Ónodi, G., Botta-Dukát, Z., Kröel-Dulay, Gy., Lellei-Kovács, E. and Kertész, M. (2018) Reduction in primary production followed by rapid recovery of plant biomass in response to repeated mid-season droughts in a semiarid shrubland. Plant Ecology, 219(5), 517-526. doi: 10.1007/s11258-018-0814-6

Reduction in primary production followed by rapid recovery of plant biomass in response to repeated mid-season droughts in a semiarid shrubland

Ónodi, G.[1,2*], Botta-Dukát, Z.[1,2], Kröel-Dulay, Gy.[1,2], Lellei-Kovács, E.[1] and Kertész, M.[1,2]

[1]MTA Centre for Ecological Research, Institute of Ecology and Botany
Alkotmány 2-4, H-2163 Vácrátót, Hungary
[2]MTA Centre for Ecological Research, GINOP Sustainable Ecosystems Group,
Klebelsberg Kuno 3, H-8237 Tihany, Hungary
*Corresponding author: Ónodi, G.
Email: onodi.gabor@okologia.mta.hu
Phone: ++36-28-360-122/159
Fax: ++36-28-360-122/110

Acknowledgements

This study was funded by the VULCAN project (EU FP5 grant EVK2-CT-2000-00094)), the INCREASE project (EU FP7 grant 227628), the Hungarian Scientific Research Fund (OTKA K112576), and the National Research, Development and Innovation Office (GINOP 2.3.3-15-2016-00019). We are grateful to the Kiskunság National Park (Hungary) for the support of our field work. The authors thank the anonymous reviewers of this manuscript for their valuable comments which have helped us to improve the quality of the paper.

Abstract

The frequency and severity of extreme weather events, including droughts, are expected to increase due to the climate change. Climate manipulation field experiments are widely used tools to study the response of key parameters like primary production to the treatments. Our study aimed to detect the effect of drought on the aboveground biomass and primary production both during the treatments as well as during the whole growing seasons in semiarid vegetation.

We estimated aboveground green biomass of vascular plants in a Pannonian sand forest-steppe ecosystem in Hungary. We applied non-destructive field remote sensing method in control and drought treatments. Drought treatment was carried out by precipitation exclusion in May and June, and was repeated in each year from 2002. We measured NDVI before the drought treatment, right after the treatment, and at the end of the summer in 2011 and 2013.

We found that the yearly biomass peaks, measured in control plots after the treatment periods, were decreased or absent in drought treatment plots, and consequently, the aboveground net primary production was smaller than in the control plots. At the same time, we did not find general drought effects on all biomass data. The studied ecosystem proved resilient, as the biomass in the drought treated plots recovered by the next drought treatment. We conclude that the effect of drought treatment can be overestimated with only one measurement at the time of the peak biomass, while multiple within-year measurements better describe the response of biomass.

Keywords

Aboveground Net Primary Production; Climate change experiment; Drought; Multi-seasonal biomass estimation; NDVI; Semiarid shrubland

Introduction

The ongoing climate change increases the frequency and severity of extreme weather events (IPCC 2013). One of the key ecological parameters affected by changing climate is primary production. Extreme drought events have been shown to reduce primary production in Europe (Ciais et al. 2005) and the increase in drought frequency negatively affected grassland production worldwide (Zhao and Running 2010). At plot scale, climate manipulation experiments are particularly effective way to study ecological consequences of climate change (Wu et al. 2011), especially long-term multi-site field experiments (Kröel-Dulay et al. 2015).

In climate manipulation experiments, effects of precipitation treatments on vegetation performance are often estimated once per year, during or right after seasonal treatments (Köchy and Wilson 2004; Brancaleoni et al. 2007; Mänd et al. 2010; Byrne et al. 2013; Tielbörger et al. 2014). However, the effects emerging in the treatment period may change during the rest of the growing season. Thus, additional within-year measurements may provide further information about the changes in plant biomass, either targeting legacy effects in long-term experiments before the yearly treatments, or aiming to follow the relaxation period after. Aboveground plant biomass may recover after the drought period in semiarid grassland and shrubland communities adapted to high variability in precipitation (Miranda et al. 2011). Even if drought strongly reduces aboveground biomass, it can recover quickly during the late summer, because belowground parts are less affected by the drought (Shinoda et al. 2010). Therefore, treatment effects should be checked multiple times during the growing season.

Conducting multiple within-year measurements on aboveground plant biomass is one of the major challenges in long-term field experiments. For this purpose, application of non-destructive sampling methods is suggested (Gamon et al. 1995). When effects on primary production is in focus, field spectroscopy is one of the feasible solutions for estimating aboveground biomass, or leaf area index (Goodin and Henebry 1997; Pontailler et al. 2003; Mulla 2013; Nestola et al. 2016; Ónodi et al. 2017a). The Normalized Differential Vegetation Index (NDVI) obtained by field spectroscopy is an accurate proxy for aboveground biomass estimations (Gamon et al. 1995; Ónodi et al. 2017b). However, it is rarely applied in multi-seasonal measurements in long-term ecological experiments, but see (Goodin and Henebry 1997; Filella et al. 2004; Boelman et al. 2005; Wang et al. 2016; Nestola et al. 2016).

Our goal was to study the effect of two-month drought treatments (i.e. rain exclusions) on the aboveground biomass, and primary production via proxies (NDVI, and the sum of positive NDVI increments accordingly) both during the treatments as well as during the whole growing seasons. We applied field spectroscopy to observe within-year changes in aboveground green biomass of vascular plants in the semiarid Kiskunság forest-steppe vegetation (Lellei-Kovács et al. 2008a; Kröel-Dulay et al. 2015). According to climate change scenarios for Hungary, the frequency of extreme dry and wet years is expected to increase in the study region (Bartholy et al. 2003; Bartholy and Pongrácz 2007).

