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THE RESPONSE OF SUB-MEDITERRANEAN GRASSLANDS TO RAINFALL VARIATION IS INFLUENCED BY EARLY SEASON PRECIPITATION

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Running head: Effects of precipitation variation on productivity

Abstract

Question: Climate change will likely modify patterns of precipitation, with an expected increase of intra-annual variability and increased frequency and magnitude of extreme events. The Mediterranean area is expected to be very sensitive to such events as water availability is already limited. However, the effect of precipitation variability on ecosystem services, such as plant productivity, is widely unknown.

What is the short-term effect of an experimental precipitation gradient on the above ground net primary productivity (ANPP) of two contrasting sub-Mediterranean grassland ecosystems? Are there effects of different intra-annual rainfall patterns, i.e. dry or wet early season (spring), on the ANPP? Do the functional groups of grasses and forbs differ in their reaction?

Location: Torricchio Nature Reserve, Central Apennines, Italy.

Methods: We selected two grasslands characterized by contrasting conditions in geophysical and soil chemical parameters (north- and south-facing slopes). In both sites, during two climatically different years, mid-season (summer) precipitation was manipulated in order to obtain a gradient of rainfall availability, comprising additional rainfall, ambient rainfall conditions and rainfall reduction. The above-ground biomass, subdivided according to the functional groups of forbs and grasses, was collected at the end of each treatment period.

Results: A significant increase of the ANPP due to experimental increase in summer rainfall appeared in the year with the wet spring, but only in the mesic north-facing slope. This response was driven by the increased productivity of perennial forbs while grasses showed a stable aboveground production. On the contrary, we found no positive effect of experimental increase in summer precipitation on ANPP in the year with the dry spring. The variability of the ANPP increased significantly in the xeric south-facing slope in the year with the wet spring, most likely reflecting indirect effects of small-scale heterogeneity such as variations in soil depth.

Conclusions: Intra-annual precipitation variation can have noticeable implications for sub-Mediterranean montane grassland agriculture: livestock pressure should be limited in years with an irregular spring drought, regardless of summer precipitation, especially in mesic grasslands.

Keywords: ANPP; Climate change; Experiment; Functional group; Precipitation variation; Intra-annual rainfall; Drought.

INTRODUCTION

Water availability is the main constraint to plant productivity in many terrestrial biomes (Heisler-White 2008; Hsu et al. 2012) and it is an ecosystem driver that will be strongly affected by climate change (Houghton et al. 2001). In addition to changes in mean annual precipitation, general circulation models predict increases in the intra-annual (seasonal) variability of precipitation (Hsu et al. 2012), with potential effects on plant productivity according to the timing and size of precipitation inputs (Swemmer et al. 2007; Heisler-White et al. 2009). In particular, the impact of precipitation variability on grassland productivity represents a topic of current concern due to its relevance for agricultural activities (Grime et al. 2000).

Endeavours to understand the effect of precipitation variability on productivity of grasslands include different methodologies, i.e. studying temporal and spatial natural gradients (Nippert et al. 2006; Golodets et al. 2013) as well as manipulative experiments (Fay et al. 2003; Holub et al. 2013; De Boeck et al. 2015). Experimental studies on the effects of precipitation variation have mainly been performed in European temperate grasslands and the North American temperate tallgrass prairie. From the European systems it has been concluded that aboveground productivity is hardly affected by rainfall variability (Grime et al. 2008; Jentsch et al. 2011; Dengler et al. 2014). Effects were seen in the North American tallgrass prairie where changes in rainfall, i.e. less frequent rainfall and/or a reduction of the amount of rain per rainfall event, had a negative influence on plant productivity (Fay et al. 2003). However, up to our knowledge and according to the review of Miranda et al. (2011), there are no studies on grasslands in the Mediterranean basin which represents a climatic transition zone between the temperate mid-latitude and the tropical dry climate. This represents a crucial research gap, given the assumed high sensitivity of Mediterranean systems to climatic alterations (Jongen et al. 2011). In the Mediterranean environment, water to support primary productivity is a limiting factor, making it highly likely that grassland productivity is affected by precipitation variation (Suttle et al. 2007; Jongen et al. 2011). Considering the relevance of plant functional aspects in this context (Wellstein et al. 2011), different plant functional groups, such as forbs and grasses, can respond differently to precipitation variation, which may in turn influence productivity (Zavaleta et al. 2003). Also, xeric versus mesic site conditions can make a difference for the response of productivity to precipitation variation (Holub et al. 2013; Knapp et al. 2008; Swemmer et al. 2007). Mediterranean montane regions are characterized by large topographic complexity as well as marked water availability gradients (Lavorel et al. 1998) calling for the consideration of local site conditions when studying precipitation effects on grassland productivity.

