ‘Park Grass’, at Rothamsted Research, England, UK. We evaluated the relationships between ANPP and interannual climate variations across both types of plots using a structural equation model, with the aim to understand how monthly variations in the NAO affected precipitation and temperature, and how these, in turn, affected ANPP. We observed a signal of NAO on ANPP. However, the signal differed between ‘low’ and ‘high’ nutrient addition plots. Under the ‘low’ nutrient addition level, the NAO signal from all months exerted some influence on ANPP (R^2: 0.38, P-value: 0.001), and all pathways were associated with precipitation. Under ‘high’ nutrients addition, the NAO signal exerted a small influence on ANPP (R^2: 0.17, P-value = 0.001) through April precipitation and May temperatures. These results shed light on the link between global atmospheric patterns and local ecosystem functioning. Our work also confirmed a shift from a precipitation-driven response to one mediated by temperature when shifting from ‘low’ to ‘high’ nutrient conditions. These contrasting

patterns suggest there is no simple way to explain the mechanisms by which global atmospheric patterns influence ecosystem functioning.

Introduction

Aboveground Net Primary Productivity (ANPP) is an integrative variable of ecosystem functioning that, in turn, determines many ecosystem services (Costanza et al., 1997; McNaughton et al., 1989). In temperate grasslands, both precipitation and temperature exert strong controls on ANPP (Epstein et al., 1997; Sala et al., 2012); factors that are in sync with general atmospheric oscillations, such as the North Atlantic Oscillation (NAO) (Chen et al., 2017; Hurrell and Van Loon, 1997; Trigo et al., 2002). In addition to such environmental effects, human interventions may either increase or reduce ecosystem ANPP (Burrell et al., 2020). For example, the addition of nutrients, “the eutrophication” of a grassland community, can remove ANPP limitations across broad moisture gradients (Hautier et al., 2020; LeBauer and Treseder, 2008; Yahdjian et al., 2011). However, “the eutrophication” can also destabilize grassland productivity (Hautier et al., 2020) potentially shifting the community response to be more strongly influenced by environmental factors. To this end, there is limited knowledge on how the NAO might impact ANPP interannual variations, particularly in temperate grasslands of northern Europe. Additionally, it is unknown if fertilization can blur or shift the effect of biophysical constraints, and in doing so, affects ANPP’s stability, taken as the inverse of the community’s interannual ANPP variability (ANPP stability = 1 / CVinterannual; Tilman, 1999). In this study, we explored these interactions to shed light on these current unknowns.

Interannual variation in regional climate is linked to changes in the atmosphere-ocean system at the global scale (Chapin et al., 2011). A well-known global pattern associated with such changes is the North Atlantic Oscillation (NAO), which is related to changes in the sea level pressure between the ‘Subtropical High’ (Azores) and the ‘Subpolar Low’ (Icelandic). Strong positive phases of the NAO tend to be associated with above-average temperatures and precipitation in northern Europe, while below-average temperatures occur Greenland (Hurrell, 1995; Scaife et al., 2014). Conversely, strong negative phases of the NAO result in opposite temperature and precipitation patterns for the said geographies. These phases are characterized through indices, one of which is provided monthly by the National Oceanic Atmospheric Administration (NOAA) dating back to1950 (https://www.ncei.noaa.gov/access/monitoring/nao/). The NAO affects regional environmental controls (e.g., temperature and precipitation) on ANPP. However, the relationship between NAO and precipitation and temperature, and between those and ANPP has only been partially explored across different terrestrial ecosystems in Europe (Olafsson and Rousta, 2021; Pettorelli et al., 2005; Vicente-Serrano and Heredia-Laclaustra, 2010). In all cases, the remotely sensed (RS) proxy of ANPP was used via a spectral index, the Normalised Difference Vegetation Index

(NDVI). However, regardless of satellite mission, the use of NDVI (or any RS index) is limited, as its time series is much shorter than that of the 75-year NAO indices provided by NOAA (Olafsson and Rousta, 2021; Pettorelli et al., 2005; Vicente-Serrano and Heredia-Laclaustra, 2010). Furthermore, for grasslands in general, and particularly those located in northern Europe, a comprehensive understanding of how seasonal variations in the NAO influence precipitation and temperature and, ultimately, ecosystem ANPP, remains an important evidence gap.

Annual temporal associations between ANPP and precipitation and temperature have been described across different grassland systems (Epstein et al., 1997; Lauenroth and Sala, 1992; Paruelo et al., 1999; Silvertown et al., 1994). However, there is a need to understand how finer, seasonal variations in precipitation or temperature affect total ANPP. This is evident in Mediterranean systems, where precipitation seasonality is out of phase from temperature and seasonal productivity dynamics (Bandieri et al., 2020; Fabricante et al., 2009). Moreover, in systems with stronger synchronicity between ANPP and precipitation, spring precipitation typically accounts for a larger proportion of annual ANPP than total annual precipitation (Lauenroth and Sala, 1992). However, in grasslands where monthly precipitation is relatively uniform throughout the year, such as those located in temperate regions of Europe, it remains unclear which months have the greatest influence on annual ANPP. Concurrent with changes in precipitation, temperature is increasing, following a clear global trend (Pfleiderer et al., 2019). Increases in temperature may extend the length of the growing season or stimulate leaf area development, thereby enhancing ANPP (Chapin et al., 2011). Contrary to this mechanism, higher temperatures may increase atmospheric water demand, leading to reduced ANPP. Consequently, the dominant mechanisms controlling inter-annual ANPP variations remain uncertain.

Soil nutrient status can affect biophysical constraints by reducing limitations associated with nutrient cycling, which are strongly influenced by water availability and temperature. Organic matter decomposition and nutrient mineralization are constrained by both water availability and low temperatures (Schimel & Parton, 1986, Aerts, 1997). Furthermore, nitrogen limitation is widespread in grasslands, and its significance increases with annual precipitation, from arid to sub-humid regions (Yahdjian et al., 2011). This limitation is reflected in interannual variations in ANPP, where years with low precipitation or low temperatures lead to reduced nutrient release into the soil solution, whereas years with above-average precipitation show the opposite effect (Coleman et al., 2017; Parton et al., 1994). Therefore, the long-term practice of adding nutrients annually should have two main consequences. First, it should eliminate the precipitation-associated climatic signal in interannual ANPP fluctuations. Second, its effect should be relatively greater in years with below-average precipitation if water limitation is the main constraint on the nitrogen cycle. If this is the case, stability should be higher under high nutrient additions compared to systems with low or no additions. This pattern has been observed, for example, in primary production in eutrophic lakes (Kröger et al., 2023).

