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Do successive climate extremes weaken the resistance of plant communities? An experimental study using plant assemblages

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Abstract

The probability that plant communities undergo successive climate extremes increases under climate change. Exposure to an extreme event might elicit acclimatory responses and thereby greater resistance to a subsequent event, but might also reduce resistance
[5] if the recovery period is too short or resilience too low. Using experimental plant assemblages, we compared the effects of two successive extremes (either two drought extremes, two heat extremes or two drought + heat extremes) to those of assemblages being exposed only to the second extreme. Additionally, the recovery period between the successive extremes was varied (2, 3.5 or 6 weeks).
[10] Among the different types of climate extremes, combined drought + heat extremes induced substantial leaf and plant mortality, while the effects of drought and heat extremes were smaller. Preceding drought + heat extremes lowered the resistance in terms of leaf survival to a subsequent drought + heat extreme if the recovery period was 2 weeks, even though the leaves had completely recovered during that interval. No
[15] reduced resistance to subsequent extremes was recorded with longer recovery times or with drought or heat extremes. Despite mortality on the short term, the drought + heat and the heat extremes increased the end-of-season aboveground biomass, independent of the number of events or the recovery period. These results show that the effect of a preceding extreme event disappears quite quickly, but that recurrent climate
[20] extremes with short time intervals can weaken the resistance of herbaceous plant assemblages. This can however be compensated afterwards through rapid recovery and secondary, positive effects in the longer term.

1 Introduction

In a future climate, many ecosystems will be exposed to more frequent, and more in-
[25] tense climate extremes (Fischer and Schär, 2010; IPCC, 2012; Meehl et al., 2000). Although not all extreme events will necessarily have a noticeable or immediate eco-

logical impact (Dreesen et al., 2012; Kreyling et al., 2008; Smith, 2011; Leuzinger et al., 2005), many of them, especially drought events, can lead to disastrous changes in ecosystems, as observed following naturally occurring extremes (Bréda et al., 2006; Breshears et al., 2005; Ciais et al., 2005; Peñuelas et al., 2007) and in studies exper-
5 imentally inducing climate extremes (De Boeck et al., 2011). Moreover, the increasing probability of recurrent extremes such as consecutive severe droughts and heat waves (IPCC, 2012) might impose an even stronger threat for ecosystems than single extreme events, if negative effects accumulate and eventually lead to chronic stress.

   With recurring climate extremes, the ability to recover from a first event can play
10 an important part in the effect of subsequent climate extremes. For example, trees with limited recovery from a drought event have been shown to be more sensitive to a second drought occurring several years later (Lloret et al., 2004). Lack of sufficient resilience (capacity of an ecosystem to reach pre-disturbance performance levels) can thus compromise resistance (ability of an ecosystem to withstand displacement from
15 control levels) to a subsequent event. The ability to recover is species-specific (Gallé et al., 2011; Liu et al., 2010), but is also influenced by competitive interactions, plant age or size (Lloret et al., 2004), the intensity of the past drought (Miyashita et al., 2005), and the amount of stored carbon reserves (Galiano et al., 2011). Importantly, recovery can be delayed when drought events are repeated, as reported in Liu et al. (2010). Other
20 studies that found that repeated events can impair resilience or resistance include the research of Zavalloni et al. (2009), who observed that frequent mild drought events evoked by simulated climate-warming, enhanced stress levels in grasslands and lowered the resistance to a severe drought event. In arctic tundra, loss of temperature resistance has been reported when plants had previously been exposed to successive
25 heat extremes (Marchand et al., 2006). Over time, such losses of resistance and/or resilience could lead to species shifts and even move the system into an alternative state (Scheffer et al., 2001).