In this contribution, we evaluate the effects of experimentally induced gradients of water availability on aboveground net primary productivity (ANPP) of a representative sub-Mediterranean montane grassland landscape of the central Apennine Mountains (Torricchio Nature Reserve, Italy). We compare the effects of experimental precipitation variation in two contrasting calcareous perennial grasslands with mesic (north-facing slope with deeper soil) and xeric (south-facing slope with extremely shallow soil) site conditions (Wellstein et al. 2013). Contrasting spring weather conditions during the two-year study period (2011, 2012) allowed us to examine the influence of spring precipitation on the response of ANPP to summer rainfall variation.

We expect (H1) that ANPP should increase with increasing summer precipitation, although (H2) varying spring precipitation and (H3) dry (S-facing) vs. mesic (N-facing) grassland systems may influence the response. In addition, (H4) we expect that different functional groups should respond differently, with forbs being more responsive. Lastly, (H5) we assume that the variability of ANPP should be highest on the dry and heterogeneous S-facing slope.

MATERIALS AND METHODS

Study area

The Torricchio Nature Reserve (Central Apennines, Italy; Appendix S1) provides montane calcareous grasslands on Jurassic-Cretaceous limestone and is under protection since 1970; previously, the grasslands were grazed. Mean annual precipitation reaches 1,250 mm and mean annual temperature is around 11 °C (Halassy et al. 2005).

We selected two study sites with an area of about one hectare each, representing the contrasting environmental conditions of the mesic north- and the xeric south-facing slope (Wellstein et al. 2013, Appendix S1, S2, S3). The south-facing site is characterized by a shallow/skeletal soil with low water holding capacity and higher soil heterogeneity compared to the north-facing slope (Wellstein et al. 2013). For details on the vegetation see Wellstein et al. (2014).

Experimental design

In both sites, the precipitation manipulations consisted of a gradient of rainfall availability, comprising additional rainfall (A, additional), ambient rainfall (C, control) and rainfall reduction (D, decreased rainfall). At each site, five plots were established with a distance of at least twenty meters between each other. Each plot was composed of three 1 m x 1 m sub-plots: one sub-plot in the centre of a 4 m^2 roof to simulate rainfall reduction (D); one sub-plot downstream the rainout shelter to simulate additional rainfall by receiving the additional rain which has fallen on the slope-parallel inclined roof and dropped in the centre of the sub-plot (A); one sub-plot under ambient rainfall conditions (C). Roofs were constructed with a steel frame and covered with transparent 3 mm plastic foil that permitted over 93% penetration of photosynthetically active radiation (PAR).

The duration of precipitation manipulations has been estimated applying the method of extreme value distributions (1000-year event; Jentsch et al. 2007) using climate data series covering 50 years. For the Torricchio Nature Reserve, the 1000-year drought event resulted in 58.5 days without precipitation. The experiment covered two consecutive years (2011 and 2012). According to the determined length of the extreme drought period, sub-plots with shelters were roofed from May 31^{st} to July 27^{th} 2011, and from May 22^{nd} to July 20^{th} 2012.