Given the long-term addition of nutrients across grasslands in northern Europe (Hejcman et al., 2013; Kidd et al., 2017), the relationship between NAO phases, local climate and ANPP requires further investigation. Since both temperature and precipitation tend to be above average during positive winter phases, a positive association with ANPP can be expected. However, which months best capture ANPP variation remains unclear. Moreover, the extent to which long-term fertilization blurs the climatic signal also warrants further investigation. Addressing the paucity of answers partly depends on the availability of long-term ANPP data beyond what is possible through RS indices. At 'Park Grass' in southeast England, the longest running fertilization experiment on the planet, use of its data for a 90-year period (1900−1992), has previously indicated a positive association between ANPP and total spring precipitation (Silvertown et al., 1994). However, it is unknown whether specific months provide similar explanatory power as the sum of spring precipitation. Additionally, given current and ongoing changes in climate variability (e.g., the increase of extreme weather events), incorporating more recent years (up to 2018) to our study dataset (i.e., 26 years beyond that used in Silvertown et al., 1994), could provide new insights into these critical associations.

In summary, our aim was to statistically analyse this long-term dataset to describe the main pathways through which climate variables influence ANPP and to assess how long-term fertilization impacts these pathways. To achieve this, we set two specific objectives: (1) to describe how hierarchically structured factors, such as global NAO and local precipitation and temperature, influence the interannual variation in ANPP, and; (2) to investigate how fertilization affects the biophysical signal in interannual ANPP variations.

Methods

Data collation

Both meteorological and biomass harvest time series data was obtained through the Rothamsted e-RA web portal (http://www.era.rothamsted.ac.uk/index.php data). All data were collected at Rothamsted, Harpenden, in southeast England 51.82 N 0.37 W, 128 m asl (i.e., 'Rothamsted Meteorological Station' and the experimental site, respectively). The experimental site was established in 1856, when John B. Lawes and Joseph H. Gilbert designed a 2.8 ha nutrient addition experiment at Rothamsted known as 'Park Grass' (Lawes and Gilbert, 1859). It was established to answer ways of improving hay yield via the application of inorganic fertilisers or organic manures (Lawes and Gilbert, 1863), and is the longest running ecological experiment in existence. It now provides a valuable resource to answer much broader questions than initially envisaged (Silvertown et al., 2006).

Specifically, for this study, monthly precipitation data were collected for daily records from March 1853 (prior to Park Grass's installation) to July 2018 (Perryman et al., 2018), coupled with temperature and biomass data (1878 to 2018) downloaded from e-RA (accessed 24th November 2021). Daily minimum (min) and maximum (max) meteorological values were downloaded where we found the average min and max monthly values. Monthly NOAA date from 1950 to 2018 was downloaded from NOAA (https://www.ncei.noaa.gov/access/monitoring/nao/).

To calculate ANPP, we only included data from the first harvest which accounted, on average, for 74% of the total produced biomass on an annual basis. The logic for this decision stems from the fact that the first harvest always took place during the month of June. The second harvest was disseminated across all the remaining months of the year without common criteria across plots or years, making it impossible to develop a coherent linear mixed model (LLM) to account for the different months (see Statistical Analysis section below).

The Park Grass experiment consists of several plots, where for this study, plots either under "high" or "low" levels of nutrient addition were chosen. Plot selection demanded detailed knowledge of the experimental setup and how it has changed over its lifetime. As an overview, seventeen plots with different levels, types and sources of nutrients were established in 1858, three more plots were added in 1865, and some plots changed their treatment configuration towards the end of the 19th century or early in the 20th (Table 1). These plots were further subdivided over time to correct pH at different levels where pH corrections had the objective of keeping it at different levels: plots 'a': pH 7, plots 'b': pH 6, plots 'c'; pH 5, and plots 'd': no correction (e.g., see Table 1 for plots code names '12b', '12c', and '12d'). These subdivisions created 101 subplots. To analyse the impact of the biophysical factors on ANPP, considering contrasting nutrient addition levels, we selected sixteen subplots, eight at the top and the remaining at the lowest mean ANPP levels (Table 1). This criterion included plots under the highest or second highest level of N addition for the level 'high', and it also included the addition of all other nutrients considered within the experiment (P, K, Na and Mg). Conversely, it included control subplots, with no nutrient addition apart from background atmospheric deposition (Blake and Goulding, 2002), and/or the addition of lime for pH corrections plus a subplot under the first level of N addition (Table 1).

Level used for this analysis	Code name of the plot	Current treatment establishment	Treatment description	Mean ± (SDEV) ANPP (kg / ha/yr) Period: 1950-2018
High	14/2d	1858	Unlimed: N*2 P K Na Mg	5060±(801)
	14/2c	1858	Limed to pH 5 since 1965: N*2 P K Na Mg	5160±(824)
	14/2b	1858	Limed to pH 6 since 1965: N*2 P K Na Mg	5210±(794)
	11/2c	1882	Limed to pH 5 since 1965: N3 P K Na Mg	5370±(1520)
	11/1b	1882	Limed to pH 6 since 1965: N3 P K Na Mg	5720±(1040)
	11/1a	1882	Limed to pH 7 since 1965: N3 P K Na Mg	5930±(1070)
	11/2b	1882	Limed to pH 6 since 1965: N3 P K Na Mg	6020±(1210)
	11/2a	1882	Limed to pH 7 since 1965: N3 P K Na Mg	6090±(1000)
Low	1d	1903	Unlimed N1	854±(503)
	3c	1856	Unlimed: Nil	1280±(491)
	3d	1856	Unlimed: Nil	1410±(566)
	2/2d	1863	Unlimed: Nil	1490±(587)
	12d	1856	Unlimed: Nil	1560±(597)
	12c	1856	Limed to pH 5 since 1965: Nil	1570±(625)
	12b	1856	Limed to pH 6 since 1965: Nil	1880±(638)
	3a	1903	Limed to pH 7 since 1965: Nil	2010±(623)

Table 1: Nil: no fertilizer or manure. N1: 48 kg N as ammonium sulphate. N*2: 96 kg N as sodium nitrate and supplying 157 kg Na. N3: 144 kg N as ammonium sulphate. P: 35 kg P as triple supephosphate until 2015, when it changed to a rate of 17 kgP/ha.yr, K: 225 kg K as potassium sulphate, Na: 15 kg Na as sodium sulphates, and Mg: 10 kg Mg as magnesium sulphate. The pH level correction was carried out through different rates across the years.

