

# North Atlantic Oscillation modulates long-term ANPP dynamics via precipitation or temperature, depending on soil nutrient levels

JGN Irisarri<sup>a,c,\*</sup>, M Texeira<sup>b</sup>, P Harris<sup>a</sup>, PE Gundel<sup>d</sup>, AL Collins<sup>a</sup>

<sup>a</sup> Rothamsted Research, North Wyke, UK

<sup>b</sup> IFEVA, CONICET & Departamento de Métodos Cuantitativos y Sistemas de Información, Facultad de Agronomía, Universidad de Buenos Aires, Buenos Aires, Argentina

<sup>c</sup> Department of Ecosystem Science and Management, University of Wyoming, Laramie, USA

<sup>d</sup> Instituto de Biología Funcional y Biotecnología (BIOLAB)-INBIOTEC-CONICET-CICBA, Facultad de Agronomía, Universidad Nacional del Centro de la Provincia de Buenos Aires (UNICEN), Buenos Aires, Argentina

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## ABSTRACT

The North Atlantic Oscillation (NAO) is a dominant mode of atmospheric variability in the North Atlantic region, influencing winter and spring precipitation and temperature across Europe. These seasonal variations strongly control interannual dynamics in Aboveground Net Primary Production (ANPP). However, long-term fertilization (>100 years) may interact with these drivers and alter their influence on ecosystem functioning. To investigate this, we analysed a long-term dataset statistically to: (1) describe how hierarchically structured factors—global NAO and local precipitation and temperature—affect interannual variation in ANPP, and (2) assess how fertilization modifies the pathways through which climate influences ANPP. Data were taken from plots with ‘high’ and ‘low’ nutrient addition at the world’s longest ecological experiment; the ‘Park Grass’ experiment (Rothamsted Research, England, UK; analysis period: 1950–2018). We used a structural equation model to evaluate relationships between ANPP and interannual climate variations, testing how monthly NAO changes affected precipitation and temperature, and how these, in turn, influenced ANPP. We detected a clear NAO signal on ANPP, but its influence varied by nutrient level. Under low nutrient addition, NAO effects were consistently mediated through precipitation ( $R^2 = 0.38$ ,  $p < 0.001$ ). In contrast, under high nutrient addition, the NAO had a weaker effect ( $R^2 = 0.17$ ,  $p < 0.001$ ), acting through April precipitation and May temperature. These results clarify how global atmospheric patterns influence local ecosystem functioning, revealing a shift from a precipitation-driven to temperature responses under ‘high’ nutrient conditions. These contrasting patterns suggest there is no simple way to explain the mechanisms by which global atmospheric patterns influence ecosystem functioning. They also reveal that long-term fertilization alters community composition and stability in ways that may differ from those observed in shorter-term experiments, with concomitant implications for interpreting ecosystem responses to human drivers.

## 1. 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

\* Corresponding author.

E-mail address: [irisarri@agro.uba.ar](mailto:irisarri@agro.uba.ar) (J. Irisarri).

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community's interannual ANPP variability (ANPP stability =  $1 / \text{CV}_{\text{interannual}}$ ; Tilman, 1999). While shorter-term experiments have shown that eutrophication can destabilize productivity and reduce diversity, it remains unclear whether these effects persist or shift over longer time-scales. Here, we address this gap using productivity data from an experiment with over a century of fertilization.

Interannual variation in regional climate is linked to changes in the atmosphere-ocean system at the global scale (F.S.I. Chapin et al., 2011). A well-known global pattern associated with such changes is the NAO, which is related to changes in the sea level pressure between the 'Sub-tropical 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 to 1950 (<https://www.ncei.noaa.gov/access/mo/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; Pettoirelli 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; Pettoirelli 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. We focused on the NAO because it is the dominant mode of atmospheric variability in the North Atlantic region, with well-documented impacts on European climate, particularly temperature and precipitation patterns during winter and spring (Hurrell, 1995; Trigo et al., 2002).