   In contrast to losing resistance, plants might also become more resistant to future exposures after being subjected to a first event, through physiological, genetic or bio-

chemical acclimation (Bruce et al., 2007). For example, pre-treatment with heat often brings greater tolerance to subsequent heat (Wahid et al., 2007; Xu et al., 2006). Several plant species have also been found to acclimate to multiple drought cycles (Gallé et al., 2011; Luo et al., 2011), even when the aboveground parts were harvested before the following drought period (Walter et al., 2011). Drought preconditioning is sometimes applied to improve the drought resistance of seedlings or young plants used for restoration or plantations (Guarnaschelli et al., 2006; Ruiz-Sánchez et al., 2000; Vilagrosa et al., 2003; Villar-Salvador et al., 2004).

Most of our knowledge on the impact of recurring climate events relates to repeated droughts. However, the incidence of higher temperatures (e.g. heat waves) during drought will exacerbate the response, as warming accelerates soil drying and increases plant water demands. In this study, plant assemblages were subjected to two successive extreme events with the same historical intensity. These events were either two drought periods, two heat waves or two periods with combined heat and drought. We varied the time interval between the two events (either 6, 3.5 or 2 weeks) in order to study the effect of the recovery period between the events, on mortality and productivity. The responses to the two successive extremes were compared with responses of assemblages being exposed to only the second extreme, to evaluate whether a preceding event increased, decreased or did not affect the vulnerability. We expected that the impact caused by the second extreme event would depend on the elapsed time interval. In the scenario with the longest delay between the successive extremes we hypothesized that acclimation could occur, enhancing the resistance to drought and/or heat. With short time intervals between the extremes, on the other hand, we anticipated additional detrimental effects on plant and leaf mortality, and hence a lower end-of-season biomass.

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2   Materials and methods

2.1   Experimental design

The experiment was conducted in 2010 at an experimental field site located at the University of Antwerp (Belgium, 51°09′ N, 4°24′ E). Mean annual air temperature at this
location with temperate maritime climate is around 9.6 °C and mean annual precipitation is 780 mm, equally distributed over the year. Synthesized plant assemblages were
used, which were constructed in separate containers (20 cm diameter, 40 cm depth).
These assemblages consisted of 10 individuals belonging to three perennial herbaceous species (*Plantago lanceolata* L., *Rumex acetosella* L. and *Bellis perennis* L.).
Plant individuals were sown in the previous year and were transplanted to the containers in spring in a hexagonal grid with only interspecific neighbours. We opted to use
experimental plant assemblages because this ensures good comparability between
treatments, and thus a more easy detection of mechanisms than in natural systems,
where differences in soil structure, nutrient availability, species composition and plant
density can more easily obfuscate results. The plant species used were common in
local grasslands and small-stature, ensuring uniform exposure to the infrared heating
treatment (see below). The containers were filled with sandy soil (96 % sand, 1.5 % silt
and 2.5 % clay; pH 7.6; 1.3 % C, 19 mg nitrate-N, 1.1 mg ammonium-N and 550 mg
Kjeldahl-N per kg dry soil) and were placed in watertight boxes (135 × 135 cm). These
boxes, six in total, were embedded in the soil to ensure natural soil temperature profiles. When not exposed to drought, the boxes were provided with a constant water
table (34 cm below the soil surface) to ensure that all assemblages had sufficient water. A perforated lid at the bottom of each container allowed either water drainage or
inflow. Permanent rain shelters were installed above each box to eliminate precipitation.
The shelters (3.60 m × 3.60 m) had transparent polycarbonate roofs (thickness 4 mm,
light attenuation around 5–15 %, depending on solar angle) and a height of 2.40 m
but slanted down to 1.80 m in south-west direction and to 2 m in north-east direction.
The height of the shelters ensured full air exchange with the surroundings and both

the build-up of heat (+0.2 °C on average) and changes in relative humidity (+3 % on average) were modest.