Statistical analysis

To achieve the first study objective, we explicitly considered the hierarchy among NAO, precipitation, temperature and annual ANPP, via piecewise structural equation modelling (pSEM) (Lefcheck, 2016). The estimated parameters from the proposed SEMs, (Fig. 1) allowed us to understand how monthly global climate oscillations, mediated by local precipitation, or temperature, could influence interannual variations of ANPP. The pSEM was fitted using functions of the "piecewiseSEM" R package (Lefcheck, 2016) using R version 3.4.4 (R Core Team, 2018). Within the pSEM, we considered both the hierarchical effect of NAO on both precipitation and temperature, and its seasonal component. Specifically, we addressed the potential effect of the NAO signal on precipitation and temperature from January to June, where the third and fourth week of June is the targeted moment of harvest (see Fig.1). Furthermore, we considered the different plots within each fertilization level. To do so, and within the pSEM we fitted a linear mixed model where the fixed factors were monthly precipitation and temperature, while the plots were treated as a random factor.

For each fertilization level (high or low), we used a stepwise approach to identify the most parsimonious model structure. First, we constructed an initial model that incorporated all hypothesized pathways linking the NAO to ANPP, mediated by precipitation and temperature (Figure 1). Next, we applied a stepwise model selection procedure by systematically removing non-significant paths based on individual component model statistics and overall model fit, assessed using the Chi^2 statistic (Grace, 2006). We continued this iterative refinement until the Chi^2 test was non-significant, indicating an adequate model fit. Finally, we evaluated the fit of the selected model by comparing observed and predicted values from the fitted pSEM model.

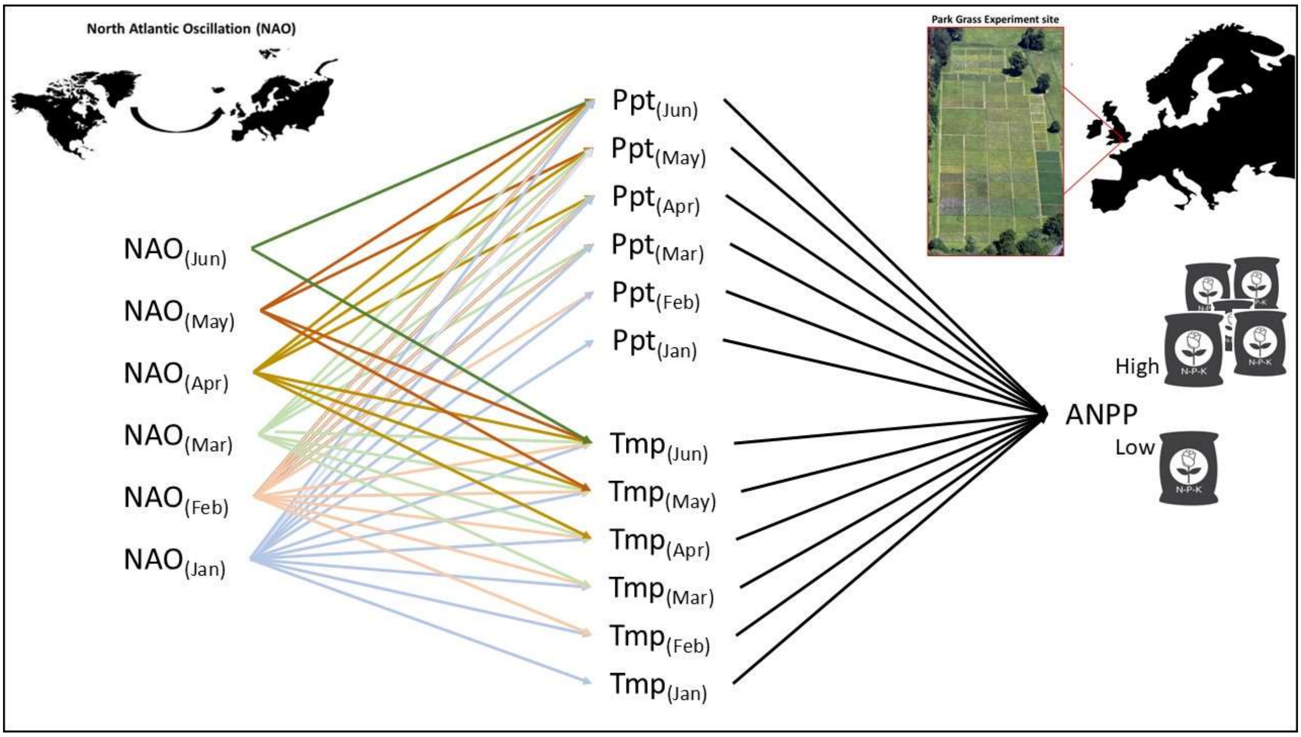

***Figure 1**. Conceptual framework of the structural equation model (SEM) used to address the effect of climate, at the global scale, mediated through the North Atlantic Oscillation (NAO), and at the regional scale through precipitation (Ppt) and temperature (Tmp) on aboveground net primary production (ANPP) for plots under high or low nutrient additions from the long-term experiment Park Grass.*

To achieve the second study objective, for describing how fertilization affects the biophysical signal on interannual variations of ANPP, we took a four-step approach. First, we estimated the average ANPP value per level of fertilization for each year under study (1950-2018). Second, we estimated the association between ANPP and the accumulated precipitation, from January to June, for each treatment ('low' or 'high' nutrient addition). We tested this association through a linear regression (using the lm function in base R). Third, we quantified the fertilization relative effect (FRE) (defined as: FRE = $ANPP_{fertilized} - ANPP_{control}$) / $ANPP_{control}$) and investigated the association between FRE and the accumulated precipitation. Here, a negative association between FRE and the accumulated precipitation, would suggest that fertilization had a major effect under lower precipitation. Fourth, we described the change in stability over time. W quantified stability as 1/CV where CV represented the inter-annual coefficient of variation of ANPP for each plot within a five-year window. Furthermore, we evaluated the differences in stability between levels through a Mann-Whitney non-parametric test.