Our specific questions were as follows: What is the effect of drought treatment on the aboveground biomass estimate (NDVI) in different seasons in a long-term climate manipulation experiment? What is the effect of drought treatment on annual primary production and production of different seasons, i.e. treatment and post-treatment changes of biomass calculated as the sum of positive NDVI increments?

Methods

Study site and experimental design

Our study site is part of the EU FP5 VULCAN and the EU FP7 INCREASE projects (Beier et al. 2004; Peñuelas et al. 2007; Kröel-Dulay et al. 2015) representing the continental semi-arid forest-steppe vegetation of Central Europe in the multi-site surveys. The site is in the Kiskunság National Park (N46°52’, E19°25’), in a Pannonian sand forest-steppe vegetation mosaic (Lellei-Kovács et al. 2008b) of high plant diversity and nature protection value (Fekete et al. 2002; Molnár et al. 2012). In our study plots, we sampled open grassland patches where also shrubby root suckers of white poplar (*Populus alba*) occurred. The soil is calcaric arenosol which enhances the semi-desert character of the vegetation. Climate of the study area is temperate continental. The vegetation period starts in April and finishes in October. Based on regional 30-years average values (1961-1990), mean annual temperature is 10.4°C, mean monthly temperature ranges from -1.9 °C in January to 21.1 °C in July, while mean annual precipitation is 505 mm with a peak in June (Kovács-Láng et al. 2000).

The climate manipulation experiment described by Lellei-Kovács et al. (2008) were conducted in three replications of controls and drought treatments. The vegetation of the replicates differed from each other in the abundance of poplar shoots, but within each control - drought treatment pair, the plots were similar in this respect. Plot size was 4 m x 5 m, and the experiment started in 2002. Automatically controlled rain exclusion during May and June was applied as drought treatment.

Sampling design and data collection

In our study, we estimated aboveground green biomass of vascular plants (referred as plant biomass hereinafter) by means of NDVI in the control and drought treatment plots in 2011 and 2013. The planned 2012 measurements had to be cancelled for technical reasons. We applied a multi-seasonal non-destructive plant biomass sampling method (Fig. 1). As the first step, we measured a baseline of the plant biomass at the beginning of the vegetation period of the first year (M0 in Fig. 1), when plant activity is still very low as the soil surface is covered by litter. Afterwards, we estimated the plant biomass three times a year: at the turn of April and May (before treatment measurement, M1), at the turn of June and July (after treatment measurement, M2) and after a relaxation period at the turn of August and September (end-of-summer measurement, M3). Precipitation was monitored in all plots separately. Rain exclusion data were calculated as differences between average values collected in the three control and the three drought treatment plots. Annual and monthly precipitation data were calculated as average values of the control plots (Online Resource 1).

In 2011, drought treatment started at 30 April and ended at 07 July. During this period we excluded 88.8 mm out of the 112.8 mm precipitation (78.7%). Annual precipitation in 2011 was 408.0 mm. Dates of the biomass estimation measurements were: (M0) 01 April, (M1) 02 May, (M2) 28 June, and (M3) 30 August.

In 2013 drought treatment started later, it was conducted between 15 May, and 30 June. During this period we excluded 111.7 mm out of the 118.4 mm precipitation (94.4%). However, 30.6 mm rain was not excluded during the first two weeks of May. Annual precipitation in 2013 was 597.8 mm. Dates of the biomass estimation measurements were: (M1) 29 April, (M2) 10 July, (M3) 04 September. Thus, 111.7 mm precipitation out of 149.0 mm (75.0%) was excluded between the M1 and M2 measurements.

We estimated the amount of plant biomass by non-destructive field spectroscopy techniques in each measurement event (Online Resource 2). We applied a portable Cropscan MSR87 multispectral radiometer (Cropscan, Inc., Rochester, MN) for measuring incoming and reflected light intensity. We used an aluminium frame for moving the sensor above the plots at a height of 1.5 meter. In each of the six plots (three control and three drought treated plots) we sampled twelve subplots arranged in a 3 x 4 grid. The area of the circular subplots were 0.44 m^2 (diameter: 0.75 m), and the distance between centre points of the neighbouring subplots were 1 meter. The frame allowed us to repeat the sampling of each subplot at the same position during the different measurement events. We calculated NDVI (Rouse et al. 1974) values based on the measured light intensity data at red (660 nm) and near infrared (810 nm) wavelengths. According to our previous investigation, NDVI provides an accurate proxy for plant aboveground green biomass estimation in the studied vegetation complex (Ónodi et al. 2017b). Thus, differences in NDVI values are interpreted as differences in aboveground green biomass henceforth. Baseline NDVI data collected at the first (M0) measurement event ($NDVI_{AVG \pm SE} = 0.205 \pm 0.003$) provides an empirical zero point for calculation of increments of yearly plant biomass. The 0.205 average is in agreement with our long term experience (Ónodi et al. 2017a) and the low standard error value we got shows that the baseline is not sensitive to the differences in litter cover and composition. We consider the increase in NDVI as proxy for aboveground primary production. Thus, we count the sum of the positive increments as proxy for the annual aboveground net primary production (ANPP), according to Sala and Austin (2000).

Statistical analyses

In the first analysis, dependence of the measured NDVI values on treatments, years and measurement events and their interactions (including three-way interaction) were analysed by fitting linear mixed models (Zuur et al. 2009). In this analysis, subplots nested in plots were random factors in the model, since simplification of the random part would result in higher AIC values. In order to avoid this, while not losing the inside-plot variation information, we applied the nested design, in line with Colegrave and Ruxton (2018). Significance of fixed factors was tested by maximum likelihood ratio tests (Zuur et al. 2009).

The following null-hypotheses were tested using contrasts. The hypothesis 1 refers to the measured NDVI values in each sampling date. The hypotheses 2-4 refer to the changes of the NDVI values in time, and they are arranged into pairs where (a) probe whether there is significant increase or decrease in the given time span at the level of a certain treatment, and (b) compare the changes between control and drought.