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 (Hajek and Knapp, 2022). 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 (Craine et al., 2012; 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 (F.S.I. 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 and 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 (Hejman 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. Although our study focuses on a single grassland site, Park Grass offers a uniquely long and detailed dataset that allows disentangling of the effects of global atmospheric patterns from local biophysical constraints. Its unparalleled temporal duration and controlled fertilization treatments make it an ideal system to explore how teleconnections modulate ANPP under contrasting nutrient regimes.

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.

## 2. Methods

### 2.1. Data collation

Both meteorological and biomass harvest time series data was obtained through the Rothamsted e-RA web portal (<https://www.era.rothamsted.ac.uk/experiment/rpg5#datasets/>). 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 site has a mean annual air temperature of 10.2 °C and a mean annual precipitation of 763.5 mm. 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). To assess community-level responses, we compiled species-level cover data to calculate functional group abundance, species richness, and ANPP stability (1/CV interannual) per plot.

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 24<sup>th</sup> November 2021). Daily minimum (min) and maximum (max) meteorological values were downloaded where we found the average min and max monthly values. Monthly NOAA data from 1950 to 2018 was downloaded from NOAA (<https://www.ncdc.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 main plots, originally established in 1856 and expanded in 1865, each representing distinct fertilization regimes defined by the type and quantity of nutrients applied (see Table 1). These include combinations of nitrogen (at different rates and chemical forms), phosphorus, potassium, sodium, magnesium, and lime. In 1903, the main plots were subdivided to study the effect of liming: 4.0 t/ha lime (chalk) was applied every 4 yrs. Plots were further split in 1965 into four subplots (a–d) and lime applied every 3 yrs, if necessary, to maintain target pH levels of 7, 6, and 5, respectively, while subplot d receives no ground chalk, allowing pH to vary naturally. This subdivision resulted in a total of 101 subplots, enabling long-term assessment of nutrient and pH interactions on productivity and species composition. For this study, we selected 16 subplots representing the extremes of ANPP response—eight with high nutrient addition and eight with low or no fertilization—based on historical treatment records and mean ANPP values (see Table 1).

## 2.2. 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. Given that all 16 subplots are geographically co-located at the Rothamsted site, the same monthly precipitation and temperature data were applied to all subplots, meaning the climate data are non-replicated at the plot scale. To account for this inherent non-independence (i.e., pseudo-replication) and to capture the variance associated with subplot-specific characteristics, the component of the pSEM linking monthly climate to ANPP was fitted using a LLM where the fixed factors were monthly precipitation and temperature, while the plots were treated as a random factor. We selected NAO signals from January to June to capture both immediate and lagged effects on precipitation and temperature leading up to the June harvest. This window aligns with previous studies showing that winter and early spring NAO phases influence growing season climate (Scaife et al., 2014; Gouveia et al., 2008).