Results

Objective 1: Effect of climate on ANPP and the influence of long-term fertilization

For the study period (1950-2018), an analysis of January, February, and March interannual dynamics revealed a shift in the NAO signal from an initial sequence characterized by negative values to a final sequence dominated by positive ones (Fig. 2a). Conversely, in the spring-to-summer transition from May to June, the observed pattern exhibited the opposite trend (that is, an initial sequence dominated by positive values to a final sequence characterized by negative ones) (Fig. 2a). For the meteorological data, monthly temperature showed similar values in January and February, increasing to a highest value in June. A clear and strong rise occurred between April and May, followed by another change between May and June. Across all years and consistently across all months, temperature decreased from 1950 to 1980, then increased, stabilizing around 2010 (Fig. 2b). Precipitation showed similar values across different months. Except for January, monthly precipitation did not exhibit any clear trends across the study years. In January, however, a positive trend in precipitation was observed, causing its monthly value to increase from 50 to nearly 80 mm, setting it apart from the other months (Fig. 2c). Finally, ANPP was, on average, six times higher under 'high' nutrient level compared to "low" nutrient level. Under the 'high' nutrient level, ANPP increased from the 1950s to the 1970s, followed by a decrease with minimum values in the 1990s. Subsequently, a second increase occurred, stabilizing by the 2010s. Conversely, under the 'low'nutrient level, ANPP gradually increased until the mid-1980s, remained stable, and then increased again in the 1990s (Fig. 2d).

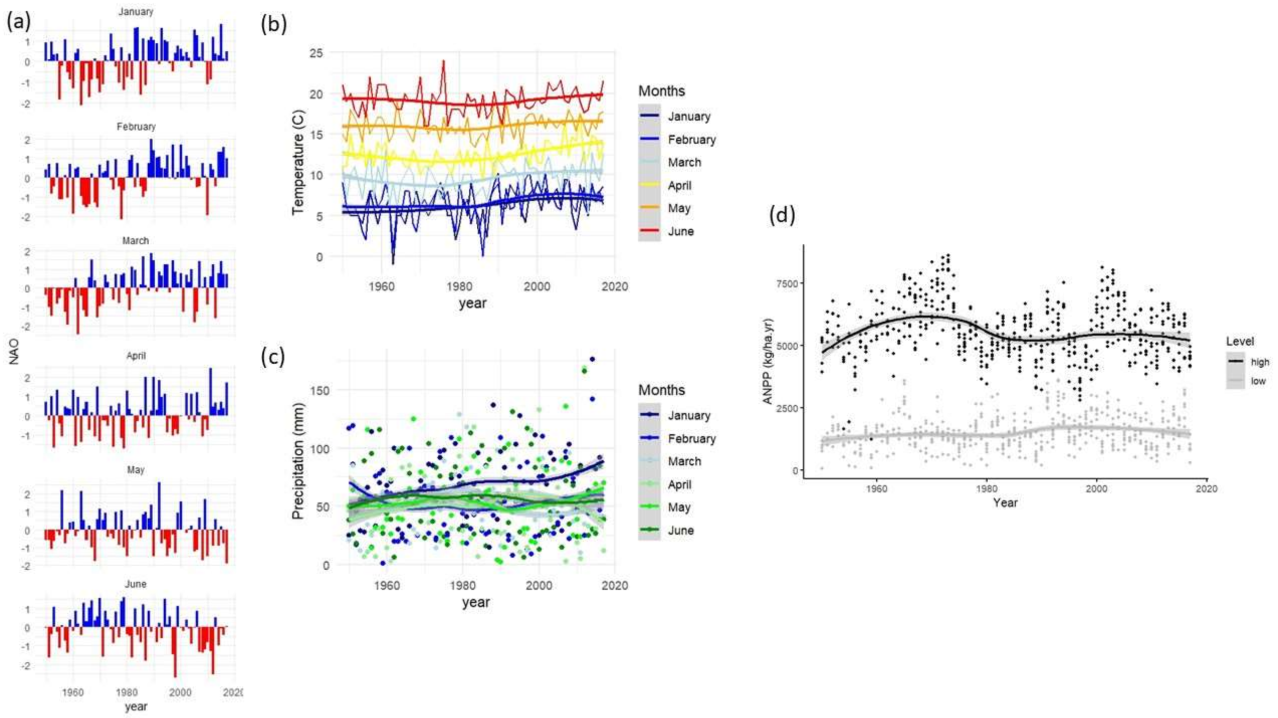

Figure 2. *(a) North Atlantic Oscillation (NAO) values, (b) monthly mean temperature, (c) monthly precipitation, and (d) Aboveground Net Primary Production (ANPP) for plots with 'high' and 'low' nutrient additions in the 'Park Grass' long-term experiment over a 68-year period (1950-2018). Trend lines in b, c and d were fitted using local regressions (loess) and are shown with standard errors. In (d), each dot represents the annual value of the 16 selected plots.*

The pSEM indicated that the NAO signal exhibited partially contrasting pathways of influence on ANPP depending on nutrient addition level (Fig. 3). Under the 'low' level, the NAO signal from all months exerted some influence on ANPP (predicted vs observed fitted parameters, R^2: 0.38, P-value: 0.001). Here, all pathways were associated with precipitation (Fig. 3). Specifically, April, May and June precipitation had a positive effect on ANPP. However, the NAO signal on precipitation was not the same across months. For example, April precipitation was associated with the NAO signal of January, March and April. For, January and March, the association was positive, but negative with the April NAO signal. In other words, as the January and March NOA signals reach positive values, April precipitation increased. On the contrary, when the NAO signal of April reached negative values, April precipitation increased. May precipitation was associated with the February and March NAO signals. In this case the association was negative for February but positive for March. Finally, June precipitation was associated with the NAO signal of January, February, March, May and June. Here, all associations were negative except for March.