The extreme climatic treatments included drought (D), heat (H) and the combination of drought and heat (DH). The plant assemblages were exposed to either: (i) a control situation without extremes (C), (ii) two consecutive climate extremes (D+D, H+H, DH+DH), or (iii) only the second climate extreme (C+D, C+H, C+DH). Key to the design is the comparison between (ii) and (iii), which allows to determine whether a preceding extreme affects the response to a subsequent extreme. The second extreme event was applied at the same time in all plant assemblages (12 August–6 September, see 2.2), but the time between the end of the first event and the start of the second was varied (42, 25 or 14 days). The assemblages that were exposed to the two consecutive extremes, thus included three different climate scenarios combined with three different interval times. The entire setup consisted of 189 plant assemblages of which 45 assemblages were exposed to the two subsequent extreme events with 42 days interval (further referred to as scenario IV), at 15 replicate assemblages per climate treatment (D+D, H+H or DH+DH, see Table 1). A similar number of plant assemblages (3 × 15) was exposed to the two extreme events with 25 days interval (scenario III) and with 14 days interval (scenario II). In addition, 27 assemblages were exposed only to the common extreme in August (scenario I), at 9 replicate assemblages per treatment (C+D, C+H or C+DH). The remaining 27 assemblages were subjected to the control climate (see Table 1 for overview of treatments and scenarios).

Each of the six watertight boxes enclosing the plant assemblages was separated in two halves. In each box, the water table was maintained in one half (C and H treatments), while in the other half, drought was induced at the appropriate time by removing the water table and withholding irrigation (D and DH treatments). Of the 12 halves in total, three were filled with control assemblages (initially 54 control assemblages) and the other nine halves were assigned to the treatments D, H or DH in either scenario IV, III or II. Before the common second extreme event was initiated, 27 control plant assemblages were spread over the nine non-control halves. These 27 former control

assemblages became the plant assemblages used for scenario I (9 per treatment), which were thus subjected to the second climate extreme only (see Table 1). In the period between the two successive events, all assemblages were relocated between the halves (to avoid pseudo-replication).

⁵ Above three of the six boxes (containing the H and DH treatments), a set of six 1500 W infrared lamps (spectrum 0.7–3 µm) was suspended at a height of circa 120 cm, to allow direct and uniform heating of the canopy in a non-intrusive way. The three other boxes (C and D treatments) had dummy lamps and were exposed to ambient air conditions. The power output of the heaters was adjusted to match the target maximum

¹⁰ daily air temperatures (see 2.2).

Campbell CS616 soil water content (SWC) reflectometers (Campbell Scientific Ltd, Loughborough, UK) were installed in four assemblages per half box (i.e. 48 sensors in total). These sensors were 30 cm long, covering most of our soil profile. The values were recorded hourly by a data logger (DL2E, Delta T, Cambridge, UK) and corrected

¹⁵ using an in situ calibration. Water retention curves were established by an external soil laboratory to determine the soil moisture content at field capacity (pF 2.5) and at permanent wilting point (pF 4.2), which was 15 vol % and 3.7 vol %, respectively. Air temperature sensors, shielded from direct radiation, recorded air temperature at the height of the canopy at half-hourly intervals.

2.2 Intensity of climate extremes

We simulated extremes with a return time of 50 years. The required length of the drought was determined by interpolation of return time data from the long-term climate database of the Royal Meteorological Institute of Belgium (records from 1880–2008), as the number of consecutive days with daily precipitation less than 1 mm. For

²⁵ a 50-year drought extreme occurring in August, this yielded 25 days. The duration of the heat extremes was set to ten days, which is a realistic length for the region (De Boeck et al., 2010). The maximum daily air temperatures (T_{max}) corresponding with heat extremes of that length were calculated, likewise by interpolation of return time

data, using the same database. The 10-day heat extremes were applied towards the end of the rain-free period, in agreement with the meteorological characteristics of heat waves in Western Europe (De Boeck et al., 2010).