1 NDVI values in control and drought treatments do not differ (tested in each measurement event);
2 (a) changes in NDVI between M1 and M2 (hereafter called treatment change) do not differ from zero;
2 (b) treatment changes do not differ between control and treatment plots;
3 (a) changes in NDVI between M2 and M3 (hereafter called post-treatment change) do not differ from zero;
3 (b) post-treatment changes do not differ between control and treatment plots;
4 (a) changes in NDVI between M1 and M3 (hereafter called whole-season change) do not differ from zero;
4 (b) whole-season changes do not differ between control and treatment plots.

P-values were corrected by single-step procedure (Hothorn et al. 2008) to avoid their inflation due to multiple testing.

In the second analysis, the sum of positive NDVI increments for each subplot, as a proxy for ANPP was the dependent variable, while year and treatment were fixed factors in the model. The random part was the same as in the previous analysis. Significance of fixed factors was tested by series of maximum likelihood ratio tests (Zuur et al. 2009).

All calculations were done in R statistical environment (R Core Team 2017) using nlme (Pinheiro et al. 2017), multcomp (Hothorn et al. 2008) and lsmeans (Lenth 2016) add-on packages for fitting models, doing post-hoc tests and drawing figures, respectively.

Results

We found significant three-way (treatment × year × measurement event) interaction (likelihood ratio = 12.875, d.f. = 2, p = 0.002) on the NDVI data, thus treatment effects had to be tested in each sampling time by post-hoc test using contrasts. Post-hoc tests showed that drought treatments significantly affected NDVI values after treatment measurements (M2), in both years and also at the end-of-summer measurement (M3) in 2013 (Table 1, upper six rows, NDVI with C vs. D comparisons). However, the differences are not significant in the other sampling times, even if NDVI values were higher in control plots in all six measurement events (Fig. 2, positive estimates in Table 1).

Regarding the increase or decrease of plant biomass between the measurement events, we found significant increase of NDVI values during the treatment change (M2-M1 in Fig. 3; M1 vs. M2 in Table 1) and its significant decrease during the post-treatment change (M3-M2 in Fig. 3; M2 vs. M3 in Table 1) except the drought treatment in 2011. There were no significant changes in the NDVI values in the whole-seasons (M3-M1 in Fig. 3; M1 vs. M3 in Table 1).

Regarding the treatment effects on the changes of plant biomass during the treatment periods, we found significantly higher biomass increase in the control than in the drought treatment in both years (M2-M1 in Fig. 3; C vs. D comparisons of ΔNDVI (M2-M1) in Table 1). In the post-treatment periods the plant biomass decrease was significantly greater in the control than in the drought treatment in 2011 (M3-M2 in Fig. 3; C vs. D comparisons of ΔNDVI (M3-M2) in Table 1).

In the analysis of the sums of the positive increments as proxy variables for ANPP (Fig. 4), the two-way interaction between treatment and year proved to be significant (likelihood ratio = 8.809, df = 1, $p = 0.003$). Effect of treatment (likelihood ratio = 16.046, df = 1, $p < 0.001$) was significant in both years (2011: $z = 2.224$, $p = 0.040$; 2013: $z = 3.823$, $p < 0.001$), however it was stronger in 2013 ($t = 3.018$, df = 70, $p = 0.004$).

Discussion

Based on multiple NDVI measurements, we found consistent negative effects of drought treatment both on yearly peak plant biomass and on the ANPP, in line with Estiarte et al. (2016) and Reinsch et al. (2017). Drought treatment decreased the biomass in both years in June (M2 in Fig. 2), and at the end of summer in 2013 (M3 in Fig. 2). However, NDVI values showed no overall significant treatment effect. Treatment and measurement event had interactive effects on biomass, similarly to Hoover et al. (2014) who also found both significant year effect and significant year × drought treatment interactions in their two-year extreme drought and heatwave experiment in central U.S. grassland. In our study, we showed that besides the significant treatment effect in June, the plant biomass did not differ in the treated and the control plots at the beginning of the studied vegetation periods (M1 in Fig. 2) and at the end of summer in 2011 (M3 in Fig 2). The treatment and post-treatment changes of NDVI values (Fig. 3) show also strong effects of drought. While the biomass increased markedly in the control plots, we did not find increment in drought plots in both years (M2-M1 in Fig. 3), only in 2013, when it was significantly less than in the control. Furthermore, the post-treatment biomass decrease was also less in 2011 compared to the control (M3-M2 in Fig. 3). Consequently, the estimated ANPP decreased in the case of our drought treatment (Fig. 4), similarly to the findings of most studies in arid or semiarid ecosystems (Beier et al. 2012).

The NDVI values responded sensitively to the treatments. The detected treatment effects depended on the relative timing of treatments and measurement events. Delay of starting the treatment resulted in detection of significant biomass increase during the treatment period also in the drought treatment plots in 2013 (M2-M1 in Fig. 3), even if this increase was significantly smaller compared to that in the control plots. We assume that the reason for the biomass increase is that the study site had 30.6 mm precipitation during the two weeks long delay period, which promoted significant vegetation growth also in the drought treated plots.

We applied multiple sampling of biomass in a year in order to gain deeper knowledge on the pattern of plant biomass changes in grasslands. First of all, multiple biomass estimates are required for monitoring the amount of biomass in the course of the vegetation season, revealing which periods of the growth season were affected by the treatment. We found that drought eliminated peak biomass in June (M2 in Fig. 2, as well as M2-M1 in Fig. 3), characteristic for the open sand grasslands (Kovács-Láng 1974), while it has slight or no effect at early and late season stages. On the other hand, multiple estimates are required for assessing the primary production following the method of the sum of positive increments in plant biomass (Sala and Austin 2000). This allows a more reliable comparison of ANPP than estimation only using a measurement of peak biomass (Scurlock et al. 2002). The method we applied is based on the calculation of the positive increments between repeated measurement events and it needs an estimate for the baseline. For this purpose, we executed a sampling plan which covers the starting point (M0) and three measurement events (M1, M2, M3) during the vegetation period. Application of the sum of positive increment method allowed us to take the biomass at the time of all the three measurement events into account. Besides the already mentioned drought effect (Fig. 4), we detected that difference between ANPPs in control and drought plots was higher in 2013. This is in accordance with the fact that spring precipitation in 2013 was much higher than in 2011 (Fig. 1), which resulted in higher peak biomass in the control. Furthermore, the late summer drought in 2013 (Fig. 1) prevented the regeneration in the drought treated plots. However, our ANPP estimate, being mostly governed by M2-M1 difference, is not sensitive to the regeneration of the plant biomass by the time of the next treatment.