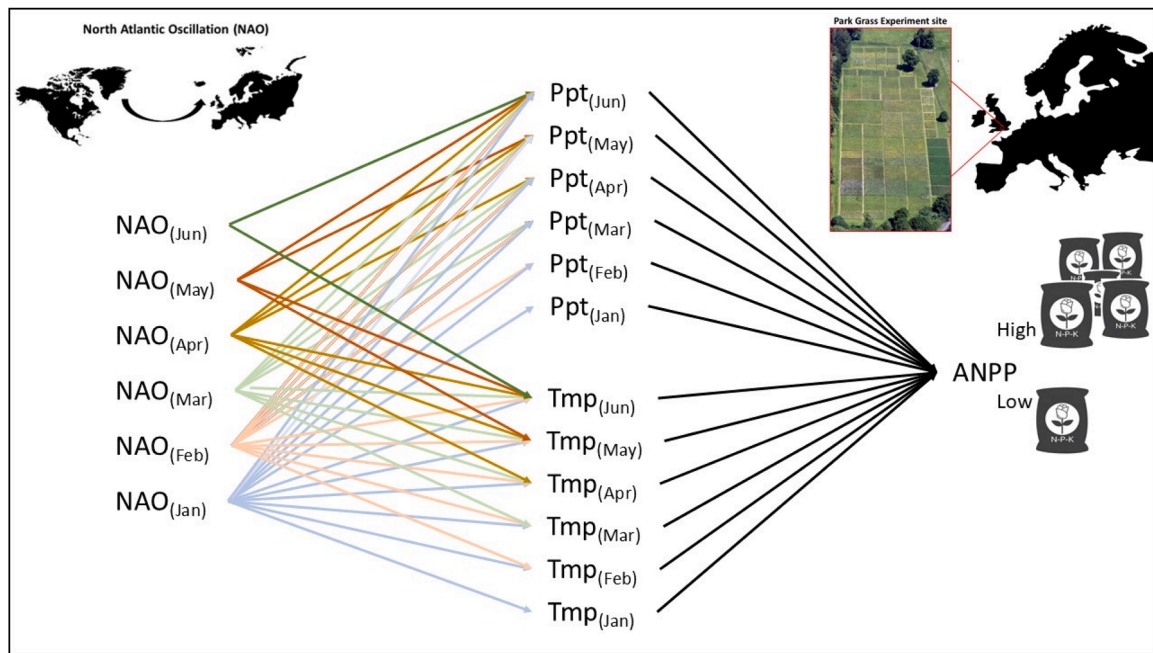
For each fertilization level (high or low), we used a stepwise approach to identify the most parsimonious model structure. First, we constructed an initial model that incorporated all hypothesized pathways linking the NAO to ANPP, mediated by precipitation and temperature (Fig. 1). Next, we applied a backward-selection procedure to iteratively refine the model structure. In each step, we systematically removed the single non-significant path ( $\alpha > 0.05$ ) based on the individual component model statistics. We continued this iterative refinement until the overall model fit, assessed using the Chi-squared ( $\chi^2$ ) statistic, was non-significant ( $p > 0.05$ ), indicating an adequate representation of the observed covariance matrix. Only the significant pathways were retained in the final pSEMs. The full dataset for the time series analysis covers  $N = 69$  years (1950–2018). Thus, both the “High Nutrient” and “Low Nutrient” pSEMs were constructed using 69 annual observations for the NAO, monthly climate variables, and ANPP means. The final component model for ANPP, which uses a LMM, utilizes the  $N$  total=552 data points (69 years  $\times$  8 plots) to estimate its parameters. Finally, we evaluated the fit of the selected model by comparing observed and predicted values from the fitted pSEM. The analysed time series for ANPP (1950–2018) represents the final 68 years of the 165-year-old Park Grass experiment. It is essential to recognize that the substantial initial differences and the current ANPP levels (Table 1) are not solely due to the immediate effects of fertilization but also represent a profound heritage effect from over a century of differential management including plants biodiversity (Table 1). This heritage effect establishes the distinct ecological baselines (high- vs. low-nutrient status) against which we test whether the mechanism (the structural pathway through the pSEM) by which NAO-driven climate variability influences ANPP dynamics differs between the two groups.

To achieve the second study objective, for describing how fertilization affects the biophysical signal on interannual variations of ANPP, we

**Table 1**

Description of the 16 plots and their fertilization history, which led to the selection of 8 plots with high nutrients addition and 8 with low or no nutrients addition, and the resulting changes in plant community composition and mean ANPP. For the number of species and the relative abundance the expressed values are from the period 1991–2012. For ANPP the expressed values are the same as the NAO information, 1950–2018.