Under 'high' nutrients addition, the NAO signal exerted a small influence on ANPP (predicted vs observed fitted parameters, R^2: 0.17, P-value = 0.001) through April precipitation and, different from the low nutrients' situation through May temperature (Figure 3). Here, ANPP increased as April precipitation increased. ANPP decreased as May temperature increased. The association pathway between April precipitation and the NAO signal was the same as the one descripted for the low nutrients condition. May temperature was associated with the NAO signal of all months from January to May. Here, the association was negative between May temperature and the January NAO signal. But, for the rest of the months, the association was positive.

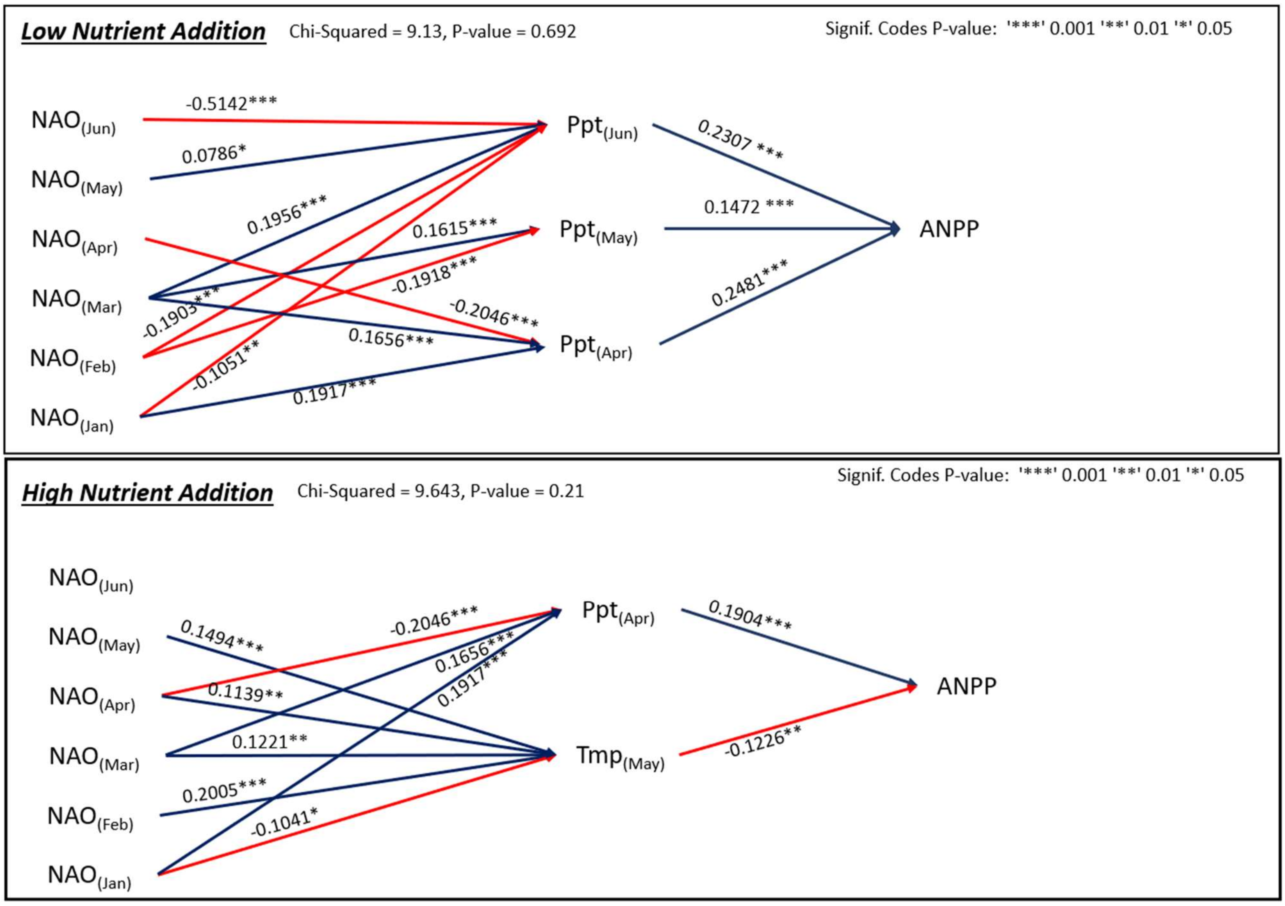

Figure 3. *Results of the structural equation model (pSEM) associating North Atlantic Oscillation (NOA), precipitation (Ppt), temperature (Tmp), and Aboveground Net Primary Productivity (ANPP) under low (upper panel) and high (lower panel) nutrient additions. Values on the arrows show standardized path coefficients. Red and blue arrows indicate negative and positive associations, respectively. The analysis covers the period from 1950 to 2018.* *$^*p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$.*

Objective 2: Nutrient addition relative effect on interannual variations of ANPP

A prominent outcome of the 'high' nutrient condition was the temporal decoupling of ANPP variation from precipitation variation (Fig. 4). In contrast, under the 'low' nutrient addition it maintained the expected positive association between these variables. Further, the relative impact of 'high' nutrient addition reduced with rising precipitation levels (Fig. 4). That is, as precipitation intensified, the influence of nutrient addition diminished. The relative effect of nutrient addition was highest at an estimated 400% when precipitation was around ≈100 mm and dropped to below 100% when precipitation reached ≈400 mm (Fig. 4).