We emphasize the importance of biomass measurements multiple times in the growing season in an experiment where yearly drought treatments are applied, in contrast to most of the studies from which only annual data are published. Our results supplement the findings of Estiarte et al. (2016) and Reinsch et al. (2017) who got consistent drought effect applying one annual biomass estimation by point-intercept method right after the treatment period. Our study reveals that in late-successional grassland-shrubland ecosystems, like ours (Kröel-Dulay et al. 2015), compensation may occur before the next drought. With one measurement per year we could only detect the effect of drought treatment on the peak biomass. Although our investigation started in the 10th year of the climate change field experiment, we could not observe general treatment effect on the biomass taking three annual measurements into consideration. While both summer drought treatments caused significant differences in NDVI by the end of the treatment periods, among four before-treatment and end-of-season measurements only one showed significant treatment effect. Furthermore, we found no whole-season (M3-M1) differences in NDVI between the control and treated plots. Thus, the studied ecosystem proved drought resistant both in terms of Vicente-Serrano et al. (2013), reacting to the drought only at a short time scale, and according Hoover et al. (2014), recovering by the end of the season. This resistance is in agreement with the findings of Tielbörger et al. (2014) in long-term experiments in Mediterranean shrublands. We suppose that the main reason for rapid recovery of biomass in the studied vegetation mosaic is that the drought treatment did not lead to regime shift which occurs after strong disturbance events (Kröel-Dulay et al. 2015). The presence of poplar shoots might contribute to the late season recovery of the grass layer after drought through shading, in line with the findings of Erdős et al. (2014). In contrast with our results, in the post-fire successional vegetation of the Catalonian VULCAN site, Filella et al. (2004) found long-term around-the-year divergence in biomass (also estimated by NDVI) due to drought treatment from the first year after the start of the experiment, which is in accordance to the findings of Kröel-Dulay et al. (2015) in early-successional ecosystems.

According to Ónodi et al. (2017a), drought can temporarily change the NDVI - biomass relationship. Several structural and physiological changes may result in lower NDVI readings, such as decreased specific leaf area, light absorptance, and green biomass to standing biomass ratio because of drought treatment (Cornic and Massacci 1996). However, Filella et al. (2004) and Mänd et al. (2010) found NDVI a reliable proxy for biomass estimation across treatments, seasons, and sites in the same experimental design. As there were not remarkable long-term compositional changes in the vegetation due to the drought treatment at our site (Kröel-Dulay et al. 2015), we conclude that the lower NDVI value after drought treatments indicated less aboveground green biomass because of increased drying and reduced sprouting.

The loss of biomass peak in consecutive years due to drought could lead to severe changes in the carbon budget of the ecosystem. Nagy et al. (2007) found that net ecosystem exchange (NEE) in semi-arid grasslands of the same ecosystem can turn to positive (i.e. carbon releasing) in dry years. However, according to Pintér et al. (2008), the NEE in the same vegetation type is negative (i.e. carbon accumulating) in years of normal or above normal precipitation. Our finding that plant biomass recovers by the next drought treatment show the resilience of this drought-adapted vegetation. Considering the long term climate prediction of increasing frequency of both extreme dry and extreme wet years (Bartholy and Pongrácz 2007), there is no direct danger of desertification in the studied community, as the carbon loss in dry years can be compensated by carbon accumulation in wet years.

In conclusion, we want to underline two of our findings. First, by means of application of field remote sensing, we demonstrated the negative effect of drought treatment on the aboveground plant biomass and the ANPP in a diverse semi-arid shrubland-grassland community. At the same time, we showed that only one yearly measurement right after the treatment may overestimate the effect of drought, disregarding the compensation processes of late-successional ecosystems, which can be detected using multiple within-year measurements.

References

Bartholy J, Pongrácz R (2007) Regional analysis of extreme temperature and precipitation indices for the Carpathian Basin from 1946 to 2001. Glob Planet Change 57:83–95.

Bartholy J, Pongrácz R, Matyasovszky I, Schlanger V (2003) 4.7 Expected regional variations and changes of mean and extreme climatology of Eastern/Central Europe. In: Combined Preprints CD-ROM of the 83rd AMS Annual Meeting. American Meteorological Society, Boston. p 10

Beier C, Beierkuhnlein C, Wohlgemuth T, Penuelas J, Emmett B, Körner C, Boeck H, Christensen JH, Leuzinger S, Janssens IA, others (2012) Precipitation manipulation experiments--challenges and recommendations for the future. Ecol Lett 15:899–911.

Beier C, Emmett B, Gundersen P, Tietema A, Penuelas J, Estiarte M, Gordon C, Gorissen A, Llorens L, Roda F, others (2004) Novel approaches to study climate change effects on terrestrial ecosystems in the field: drought and passive nighttime warming. Ecosystems 7:583–597.