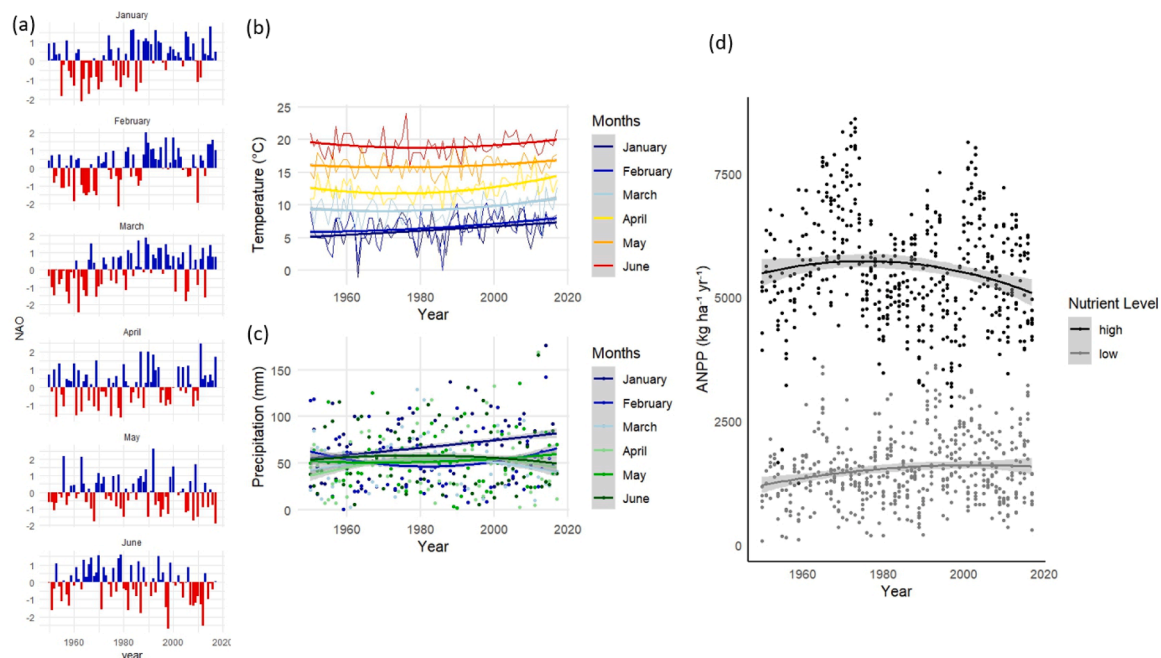
Level used for this analysis	Code name of the selected plots	Fertilization treatments summary	Relative abundance (%)					# of species per plot Mean $\pm$ (SDEV)	ANPP (kg / ha/yr ) Mean $\pm$ (SDEV)
			Grass	Forb	Legume	Rush	Sedge		
High	14/2d, 14/2c, 14/2b, 11/2c, 11/1b, 11/1a, 11/2b, 11/2a	Plots received from 96 to 144 kg N. In addition all plots received 35 kg P, 225 kg K, 15 kg Na, and 10 kg Mg and different levels of lime to correct pH to a targeted level.	92.75	7	0.25	0	0	8 $\pm$ (2) to 14 $\pm$ (2)	5060 $\pm$ (801) to 6090 $\pm$ (1000)
Low	1d, 3c, 3d, 2/2d, 12d, 12c, 12b, 3a	One plot received 48 kg N, the rest did not received any type of nutrients, except for lime to correct pH levels to a targeted level	62.5	11.25	5.25	14.6	6.4	3 $\pm$ (1) to 31 $\pm$ (2)	854 $\pm$ (503) to 2010 $\pm$ (623)



**Fig. 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.

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:  $FRE = \frac{ANPP_{fertilized} - ANPP_{control}}{ANPP_{control}}$ ) 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. We 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.



**Fig. 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 from the 'Park Grass' long-term experiment over a 68-year period (1950–2018). Trend lines in panels (b–d) were estimated using quadratic regressions to capture long-term tendencies and are shown with standard errors. In panel (d), each dot represents the annual value of the 16 selected plots.