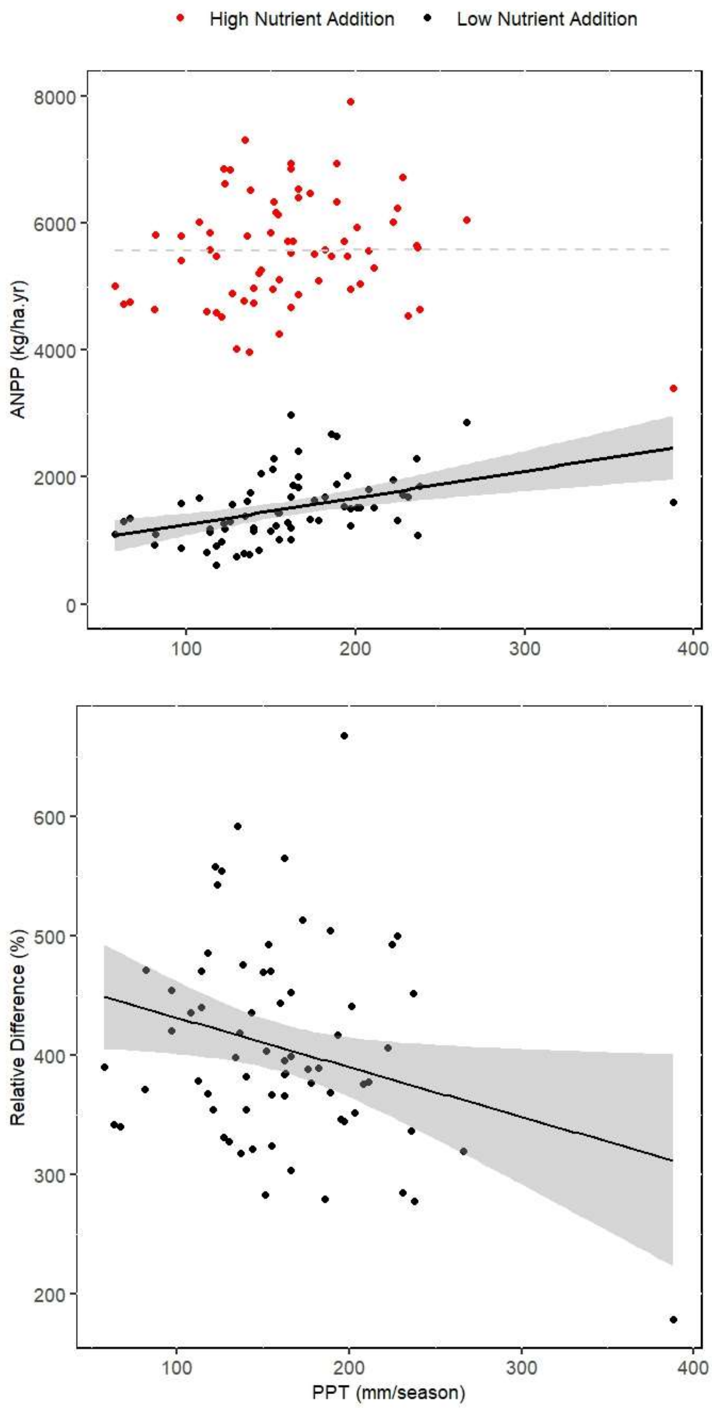

Figure 4. *(a) Association between Aboveground Net Primary Production (ANPP) and annual precipitation (Ppt, accumulated from January to a harvest in June) under high and low nutrient addition. Each point represents the average ANPP of all 8 plots for a specific fertilization level and year from 1950 to 2018. (b) The relative difference – which estimates the effect of nutrient addition on ANPP, calculated as (ANPP in 'high' - ANPP in 'low') / ANPP in low, in relation to annual precipitation. Black continuous and grey dotted lines indicate statistically significant ($p < 0.05$) and statistically non-significant relationships, respectively. Fitted models: High nutrients addition ($p = 0.9788$) Low nutrients addition ($ANPP = 4.20PPT + 831.8$; $p < 0.001$; Adjusted R2:0.17). Relative Difference ($RD (\%) = -0.41PPT + 472.85$; $p = 0.03$; Adjusted R2:0.05).*

The stability of ANPP (1 / CV) varied over the study period, with consistently higher stability observed in ‘high’ nutrient addition plots compared to ‘low’ nutrient addition plots (Fig 5). The average (median) stability values were also higher for the ‘high’ nutrient addition plots, whereas the ‘low’ nutrient addition plots exhibited lower average stability but with greater variability (Fig 6).