Boelman NT, Stieglitz M, Griffin KL, Shaver GR (2005) Inter-annual variability of NDVI in response to long-term warming and fertilization in wet sedge and tussock tundra. Oecologia 143:588–597. doi: 10.1007/s00442-005-0012-9

Brancaleoni L, Gualmini M, Tomaselli M, Gerdol R (2007) Responses of subalpine dwarf-shrub heath to irrigation and fertilization. J Veg Sci 18:337. doi: 10.1658/1100-9233(2007)18[337:ROSDHT]2.0.CO;2

Byrne KM, Lauenroth WK, Adler PB (2013) Contrasting Effects of Precipitation Manipulations on Production in Two Sites within the Central Grassland Region, USA. Ecosystems 16:1039–1051. doi: 10.1007/s10021-013-9666-z

Ciais P, Reichstein M, Viovy N, Granier A, Ogée J, Allard V, Aubinet M, Buchmann N, Bernhofer C, Carrara A, Chevallier F, De Noblet N, Friend AD, Friedlingstein P, Grünwald T, Heinesch B, Keronen P, Knohl A, Krinner G, Loustau D, Manca G, Matteucci G, Miglietta F, Ourcival JM, Papale D, Pilegaard K, Rambal S, Seufert G, Soussana JF, Sanz MJ, Schulze ED, Vesala T, Valentini R (2005) Europe-wide reduction in primary productivity caused by the heat and drought in 2003. Nature 437:529–533. doi: 10.1038/nature03972

Colegrave N, Ruxton GD (2018) Using Biological Insight and Pragmatism When Thinking about Pseudoreplication. Trends Ecol Evol 33:28–35. doi: https://doi.org/10.1016/j.tree.2017.10.007

Cornic G, Massacci A (1996) Leaf Photosynthesis Under Drought Stress. In: Baker NR (ed) Photosynthesis and the Environment. Springer Netherlands, Dordrecht, pp 347–366

Erdős L, Tölgyesi C, Horzse M, Tolnay D, Hurton Á, Schulcz N, Körmöczi L, Lengyel A, Bátori Z (2014) Habitat complexity of the Pannonian forest-steppe zone and its nature conservation implications. Ecol Complex 17:107–118. doi: 10.1016/j.ecocom.2013.11.004

Estiarte M, Vicca S, Peñuelas J, Bahn M, Beier C, Emmett BA, Fay PA, Hanson PJ, Hasibeder R, Kigel J, Kröel-Dulay G, Larsen KS, Lellei-Kovács E, Limousin J-M, Ogaya R, Ourcival J-M, Reinsch S, Sala OE, Schmidt IK, Sternberg M, Tielbörger K, Tietema A, Janssens IA (2016) Few multiyear precipitation-reduction experiments find a shift in the productivity-precipitation relationship. Glob Chang Biol 22:2570–2581. doi: 10.1111/gcb.13269

Fekete G, Molnár Z, Kun A, Botta-Dukát Z (2002) On the structure of the Pannonian forest steppe: grasslands on sand. Acta Zool Hung 48:137–150.

Filella I, Penuelas J, Llorens L, Estiarte M (2004) Reflectance assessment of seasonal and annual changes in biomass and CO2 uptake of a Mediterranean shrubland submitted to experimental warming and drought. Remote Sens Environ 90:308–318. doi: 10.1016/j.rse.2004.01.010

Gamon JA, Field CB, Goulden ML, Griffin KL, Hartley AE, Joel G, Penuelas J, Valentini R (1995) Relationships Between NDVI, Canopy Structure, and Photosynthesis in Three Californian Vegetation Types. Ecol Appl 5:28–41. doi: 10.2307/1942049

Goodin DG, Henebry GM (1997) A technique for monitoring ecological disturbance in tallgrass prairie using seasonal NDVI trajectories and a discriminant function mixture model. Remote Sens Environ 61:270–278. doi: 10.1016/S0034-4257(97)00043-6

Hoover DL, Knapp AK, Smith MD (2014) Resistance and resilience of a grassland ecosystem to climate extremes. Ecology 95:2646–2656. doi: 10.1890/13-2186.1

Hothorn T, Bretz F, Westfall P (2008) Simultaneous Inference in General Parametric Models. Biometrical J 50:346–363.

IPCC (2013) Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, New York, NY

Kovács-Láng E (1974) Examination of dynamics of organic matter in a perennial open sandy steppe-meadow (Festucetum vaginatae danubiale) at the Csévharaszt IBP sample area (Hungary). Acta Bot Acad Sci Hung 20:309–326.

Kovács-Láng E, Kröel-Dulay G, Kertész M, Fekete G, Bartha S, Mika J, Dobi-Wantuch I, Rédei T, Rajkai K, Hahn I, others (2000) Changes in the composition of sand grasslands along a climatic gradient in Hungary and implications for climate change. In: Phytocoenologia. pp 385–407

Köchy M, Wilson SD (2004) Semiarid grassland responses to short-term variation in water availability. Plant Ecol Former `Vegetatio’ 174:197–203. doi: 10.1023/B:VEGE.0000049098.74147.57

Kröel-Dulay G, Ransijn J, Schmidt IK, Beier C, De Angelis P, de Dato G, Dukes JS, Emmett B, Estiarte M, Garadnai J, Kongstad J, Kovács-Láng E, Larsen KS, Liberati D, Ogaya R, Riis-Nielsen T, Smith AR, Sowerby A, Tietema A, Penuelas J (2015) Increased sensitivity to climate change in disturbed ecosystems. Nat Commun 6:6682. doi: 10.1038/ncomms7682

Lellei-Kovács E, Kovács-Láng E, Kalapos T, Botta-Dukat Z (2008a) Soil respiration and its main limiting factors in a semiarid sand forest-steppe ecosystem-results of a climate simulation experiment. Cereal Res Commun 36:1223–1226.

Lellei-Kovács E, Kovács-Láng E, Kalapos T, Botta-Dukát Z, Barabás S, Beier C (2008b) Experimental warming does not enhance soil respiration in a semiarid temperate forest-steppe ecosystem. Community Ecol 9:29–37.