### 3. Results

#### 3.1. Objective 1: effect of climate on ANPP and the influence of long-term fertilization

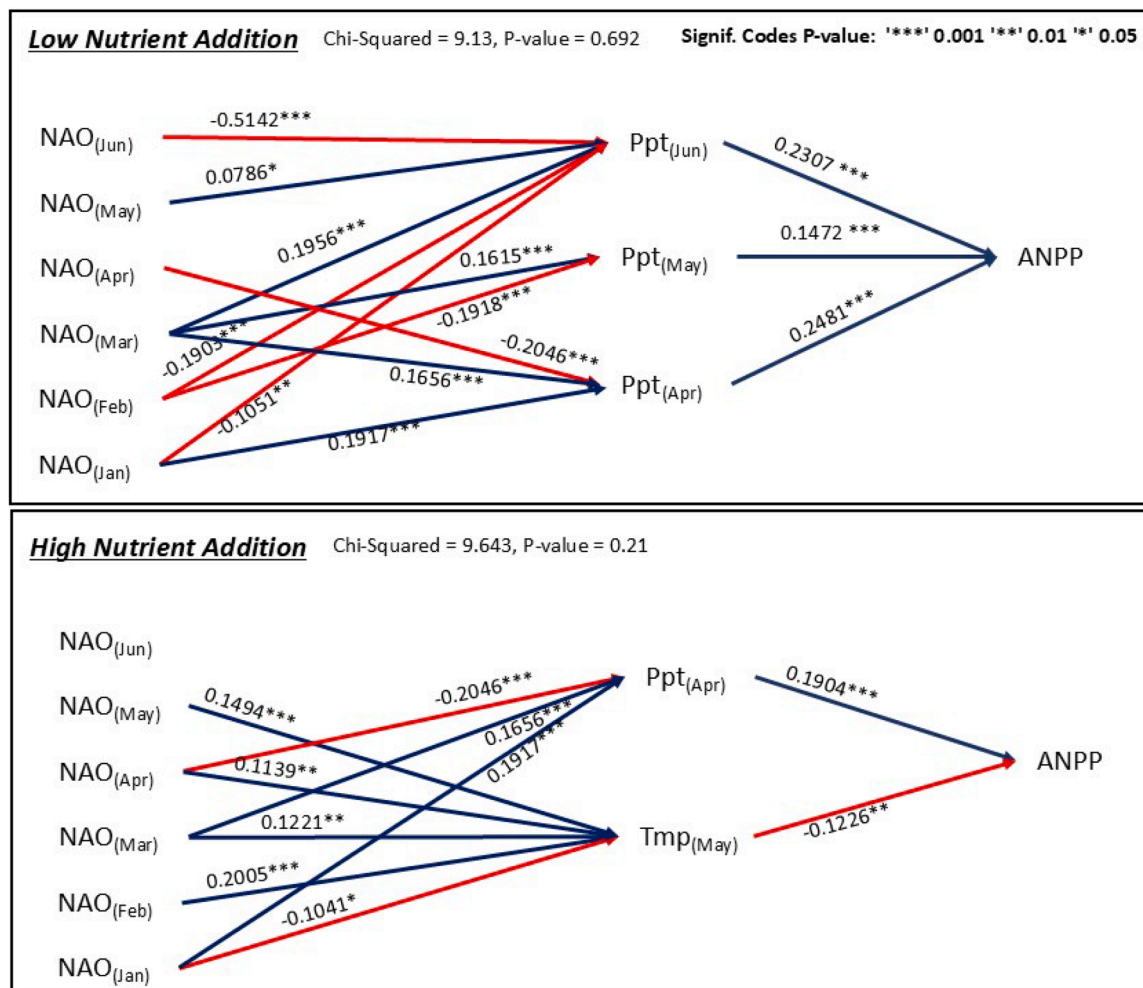
For the study period (1950–2018), an analysis of January, February, and March interannual dynamics revealed a shift in the NAO signal from an initial sequence characterized by negative values to a final sequence dominated by positive ones (Fig. 2a). Conversely, in the spring-to-summer transition from 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. Temperatures showed an overall increase across all years, with the most pronounced warming occurring during the winter months (January and February) and in April. (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. Conversely, under the low nutrient level, ANPP gradually increased (Fig. 2d).

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 NAO 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.