Following Ashcroft and Gollan (2013) we measured the microclimatic conditions of the soil. Soil temperature and relative humidity (RH) of the soil air were measured during the second year every two hours at high resolution (DS1923 iButton Hygrochron Temperature/Humidity logger, Maxim Integrated, San Jose, CA, USA; precision of 0.0625 °C/0.04% RH) at both slopes directly below the soil surface (-1 cm) with a replication of two per treatment. General meteorological data was provided by the local meteorological station of the Torricchio Nature Reserve.

The total above-ground biomass was collected in a sampling area of 400 cm² (10 cm × 40 cm) in each sub-plot once a year at the end of the treatment period (peak biomass harvest, a common measure for ANPP). The size of the sampling area was used in previous similar studies in Mediterranean grasslands (Golodets et al. 2013). Biomass samples were subdivided into the functional groups of forbs and grasses, oven dried (48 hours at 80 °C) and weighed.

Seasonal patterns of ambient rainfall

A detailed report on the timing and amount of ambient precipitation in each study year is given in Appendices S4 and S5. From these data it emerges that the rainfall pattern was completely different between study years, with the first year (2011) having a higher shortage of water underneath the roofs and a higher amount of water in the additional rainfall sub-plots during treatment. With respect to the local average precipitation of the season (Venanzoni 2003), the spring of 2011 was very dry while that of 2012 showed a higher level of precipitation (see Appendix S5 for details).

Data analysis

The hypotheses H1, H2 and H3 were tested using for each study year (2011, 2012) and each system (mesic, xeric) a trend-test for a monotonic trend, namely the Jonckheere-Terpstra Test (R package *DescTools*) (Jonckheere 1954; Terpstra 1952). To test H4, statistical tests were repeated for the functional groups of grasses and forbs separately. H5 was tested using a trend-test for monotonic trend in variance suggested by Neuhauser and Hothorn (2000) (R package *lawstat*) for the total as well as for the functional group ANPP .

For each trend test, we applied Bonferroni correction as we tested two grassland systems and two years, resulting in a significance threshold of $\alpha = 0.0125$ (= 0.05 divided by 4 tests). Furthermore, to test the effect of ambient rainfall on ANPP, we compared the productivity in control sub-plots between the two years in each slope.

For the relative humidity of the soil air, daily mean values were calculated for each site (slope), and treatment. For the soil temperature, differences between roofed and non-roofed sub-plots were tested using the Mann-Whitney U-test. Prior to analysis, both temperature and humidity observations of the iButtons were corrected using internal, sensor specific, factory supplied calibration data (iButton – DS1923). As the iButtons can saturate under humid conditions producing values higher than 100%, the humidity observations were corrected applying a scaling and correction procedure (Ashcroft and Gollan 2013).

All tests were performed using the software R 3.0.3 (R Development Core Team 2014).

RESULTS

Effects of treatments on micro-climate

The relative humidity of the soil air generally decreased during the season from spring to summer in all treatments during the experiment (Fig. 1). Differences between treatments were visible at both slopes with lower relative humidity values occurring in rainfall reduction treatment and higher values in the additional rainfall treatment. Shelters had a significant effect on soil temperature. The mean difference between roofed and non-roofed plots in the north-facing slope (-1 cm) was 0.66°C ($p = 0.009$) and in the south-facing slope 1.02°C ($p = 0.014$).

Effects of treatments on productivity

A comparison of the ambient rainfall plots (C sub-plots) was made to show the differences between the two study years under ambient conditions: the year with the wet spring (2012) showed significantly higher total ANPP under ambient rainfall than the year with the dry spring (2011). These significant differences were seen in both grassland systems but were higher in the north-facing slope (ANPP increase by 75%; $p = 0.019$) than in the south-facing slope (ANPP increase by 16%; $p = 0.049$).