Lenth R V (2016) Least-Squares Means: The {R} Package {lsmeans}. J Stat Softw 69:1–33. doi: 10.18637/jss.v069.i01

Mänd P, Hallik L, Peñuelas J, Nilson T, Duce P, Emmett BA, Beier C, Estiarte M, Garadnai J, Kalapos T (2010) Responses of the reflectance indices PRI and NDVI to experimental warming and drought in European shrublands along a north–south climatic gradient. Remote Sens Environ 114:626–636. doi: 10.1016/j.rse.2009.11.003

Miranda JD, Armas C, Padilla FM, Pugnaire FI (2011) Climatic change and rainfall patterns: Effects on semi-arid plant communities of the Iberian Southeast. J Arid Environ 75:1302–1309. doi: https://doi.org/10.1016/j.jaridenv.2011.04.022

Molnár Z, Biró M, Bartha S, Fekete G, Dúbravková D, Hajnalová M (2012) Eurasian Steppes. Ecological Problems and Livelihoods in a Changing World. In: Werger JAM, van Staalduinen AM (eds). Springer Netherlands, Dordrecht, pp 209–252

Mulla DJ (2013) Twenty five years of remote sensing in precision agriculture: Key advances and remaining knowledge gaps. Biosyst Eng 114:358–371. doi: 10.1016/j.biosystemseng.2012.08.009

Nagy Z, Pintér K, Czóbel S, Balogh J, Horváth L, Fóti S, Barcza Z, Weidinger T, Csintalan Z, Dinh NQ, Grosz B, Tuba Z (2007) The carbon budget of semi-arid grassland in a wet and a dry year in Hungary. Agric Ecosyst Environ 121:21–29. doi: http://dx.doi.org/10.1016/j.agee.2006.12.003

Nestola E, Calfapietra C, Emmerton C, Wong C, Thayer D, Gamon J (2016) Monitoring Grassland Seasonal Carbon Dynamics, by Integrating MODIS NDVI, Proximal Optical Sampling, and Eddy Covariance Measurements. Remote Sens 8:260. doi: 10.3390/rs8030260

Ónodi G, Kertész M, Kovács-Láng E, Ódor P, Botta-Dukát Z, Lhotsky B, Barabás S, Mojzes A, Kröel-Dulay G (2017a) Estimating aboveground herbaceous plant biomass via proxies: The confounding effects of sampling year and precipitation. Ecol Indic 79:355–360. doi: 10.1016/j.ecolind.2017.04.011

Ónodi G, Kröel-Dulay G, Kovács-Láng E, Ódor P, Botta-Dukat Z, Lhotsky B, Barabás S, Garadnai J, Kertész M (2017b) Comparing the accuracy of three non-destructive methods in estimating aboveground plant biomass. Community Ecol 18:56–62. doi: 10.1556/168.2017.18.1.7

Peñuelas J, Prieto P, Beier C, Cesaraccio C, De Angelis P, de Dato G, Emmett BA, Estiarte M, Garadnai J, Gorissen

A, others (2007) Response of plant species richness and primary productivity in shrublands along a north--south gradient in Europe to seven years of experimental warming and drought: reductions in primary productivity in the heat and drought year of 2003. Glob Chang Biol 13:2563–2581.

Pinheiro J, Bates D, DebRoy S, Sarkar D, R Core Team (2017) {nlme}: Linear and Nonlinear Mixed Effects Models.

Pintér K, Barcza Z, Balogh J, Czóbel S, Csintalan Z, Tuba Z, Nagy Z (2008) Interannual variability of grasslands' carbon balance depends on soil type. Community Ecol 9:43–48. doi: 10.1556/ComEc.9.2008.S.7

Pontailler J-Y, Hymus GJ, Drake BG (2003) Estimation of leaf area index using ground-based remote sensed NDVI measurements: validation and comparison with two indirect techniques. Can J Remote Sens 29:381–387. doi: 10.5589/m03-009

R Core Team (2017) R: A Language and Environment for Statistical Computing.

Reinsch S, Koller E, Sowerby A, de Dato G, Estiarte M, Guidolotti G, Kovács-Láng E, Kröel-Dulay G, Lellei-Kovács E, Larsen KS, Liberati D, Peñuelas J, Ransijn J, Robinson DA, Schmidt IK, Smith AR, Tietema A, Dukes JS, Beier C, Emmett BA (2017) Shrubland primary production and soil respiration diverge along European climate gradient. Sci Rep 7:43952. doi: 10.1038/srep43952

Rouse JW, Haas RH, Deering DW, Schell JA, Harlan JC (1974) Monitoring the vernal advancement and retrogradation (green wave effect) of natural vegetation. 390.

Sala OE, Austin AT (2000) Methods of estimating aboveground net primary productivity. In: Sala OE, Jackson RB, Mooney HA, Howarth RH (eds) Methods in Ecosystem Science. pp 31–43

Scurlock JMO, Johnson K, Olson RJ (2002) Estimating net primary productivity from grassland biomass dynamics measurements. Glob Chang Biol 8:736–753. doi: 10.1046/j.1365-2486.2002.00512.x

Shinoda M, Nachinshonhor GU, Nemoto M (2010) Impact of drought on vegetation dynamics of the Mongolian steppe: A field experiment. J Arid Environ 74:63–69. doi: https://doi.org/10.1016/j.jaridenv.2009.07.004

Tielbörger K, Bilton MC, Metz J, Kigel J, Holzapfel C, Lebrija-Trejos E, Konsens I, Parag HA, Sternberg M (2014) Middle-Eastern plant communities tolerate 9 years of drought in a multi-site climate manipulation experiment.

Nat Commun 5:5102. doi: 10.1038/ncomms6102

Vicente-Serrano SM, Gouveia C, Camarero JJ, Beguería S, Trigo R, López-Moreno JI, Azorín-Molina C, Pasho E, Lorenzo-Lacruz J, Revuelto J, Morán-Tejeda E, Sanchez-Lorenzo A (2013) Response of vegetation to drought time-scales across global land biomes. Proc Natl Acad Sci U S A 110:52–7. doi: 10.1073/pnas.1207068110

Wang R, Gamon J, Montgomery R, Townsend P, Zygielbaum A, Bitan K, Tilman D, Cavender-Bares J (2016) Seasonal Variation in the NDVI–Species Richness Relationship in a Prairie Grassland Experiment (Cedar Creek). Remote Sens 8:1–15. doi: 10.3390/rs8020128

Wu Z, Dijkstra P, Koch GW, Peñuelas J, Hungate BAR (2011) Responses of terrestrial ecosystems to temperature and precipitation change: a meta-analysis of experimental manipulation. Glob Chang Biol 17:927–942. doi: 10.1111/j.1365-2486.2010.02302.x

Zhao M, Running SW (2010) Drought-Induced Reduction in Global Terrestrial Net Primary Production from 2000 Through 2009. Science (80-) 329:940–943.

Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GM (2009) Mixed Effects Modelling for Nested Data. In: Zuur AF (ed) Mixed effects models and extensions in ecology with R. Springer, New York, NY, pp 101–142

Table 1 Comparisons tested using contrasts in the mixed effect linear model fitted to NDVI. M2-M1: treatment change, M3-M2: post-treatment change, M3-M1: whole-season change

Response variables	Subset	Comparison	Estimate	Std. Error	Z-value	p-value
NDVI	2011 M1	C vs. D	0.026	0.022	1.151	0.964
NDVI	2013 M1	C vs. D	0.065	0.022	2.911	0.063
NDVI	**2011 M2**	**C vs. D**	**0.102**	**0.022**	**4.598**	**<0.001**
NDVI	**2013 M2**	**C vs. D**	**0.104**	**0.022**	**4.666**	**<0.001**
NDVI	2011 M3	C vs. D	0.021	0.022	0.928	0.992
NDVI	**2013 M3**	**C vs. D**	**0.085**	**0.022**	**3.831**	**0.003**
NDVI	**2011 C**	**M1 vs. M2**	**0.054**	**0.009**	**6.045**	**< 0.001**
NDVI	2011 D	M1 vs. M2	0.023	0.009	-2.581	0.150
NDVI	**2013 C**	**M1 vs. M2**	**0.075**	**0.009**	**8.404**	**< 0.001**
NDVI	**2013 D**	**M1 vs. M2**	**0.036**	**0.009**	**4.011**	**0.001**
NDVI	**2011 C**	**M2 vs. M3**	**-0.074**	**0.009**	**-8.341**	**< 0.001**
NDVI	2011 D	M2 vs. M3	0.007	0.009	0.845	0.996
NDVI	**2013 C**	**M2 vs. M3**	**0.062**	**0.009**	**-6.961**	**< 0.001**
NDVI	**2013 D**	**M2 vs. M3**	**-0.043**	**0.009**	**-4.871**	**< 0.001**
NDVI	2011 C	M1 vs. M3	-0.020	0.009	-2.296	0.284
NDVI	2011 D	M1 vs. M3	0.015	0.009	-1.736	0.680
NDVI	2013 C	M1 vs. M3	0.013	0.009	1.442	0.863
NDVI	2013 D	M1 vs. M3	-0.008	0.009	-0.860	0.995
ΔNDVI (M2-M1)	**2011**	**C vs. D**	**0.077**	**0.013**	**6.099**	**< 0.001**
ΔNDVI (M2-M1)	**2013**	**C vs. D**	**0.039**	**0.013**	**3.106**	**0.034**
ΔNDVI (M3-M2)	**2011**	**C vs. D**	**-0.082**	**0.013**	**-6.495**	**< 0.001**
ΔNDVI (M3-M2)	2013	C vs. D	-0.019	0.013	-1.478	0.845
ΔNDVI (M3-M1)	2011	C vs. D	-0.005	0.013	-0.396	1.000
ΔNDVI (M3-M1)	2013	C vs. D	0.020	0.013	1.628	0.755

List of Figure Captions

Fig. 1 The timing of measurement events (M0 to M3). Horizontal bars stand for time intervals of drought treatments. Vertical bars are proportional to the monthly precipitation, while the unfilled parts of the vertical bars show the amounts of excluded precipitation during the drought treatments. The heights of the bars range from 0 mm (November 2011) to 126.3 mm (March 2013). See dates and more values in the text, as well as in Online Resource 1.

Fig. 2 NDVI values (least-square means and 95% confidence intervals estimated by the fitted mixed-effect model) for the measurement events in 2011 and 2013 in the control (C) and drought treatment (D) plots (see also Online Resource 2); before treatment: M1, after treatment: M2, end-of-summer: M3.

* denotes significant drought effect

Fig. 3 Estimated changes of NDVI values between measurement events (least-square means and 95% confidence intervals): treatment change, i.e. M2-M1; post-treatment change, i.e. M3-M2; whole-season change, i.e. M3-M1; in 2011 and 2013 in the control (C) and drought (D) treatments;

* denotes significant drought effect

Fig. 4 Sum of positive NDVI increments from the 0.205 start-of-season baseline (M0) to the end-of-summer measurements as a proxy for annual aboveground net primary production, in 2011 and 2013 in the control (C) and drought treatment (D) plots (least-squares means and 95% confidence intervals). The difference between control and drought treatment is significant in both years and its value is significantly greater in 2013.