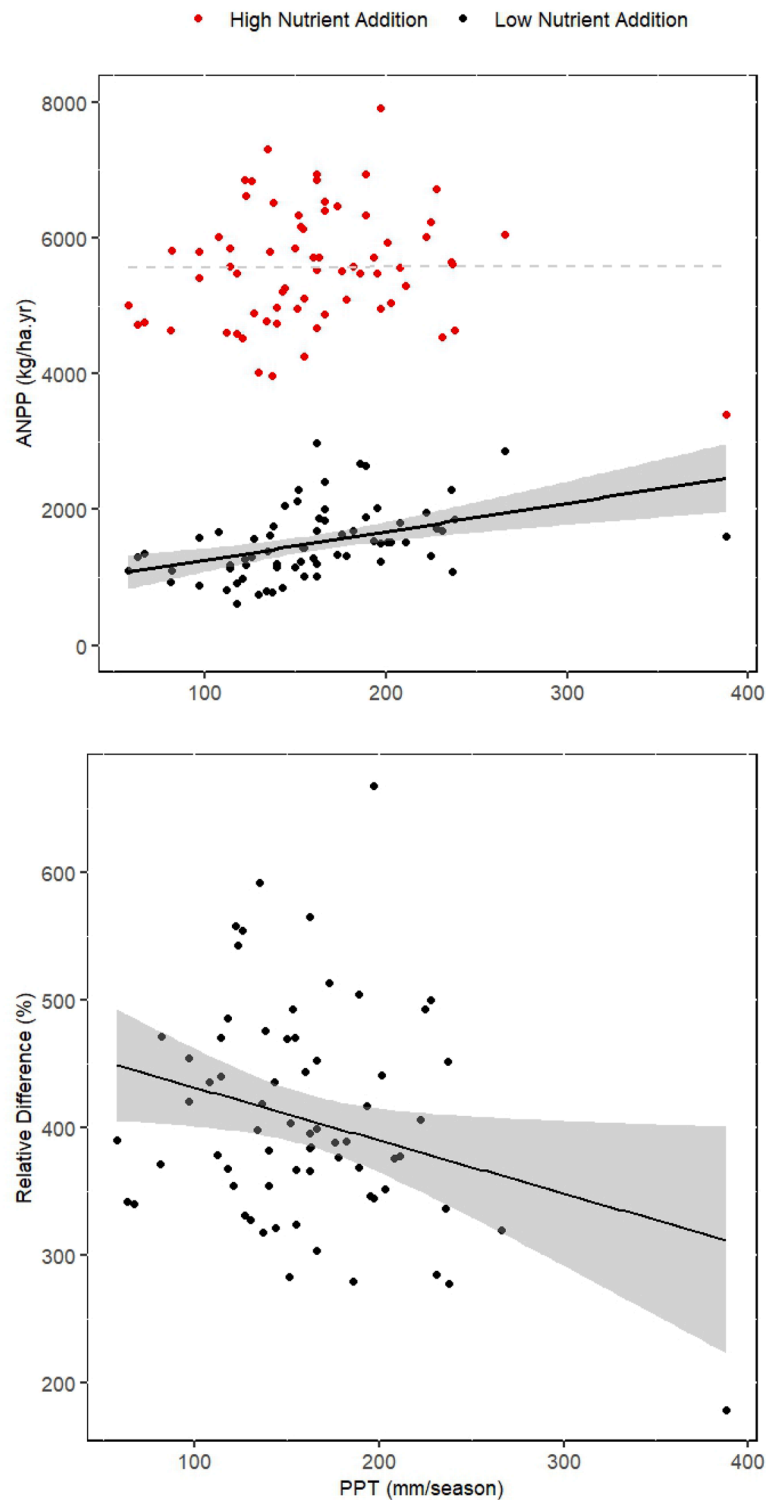
Under ‘high’ nutrients addition, the NAO signal exerted a small influence on ANPP (predicted vs observed fitted parameters,  $R^2$ : 0.17, P-value = 0.001) through April precipitation and, different from the low nutrients’ situation through May temperature (Fig. 3). Here, ANPP



**Fig. 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.

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 described 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.



**Fig. 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 ( $\text{ANPP} = 4.20\text{PPT} + 831.8$ ;  $p < 0.001$ ; Adjusted  $R^2: 0.17$ ). Relative Difference ( $\text{RD} (\%) = -0.41\text{PPT} + 472.85$ ;  $p = 0.03$ ; Adjusted  $R^2: 0.05$ ).

### 3.2. 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  $\approx 100$  mm and dropped to below 100 % when precipitation reached  $\approx 400$  mm (Fig. 4).