When testing the hypotheses on the effect of the rainfall gradient on ANPP, the total ANPP showed no significant response to the gradient of rainfall availability in the year with the dry spring in either study system (Table 1, Fig. 2a,b). A significant increase of ANPP with increasing rainfall availability was seen, however, in the year with the wet spring (2012) and this was only apparent in the grassland system of the north-facing slope (Table 1, Fig. 2a). There the total ANPP increased by more than one half (52%) with increasing rainfall availability while no significant changes of ANPP were seen at the south-facing slope (Table 1, Fig. 2b). When testing the functional groups separately, a significant increase was found only for the forbs in the north-facing slope while the grasses showed no changes in aboveground production (Table 1, Fig. 3).

The total ANPP showed a significant increase in variability with increasing rainfall availability in the second year of precipitation manipulation only on the south facing slope (Table 2). When looking at the functional groups of forbs and grasses on this slope, a significant increase in variability with increasing rainfall availability was seen only for the grasses (Table 2). The forbs showed a significant increase in the variability of ANPP only on the north-facing slope in the second year (Table 2).

DISCUSSION

Microclimate

During the two seasons of weather manipulation, fixed shelters proved to be effective tools for altering the amount of rainfall. Judging from the limited sample size of relative humidity of the soil air measurements, the treatment led to continuous differences in the levels of relative humidity of the soil air directly below the soil surface (Fig. 1). While values of relative humidity of the soil air close to 100% have no effect on plants, strong drops indicate strong changes in the water availability for plants as the permanent wilting point of plant species is highly sensitive to changes in relative humidity of the soil air (Lal and Shukla 2004).

The increase in relative soil air humidity during rainfall events in the rainfall reduction treatment (Fig. 1) depends probably on water runoff during major precipitation events. However, we did not aim to test for total exclusion of water availability but rather aimed to establish a gradient of water availability.

Furthermore, temperature alterations observed under the rainout shelters were relatively low and generally comparable to those seen in other fixed shelter designs (Fay et al. 2000 and references therein).

Early season precipitation conditioning ANPP

The positive response of ANPP towards experimental precipitation increase was seen only in the year with the wet spring (2012), rejecting H1 and confirming H2, and only on the mesic north-facing slope, confirming H3. This effect was seen despite the lower summer water availability during the experiment in 2012 compared to 2011 (Appendix S5). This confirms the findings of Swemmer et al. (2007) and Heisler-White et al. (2009) reporting that the distribution and size of precipitation events can affect ANPP independently of the precipitation amount. The fact that the response was significant only in 2012 is more likely related to the climatic differences of the spring prior to the experiment than to the recurrence of the treatments. This is supported by the significantly higher ANPP under ambient conditions in 2012 than in 2011. The response of ANPP towards experimental precipitation increase in the year with the wet spring is in line with the findings of both experimental and modelling studies. Epstein et al. (1999) found that the precipitation seasonality is the most important factor accounting for variation in ANPP in a model simulation and Suttle et al. (2007) report dramatic changes in Mediterranean grassland productivity after spring water addition.

Looking into the mechanisms behind the relevance of the water availability in spring for plant growth, we hypothesize that in the studied sub-Mediterranean context the physiological and morphological plant adaptation at the beginning of the growing season leads to a higher growth potential. This capacity can then be used to raise productivity under increased precipitation in summer. The review of Zeppel et al. (2014) emphasizes that the seasonal distribution of precipitation influences processes triggering plant growth such as tiller production, root-shoot biomass, root depth, canopy leaf area, stomatal conductance and photosynthesis.

Evidence of adaptation capacity of functional growth traits to fine-scale environmental variation (Wellstein et al. 2013) makes adaptations to environmental variations over time likely, such as changes in plant water availability due to altered precipitation patterns.