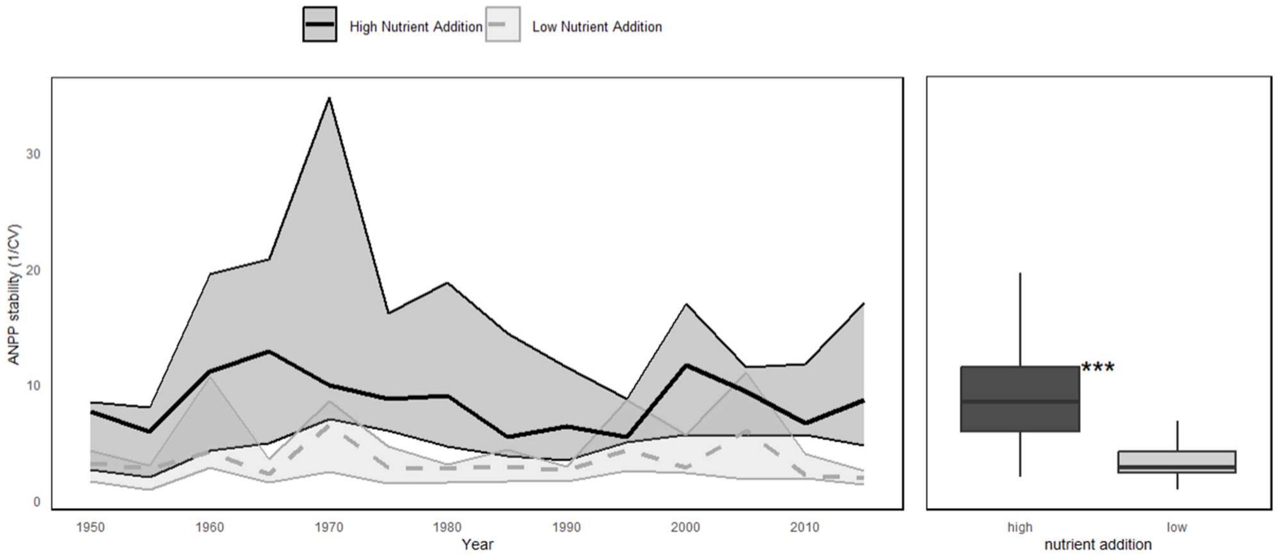

Figure 5. *Temporal stability of aboveground net primary productivity (ANPP) estimated as 1 / CV where CV = μ/σ, over a five-year window across the study period (1950-2018). The lines within the shaded areas represent the median for all plots under either ‘high’ or ‘low’ nutrient addition The shaded area represents the range of variation, defined by the maximum and minimum stability values within each nutrient addition group. *** indicates statistical significance ($p < 0.001$) for the difference between the ‘low’ and ‘high’ nutrient groups in terms of stability.*

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Discussion

Overall, we observed a direct connection between the NAO, an indicator of global climate variations, and local variations in precipitation and temperature. The NAO was positively associated with temperature, mainly in winter, and negatively associated with June precipitation. In turn, June precipitation was positively associated with ANPP. Continuous nutrient addition for over 160 years altered the association structure between climate and ANPP. On one hand, nutrient addition shifted the association between NAO and ANPP, from one totally mediated by precipitation, to one mediated by precipitation and temperature. On the other hand, via a relative effect analysis, the effect of nutrient addition on ANPP was greater under low precipitation. Furthermore, the reduced dependence on water availability appears to be the pathway leading to greater stability in ANPP under ‘high’ nutrient addition.

Our analysis partially confirmed the expected association of the NAO signal on temperature and precipitation. It supported the association between the NAO's positive phase and above-average winter temperatures (Hurrell, 1995; Scaife et al., 2014), but it did not provide evidence for a similar association with precipitation. Furthermore, our results are novel in that, until now, the NAO's influence on vegetation has been reported mainly in relation to temperature (Gouveia et al., 2008). Specifically, previous research has indicated that high winter NAO values were associated with higher values of NDVI, a RS-based proxy of ANPP, in spring, but low NDVI values in summer (Gouveia et al., 2008). Our study, however, highlights two novel aspects. First, as in previous studies (Hurrell, 1995; Scaife et al., 2014), we observed a link between the NAO's winter signal and temperature, and its association with ANPP under high nutrient addition. However, our results emphasize the negative effect on summer ANPP rather than the positive effect in spring. Second, under low nutrient addition, ANPP was more limited by water availability (Sala et al., 2012) than by temperature (Epstein et al., 1997). This result reveals a previously undescribed pathway linking global atmospheric patterns and ANPP in temperate regions of Europe.

Continuous nutrient addition for over 160 years has evidently altered the association between climate and ANPP. Given the long-established use of synthetic fertilizer across Europe (Pellegrini and Fernández, 2018; Rosa and Gabrielli, 2022), it is reasonable to speculate that the NAO signal may have a similar effect on many other temperate grasslands across the continent. However, at least two factors are currently affecting the use of synthetic fertilizers. First, the ongoing conflict between Ukraine and Russia has disrupted supply chains, increasing the costs of nitrogen-based fertilizers (Pereira et al., 2022). Second, the imperative to reduce greenhouse gas emissions has intensified efforts to limit fertilizer use, including net-zero policies advocated by the European Union and the UK (Abdalla et al., 2010; Anderson et al., 2020). These coupled factors suggest that, in the future, agricultural systems containing temperate grasslands may experience a shift in the pathways linking them to global atmospheric processes, unless alternative "green" sources of nitrogen are more widely implemented to compensate for the desired and policy-driven reductions in the use of synthetic fertilizers.

Fertilizers have brought significant benefits to Europe's grasslands, and it is essential to contextualize these effects. Data from long-term experiments (LTEs), together with LTE networks, provide valuable opportunities to compare the impact of fertilization on water yield, estimated through 'precipitation use efficiency' (PUE; ANPP/annual precipitation, Huxman et al., 2004; Verón et al., 2005), and on the stability of ANPP, estimated through its inverse to relative interannual variation (Bai et al., 2008; Jobbágy and Sala, 2000; Knapp and Smith, 2001). Within the unique LTE of this study ('Park Grass' at Rothamsted, UK), fertilization was shown to increase water yield to its highest value when contextualised across a network of LTEs spanning four continents (Europe, Asia, North and

South America Fig. 6). Additionally, the Park Grass treatments under 'high' levels of nutrient addition recorded an increase in ANPP stability, not only when compared to their local counterparts but also across different biomes, globally. This suggests that, in sites fertilized for over 160 years, eutrophication increased 'precipitation use efficiency' (PUE) and simultaneously stabilized the interannual dynamics of ANPP, effectively decoupling it from variation in precipitation. This pattern contrasts with the findings of 'NUTNET', where fertilization increased ANPP instability (Hautier et al., 2014), and suggests that eutrophication may involve an adjustment period, during which plant communities shift to the new abiotic environment.