The stability of ANPP ( $1 / CV$  interannual) 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). Furthermore, plots under high nutrient addition showed lower species richness and dominance by grasses, with near absence of sedges and rushes. In contrast, low nutrient plots exhibited higher richness and functional diversity (Table 1). Despite this, ANPP stability was higher in high nutrient plots, suggesting a decoupling of the classical stability-diversity relationship.

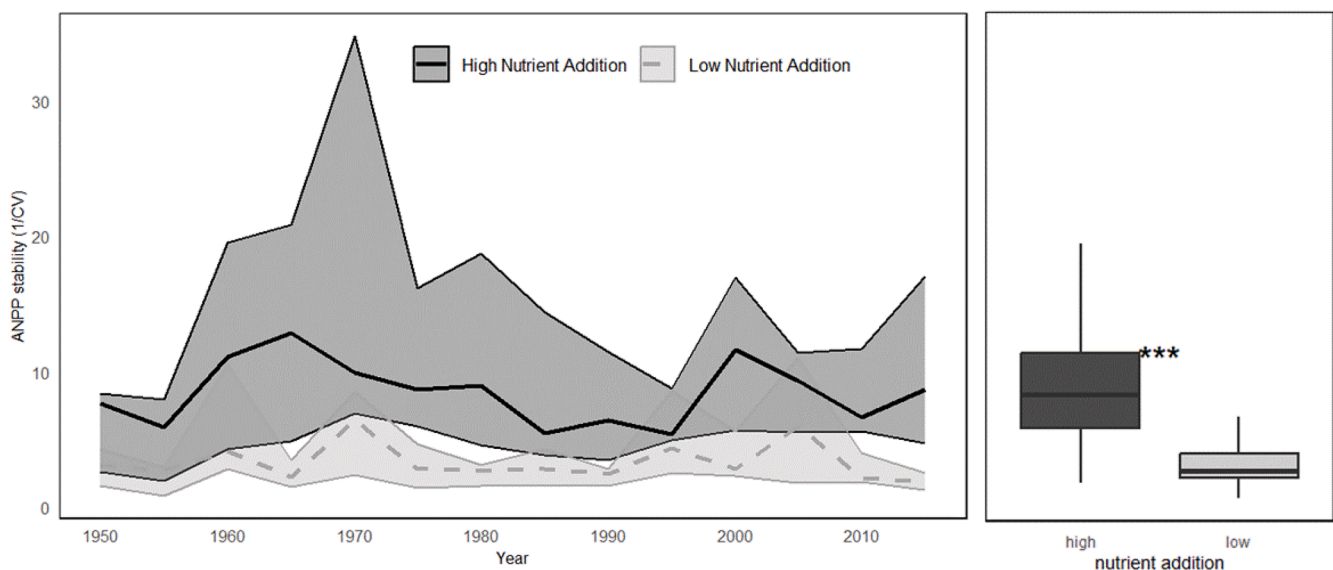
## 4. Discussion

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, but this association was found to be statistically significant only in the low-nutrient treatment. This result directly counters the suggestion that precipitation variability exerts a weak influence, instead indicating that its importance is conditional on the system’s nutrient status. 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