The second and common extreme event of all scenarios started on August 12th (DOY 225) and lasted, as mentioned above, 25 days. The calculated mean target T_{max} of the heat wave applied during the last ten days of this drought extreme was 28 °C. The calculated target T_{max} of the preceding heat waves was 30 °C in each of the three scenarios. The preceding drought extreme of scenario IV started on June 5th (DOY 156), for 25 days. Since we studied the effect of the length of the recovery period between two consecutive extremes, we wanted the impact of the three preceding climate extremes on the plant assemblages to be as similar as possible. Therefore, during the first drought of scenario IV, we determined the soil water content that was reached at the time the heat wave was initiated (i.e. after 15 days). This soil water content then became the target drought level to be reached during the preceding drought extremes of scenarios III and II at which the heat extreme was initiated. In other words, the heat extreme was induced at a fixed soil water content, independent of the number of days it took to reach this soil water content. As the target T_{max} was also the same during the three preceding heat extremes, the eventual intensity in all three preceding extremes was similar. Scenario III started on 28 June (DOY 189) with 19 days of no water supply, and scenario II on 9 July (DOY 109) followed by 20 days without water (see Table 1 and Fig. 1).

2.3 Measurements

The percentage of living leaves (leaf survival) was measured by counting all leaves present and how many of these leaves were dead, in five containers per treatment. Leaves were regarded dead if they were wilted and brown, but still attached to the plant. These counts were made weekly before and after all climate extremes, but more frequently during the extremes. The percentage of living plants (plant survival) was

determined in the same five containers per treatment (each container started with 10 individuals and all invading plants were removed).

Leaf colour was determined from colour pictures of the assemblages, made with a digital camera (Canon EOS 5D) under scattered light conditions and zenith angle. Three pictures, each comprising four plant containers, were made per treatment. Leaf colour was analyzed using Matlab 2008b software (The MathWorks Inc., Natick, Massachusetts, USA) by manually selecting pixels of leaves, to ensure that no pixels of soil, containers or sensors were included. The RGB (red, green and blue) values of the selected pixels were transformed to HSV (hue, saturation and value). In the HSV colour space, hue represents the dominant wavelength of a colour. The corresponding colours are projected on a circle (0°–360°), varying from red (0 and 360°) through yellow (60°), green (120°), cyan (180°), blue (240°), magenta (300°) and back to red. Saturation and value reflect the purity of the colour and brightness, respectively. Differences in hue were compared between treatments for the dominant species *P. lanceolata*, which comprized 74 % of the biomass.

Plant biomass was determined at the end of the growing season (2–3 November). Aboveground parts were cut from all plant assemblages and sorted per species. Belowground parts were sampled from 6 containers per treatment (but 18 for the control treatment) by carefully washing all soil from the container, leaving nothing but the roots. All biomass samples were weighed after drying at 70 °C. Three replicate samples of aboveground biomass and belowground biomass (all species combined) were analysed for leaf and root nitrogen concentration with a carbon/nitrogen element analyser (NC-2100, Carlo Erba Instruments, Milan, Italy), after being ground and sieved over a 0.1 mm mesh.

2.4 Statistical analysis

All statistical tests were made using SAS (version 9.1, SAS Institute Inc., Cary, NC, USA). Biomass was analyzed using two-way ANOVA with scenario (IV to I) and treatment (C, D, H and DH) as fixed factors. Post-hoc tests were performed with the Tukey-

Kramer correction. We analyzed the colour differences between treatments for each sampling date separately per scenario, using one-way ANOVA (note that between-scenario comparisons on specific dates are not relevant because of the different exposure time associated with each scenario). The normality of these datasets was tested with the Shapiro-Wilkinson test. To investigate differences among the treatments in the percentage of living leaves and living plants, an ANOVA model for binomially distributed data was applied. Here, a chi-square test is used (χ^2) instead of the F-test in ANOVA for normally distributed data. The significance threshold was 0.05.

3 Results

3.1 Environmental conditions

At the end of the first climate extremes of scenarios IV, III and II (i.e. DOY 181, 198 and 210), which had the same target T_{max} and the same target drought level, the soil water content was similar (Fig. 1). The D treatment reached SWC values around 5 % in all three scenarios, while in the DH treatment SWC values ranged from 3.7 % in scenario III to 4.7 % in scenario II, so almost dropping to wilting point (3.7 % in this soil). After re-watering, the soil water levels of the drought treatments (D and DH) fairly quickly reached field capacity again. During the second and common climate extreme, the mean SWC dropped to 7.4 % in D and 5.6 % in DH.