Response of ANPP to increased rainfall in mesic vs. xeric grassland

While in the year with the wet spring, the mesic north-facing slope showed a strong increase (> 50%) of the ANPP with experimentally increased precipitation, we did not find such positive effects on the xeric south-facing slope, most likely due to the extremely shallow soil with low water holding capacity (Wellstein et al. 2013). This is in line with the results of Buckland et al. (1997) who claimed that plants growing on shallower soils benefit less of water addition. However, Zavaleta et al. (2003) found that the timing of rainfall events and midseason droughts can influence species productivity in a relatively xeric Mediterranean grassland. In conditions with much higher amount of precipitation (climatic gradient from 90 to 780 mm mean annual precipitation) than in our study, Golodets et al. (2013) demonstrate that arid pastures profited more from increased precipitation during the growing season than mesic ones. Similarly, Holub et al. (2013) found a significant effect of increased water availability at the driest site, while the moistest site did not respond. These contrasting findings reinforce the hypothesis that it might generally depend on ecosystem properties such as soil characteristics as well as on the amount of precipitation variation whether ANPP reacts to rainfall variation or not.

Forbs vs. grasses response in ANPP

Looking into the functional groups, we found that forbs profit more from increased water availability than grasses as a significant ANPP increase was found only for forbs (Tab. 2, Fig. 3) confirming H4 for the mesic north-facing slope in the year with the wet spring. This finding is in line with results of another study showing that increased precipitation enhanced forb production but affected grasses little (Zavaleta et al. 2003). The study of Suttle et al. (2007) also points towards the hypothesis of the responsiveness of forbs to precipitation demonstrating that the strongest initial productivity response after an extended spring rainfall is by forbs followed by a more complex community response in the subsequent years. Our result of a stable productivity of grasses was also seen in other systems (Fay et al. 2003). Our findings emphasize the importance to include plant functional aspects when studying the effect of climate change on ecosystem services (Wellstein et al. 2011).

ANPP variability

Only on the xeric south-facing slope the variability of ANPP increased with experimentally increased precipitation in the year with the wet spring (Tab. 2) confirming hypothesis H5 of a higher variability in the system with higher soil heterogeneity (Wellstein et al. 2013). Depending on the fine-scale variability of the water retention capacity of the soil (Wellstein et al. 2013), the plants could or could not profit from rainfall events making a high variability in the ANPP response likely. Looking into the differences of functional groups, we found an increase of ANPP variability with increasing precipitation for the forbs only on the north-facing slope. This result was unexpected as the N-facing slope does not have as high soil heterogeneity as the S-facing slope. . We suggest that plant-plant interactions such as the competition with the dense grass carpet in the mesic system (Wellstein et al. 2014) might be responsible for the significant ANPP variation of forbs meaning that the growth of some, but not all, forb species was affected by competition. However, on the S-facing slope grasses ANPP variability increased, most likely triggered by soil heterogeneity.

CONCLUSIONS

Climate models predict an increase of intra-annual precipitation variability including both the quantity and the timing for the European Mediterranean basin (Bolle 2012). The results of our study show that intra-annual precipitation variation can have important implications for sub-Mediterranean montane grasslands. The relatively low yield of the mesic grasslands could be strongly increased in wet springs. On the contrary, dry springs could inhibit this positive effect by affecting the growth capacity of plants. In particular, functional groups should be considered as they can play a key role in driving these responses.

This might have implications for adapting montane agriculture to climatic change: livestock pressure should be limited in years with an irregular spring drought, regardless of summer precipitation, especially in mesic grasslands. This is in line with the recommendation of Catorci et al. (2012) to strongly reduce grazing in dry periods in sub-Mediterranean grasslands.

Lastly, our results call for caution when interpreting the outcome of experimental climate manipulations as the climatic conditions of the period prior to the experiment can influence the responses of plant species and vegetation. For this reason we encourage studies dealing with precipitation manipulation at the beginning of the growing season.

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List of electronic appendices

Appendix S1. Land use types, topography and position of the plots in in the north-facing and the south-facing slope of the study area.

Appendix S2. Geo-physical characterization of the sampling sites.

Appendix S3. Mean number of species per treatment per year for each sampling unit of each slope

Appendix S4. Estimation of the rainfall, for each treatment and year, from the beginning of the growing season to the end of the experiment.

Appendix S5. General overview of the precipitation patterns in the two experimental years.