Figures

Fig. 1

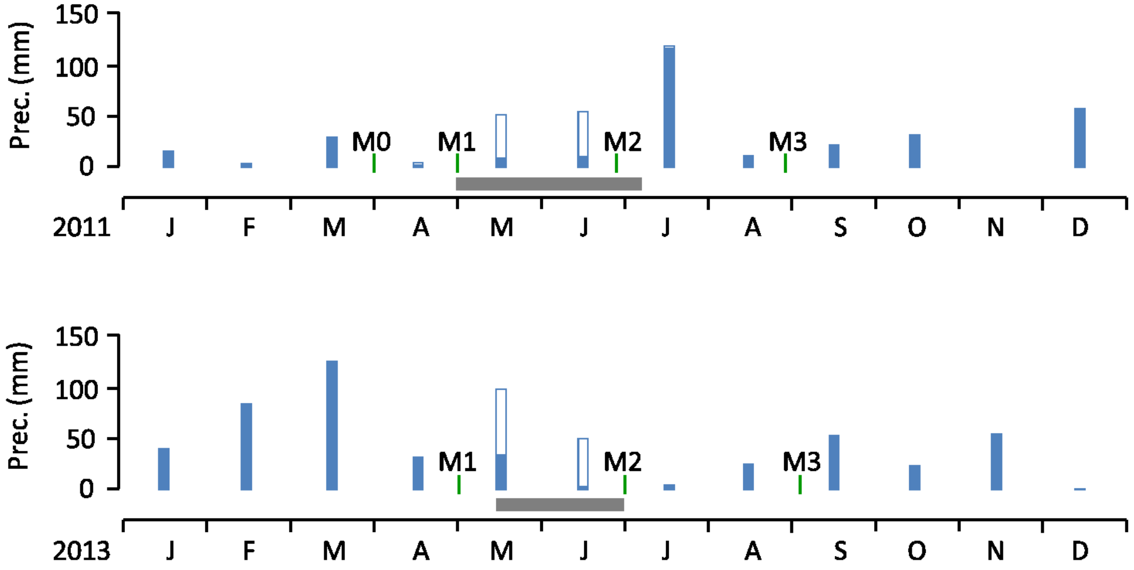


Fig. 2

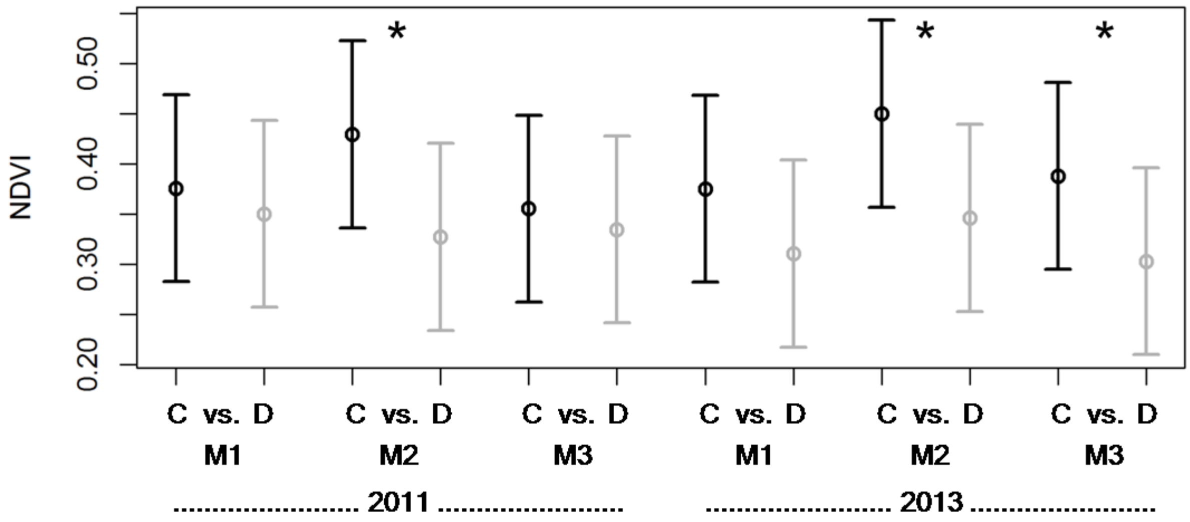
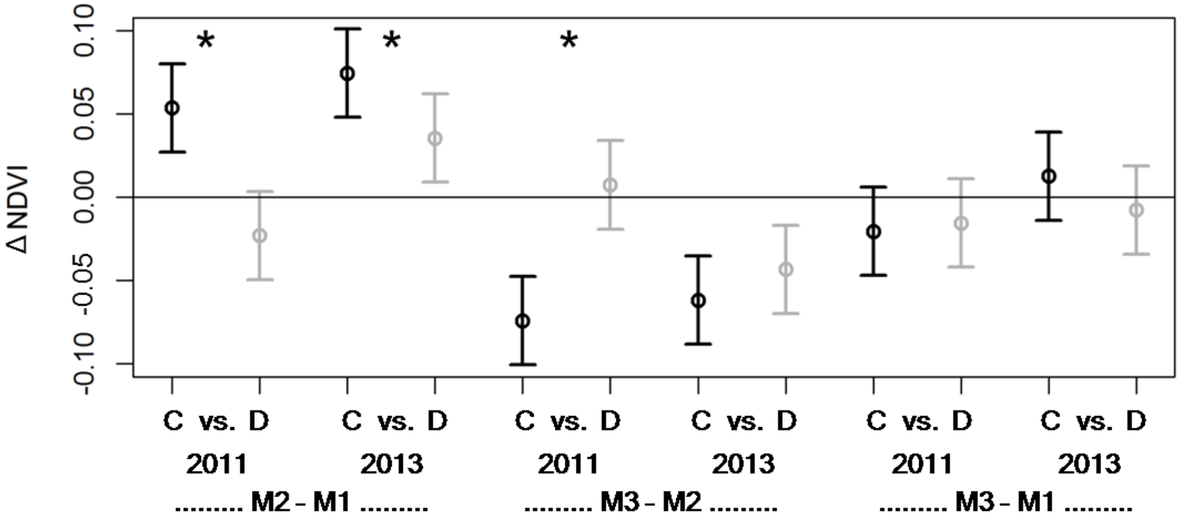

NDVI
0.20
0.30
0.40
0.50
*
*
*
C vs. D
M1
C vs. D
M2
C vs. D
M3
C vs. D
M1
C vs. D
M2
C vs. D
M3
.... 2011 ....
.... 2013 ....

Fig. 3



0.10
0.05
0.00
-0.05
-0.10
Δ NDVI
*
*
*
C vs. D
2011
C vs. D
2013
C vs. D
2011
C vs. D
2013
C vs. D
2011
C vs. D
2013
.... M2 - M1 ....
.... M3 - M2 ....
.... M3 - M1 ....

Fig. 4