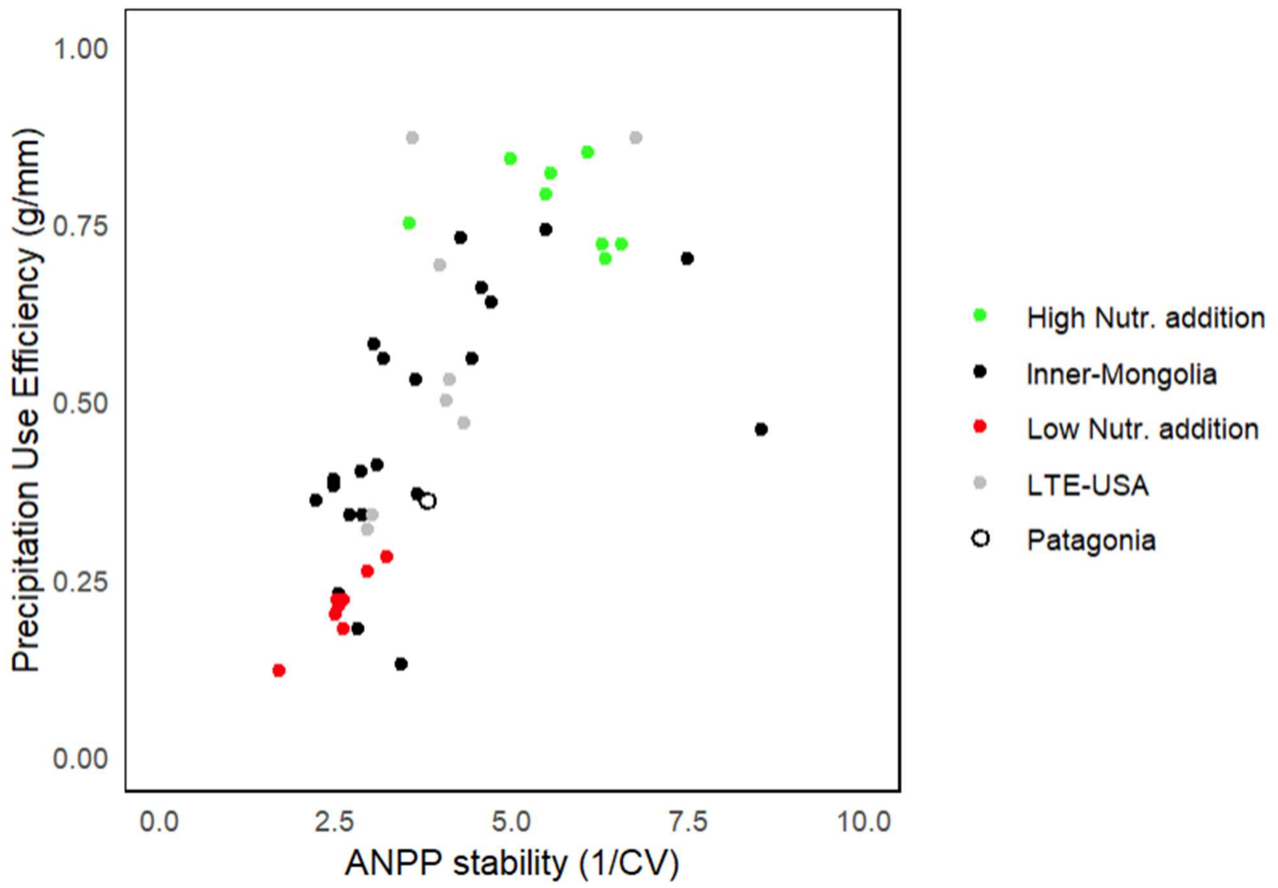

Figure 6. *Relationship between precipitation use efficiency (PUE; ANPP / mean annual precipitation) and ANPP stability (1 / inter-annual relative variation, CV) across different long-term experiments (LTEs) in different biomes and different continents. Green and red round symbols represent plots from the present study under 'high' or 'low' nutrient addition, respectively (UK/ Europe LTE). The LTE-USA (North America) covers different biomes across the United States (Knapp and Smith 2001). The Inner-Mongolia (Asia) LTE covers several types of grassland and steppes (Bai et al. 2008). The single LTE in Patagonia (South America) represents a co-dominated shrub-grass steppe (Jobbágy and Sala, 2000). Only sites with a mean annual precipitation lower than 1000 mm were considered in this figure. (Pearson correlation: 0.703, p-value < 0.0001).*

Our study offers valuable insights into the relationship between global atmospheric patterns, local climatic variables, and the long-term effects of nutrient addition on ANPP interannual dynamics. However, two key limitations must be acknowledged. First, the use of observed results for long-term predictions of ANPP in absolute terms is limited when compared to other studies. For example, our findings suggest that high NAO values in June are likely correlated with below-average ANPP in similar situations in Northern Europe; however, these findings should not be directly used to predict future scenarios, such as those given by the Bayesian modelling framework used in Addy et al. (2022). Second, the unexplained variability in ANPP by climatic factors (bottom-up factors) may also be influenced by biological factors (top-down factors). Herbivory could differentially regulate interannual variations in ANPP between the nutrient-poor and nutrient-rich LTE plots. The low nutrient addition plots, which are nutrient-poor, are dominated by non-grass herbaceous plants, while the fertilized plots are dominated by grasses (Baca Cabrera et al., 2021). Additionally, many grasses form mutualistic relationships with endophytic fungi which are known to confer resistance to herbivory (Dirihan et al., 2016; Gundel et al., 2011). The abundance of grasshoppers at the 'Park Grass' site has been shown to negatively correlate with ANPP (Morris, 1992), suggesting that the increased stability in ANPP under fertilization is, in part, due to reduced top-down controls, mediated by changes in plant functional types associated with nutrient availability.

Conclusions

Our study has described, for the first time, the pathway through which the global atmospheric pattern, the NAO, affects long-term ANPP interannual dynamics at the 'Park Grass' long-term experiment in southeast UK. We identified a novel signal between spring's precipitation and the NAO, and how this signal influences ANPP. Specifically, the main path indicated that under its negative NAO phase in June, above-average precipitation positively affected ANPP. This pattern was observed in LTE plots with low or no direct nutrient addition. In contrast, for plots with long-term high nutrients addition, the NAO signal was mediated by temperature, and precipitation. Our study provides two novel insights. First, from an ecosystem perspective, the results suggest that, under "real world" conditions, the NAO signal on ANPP in Europe's temperate grasslands may be weak, given the historically high levels of nutrient addition. Second, from a management perspective, the results indicate that the direct addition of nutrients at high rates over multiple years may not be the most efficient approach. In other words, nutrient additions to temperate grasslands in the temperate areas of Europe would be more beneficial if applied during below-average precipitation conditions. Finally, our study provides quantitative insights into how much precipitation can compensate ANPP during wetter years.

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