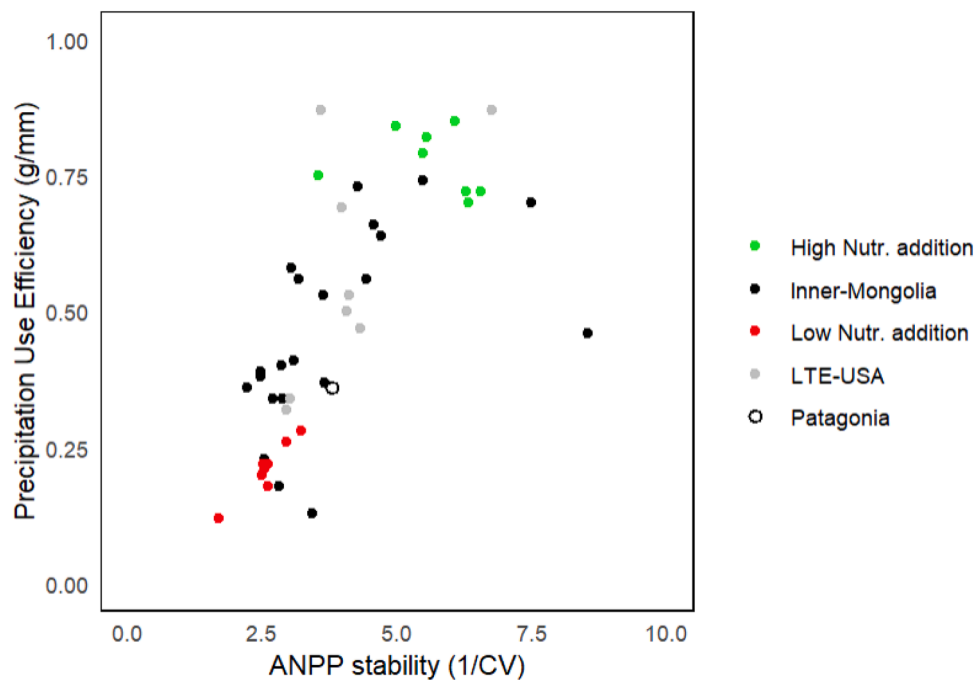
precipitation (under low fertilization), to one mediated by precipitation and temperature (under high fertilization). On the other hand, via a relative effect analysis, the effect of nutrient addition on ANPP was greater under low precipitation.

The reduced dependence on water availability appears to reflect a fundamental shift in resource-use strategy following chronic fertilization. A plausible physiological interpretation aligns with the “least-cost” hypothesis of photosynthesis (Wang et al., 2017), which describes how plants balance the marginal costs of nitrogen investment in carboxylation and water loss through stomatal conductance to minimize the overall cost of carbon assimilation. Under low nutrient availability, this balance may favour higher stomatal conductance and stronger precipitation sensitivity, whereas long-term nutrient enrichment could relax nitrogen constraints, leading to dominance by dense, fast-growing canopies whose productivity is less dependent on interannual water variation. Such changes might reduce climatic sensitivity through structural and compositional feedback rather than through direct resource substitution. Although speculative, this perspective aligns with the long-term divergence observed at Park Grass and offers a physiological framework linking nutrient-driven community shifts to altered ANPP–climate relationships (Prentice et al., 2014; Wang et al., 2017). These findings also underscore the importance of considering global climate drivers in ecosystem models, particularly under scenarios of reduced nutrient input and highlight that the significance of precipitation is lost after decades of nutrient saturation. The NAO–ANPP interaction provides a mechanistic link between large-scale atmospheric variability and local ecosystem functioning, which is critical for forecasting productivity under changing climate and management regimes.

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



**Fig. 5.** Temporal stability of aboveground net primary productivity (ANPP) estimated as  $1 / CV$  interannual, where  $CV = \mu/\sigma$ , over a five-year window across the study period (1950–2018). Solid and dashed lines 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.



**Fig. 6.** Relationship between precipitation use efficiency (PUE; ANPP / mean annual precipitation) and ANPP stability ( $1 / \text{inter-annual relative variation, CV}$ ) 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  $< 0.0001$ ).

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. The stronger NAO–ANPP signal under low nutrient conditions suggests that fertilization may buffer ecosystems against climate variability. This has practical implications: in regions where fertilizer use is being reduced due to environmental or economic constraints, understanding teleconnection impacts becomes increasingly relevant for predicting productivity and planning adaptive management.

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.

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 (Diriham 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.

## 5. 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.

## CRedit authorship contribution statement

**JGN Irisarri:** Writing – review & editing, Writing – original draft, Validation, Supervision, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **M Texeira:** Writing – review & editing, Methodology, Investigation, Formal analysis, Data curation. **P Harris:** Writing – review & editing, Investigation, Formal analysis, Conceptualization. **PE Gundel:** Writing – review & editing, Visualization, Methodology, Investigation, Conceptualization. **AL Collins:** Writing – review & editing, Supervision, Methodology, Funding acquisition, Formal analysis.

## Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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## Data availability

All data is publicly available.

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