TABLES

Table 1

Results of the trend test for monotonic decline in aboveground net primary productivity (ANPP) with reduced rainfall availability (Jonckheere-Terpstra test) in the mesic north-facing (site N) and the xeric south-facing (site S) grassland system in the two years of precipitation manipulation. Results are shown for the total ANPP and for the functional groups of grasses and forbs.

			Aboveground biomass mean (g/m^2)				
site	year	functional group	reduced rainfall	ambient rainfall	additional rainfall	JT test-statistic	p-value
N	2011	all	182	189	215	49	0.118
		grasses	135	155	160	33	0.703
		forbs	47	34	55	42	0.348
N	2012	all	226	332	475	66	**0.001**
		grasses	192	269	273	46	0.199
		forbs	34	63	202	72	**0.000**
S	2011	all	150	187	241	43	0.306
		grasses	119	58	169	47	0.180
		forbs	31	128	72	52	0.066
S	2012	all	139	216	299	54	0.044
		grasses	103	58	157	36.5	0.554
		forbs	36	158	142	59	0.013

Significant p-values are given in bold ($p < 0.0125$ after Bonferroni correction)

Table 2

Results of the Neuhauser-Hothorn test for monotonic trend in variances of aboveground net primary productivity (ANPP) with increasing rainfall availability in the mesic north-facing (site N) and the xeric south-facing (Site S) grassland system in the two years of precipitation manipulation**.** Significant p-values suggest increasing variance with increasing water availability. Results are shown for the total ANPP and for the functional groups of grasses and forbs.

site	year	functional group	test-statistic	p-value
N	2011	all	0.683	0.340
		grasses	2.572	0.023
		forbs	0.600	0.370
N	2012	all	1.915	0.066
		grasses	1.346	0.151
		forbs	3.277	**0.008**
S	2011	all	1.800	0.078
		grasses	1.171	0.191
		forbs	2.168	0.044
S	2012	all	3.715	**0.004**
		grasses	2.999	**0.012**
		forbs	1.763	0.083

Significant p-values are given in bold ($p < 0.0125$ after Bonferroni correction)

FIGURES

Fig. 1. Daily relative humidity of soil air (relative humidity of the soil air %) in the year 2012, measured directly below the soil surface in each treatment at (a) the north-facing slope and (b) the south-facing slope. Arrows represent rainfall events.

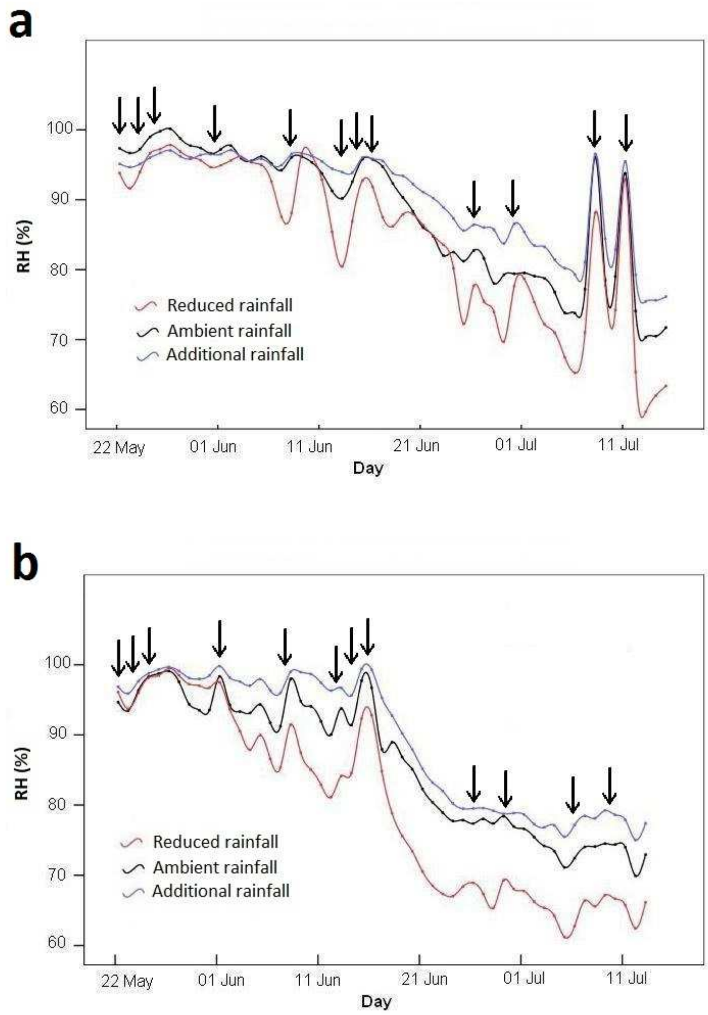

Fig. 2. Aboveground net primary productivity (ANPP) in the mesic north-facing (a, site N) and the xeric south-facing (b, site S) slope for three treatments of precipitation manipulation in each year (2011 in light grey, 2012 in dark grey).

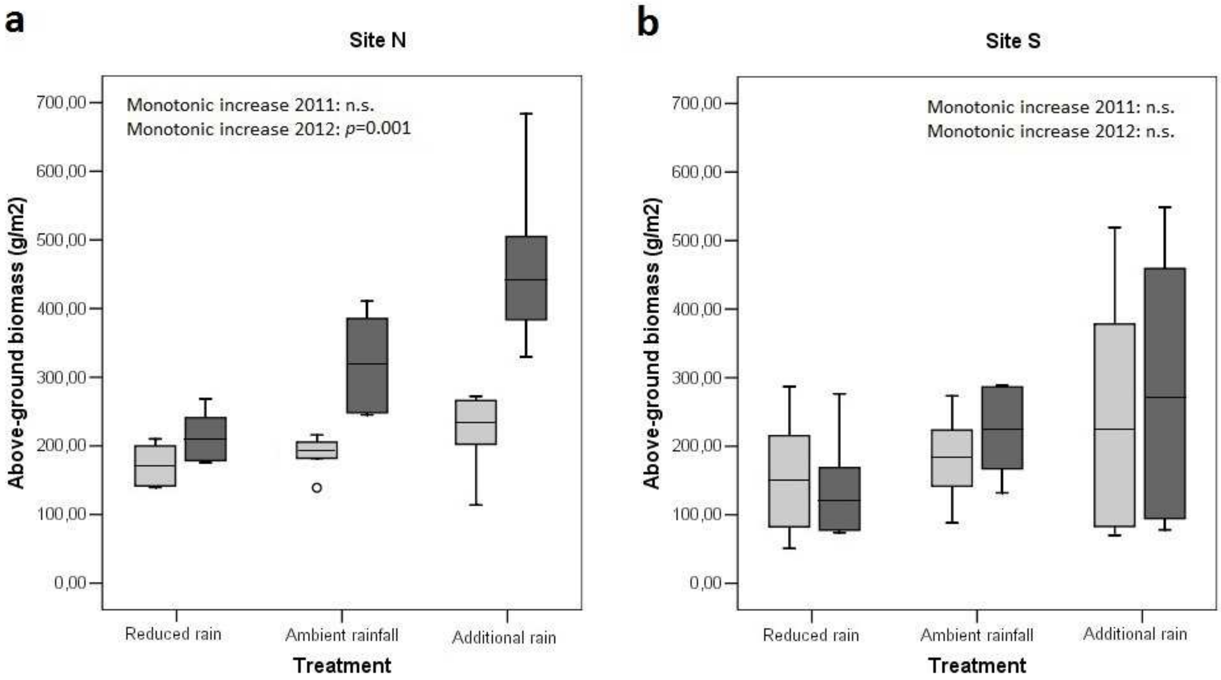

Fig. 3. Aboveground net primary productivity (ANPP) of the functional group of grasses in the north- (a) and south-facing slope (b) and the functional group of forbs in the north- (c) and south-facing slope (d). The ANPP is displayed for the three treatments of precipitation manipulation in each year (2011 in light grey, 2012 in dark grey).