Air temperatures at the height of the canopy during the heat extremes (same in H and DH) reached a mean daily maximum of 32.6 °C, 34.5 °C and 32.9 °C for the first extremes of scenarios IV, III and II, respectively. During the common extreme, the daily mean maximum air temperature of the heat extreme equalled 30.2 °C, or 6.8 °C above normal daily mean T_{max} (Table 1).

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3.2 Leaf and plant survival

The preceding climate extremes (i.e. the first extremes of scenarios IV, III and II) reduced the percentage of living leaves compared to the controls (Fig. 2a). The first D treatment impaired leaf survival by 12.8 % in scenario IV ($\chi^2 = 6.26$, $P = 0.01$) and 7.0 % in scenario III ($\chi^2 = 3.90$; $P = 0.048$), while it increased leaf survival with 9.2 % in scenario II ($\chi^2 = 4.65$, $P = 0.03$). The first H treatment reduced the percentage of living leaves with 7.3 % in scenario IV ($\chi^2 = 4.12$, $P = 0.04$), while it had no effect in the other scenarios. The loss of living leaves caused by the first DH extremes was more substantial and quite similar in all three scenarios: 24.1 %, 20.9 % and 17.5 % in scenarios IV, III and II, respectively ($\chi^2 = 9.88$, $P = 0.002$; $\chi^2 = 19.92$, $P < 0.0001$ and $\chi^2 = 6.37$, $P = 0.01$). After re-watering, the percentage of living leaves increased again in all treatments that had suffered from losses. In the D treatments of scenarios IV and III and the DH treatment of scenario II, this resulted from leaf fall only, lowering the number of dead and total leaves, while the number of living leaves stayed the same. In the H treatment of scenario IV and the DH treatments of scenarios IV and III, the recovery of living leaves was caused by a combination of both leaf fall and regrowth. When the second, common, climate extreme was initiated (on DOY 222), no differences in the percentage of living leaves remained between the treatments and the control, in any of the scenarios (see Fig. 2a). By the end of the second extreme, however, the plant assemblages of the DH treatment of scenario II again experienced leaf loss (17 % decline, $\chi^2 = 7.55$, $P = 0.006$). When the second climate extreme was applied without any preceding extremes (scenario I), no leaf losses were observed (Fig. 2a). These observations suggest that a previous event can induce memory effects during later events, even though recovery after that first event seems complete.

Larger differences between the various scenarios in the impact of the preceding extremes were found in plant survival, notably in DH. The greatest reduction in living plants caused by the preceding DH treatments reached 58 % in scenario IV ($\chi^2 = 18.58$, $P < 0.0001$) and 30 % in scenario II ($\chi^2 = 7.12$, $P = 0.008$), whereas no

significant effect was observed in scenario III (Fig. 2b). Note that the percentage of living plants slightly increased again after the DH extreme in scenarios IV and II, owing to regrowth of plants previously appearing dead. The other climate treatments (D and H) never influenced plant survival. As with leaf mortality, the second climate extreme had no effect on plant survival when applied without preceding extremes (scenario I, Fig. 2b).

Our central question was whether herbaceous vegetation becomes more vulnerable or more resistant to a climate extreme after having faced an earlier one, and whether this effect would be influenced by the interval between them. In Fig. 3a and b, we therefore plot the influence on plant and leaf survival caused by the second extreme only (i.e. the difference in the percentage of living leaves or living plants before and after the second extreme) as a function of the number of days since the end of the first extreme. The second extreme had no effect on plant survival in any of the scenarios (Fig. 3a). In other words, for plant survival, it made no difference whether the plant assemblages had been exposed to two recurring or to only one climate extreme, or whether the recovery period in between the two extremes was shorter or longer. Resistance to the second extreme was thus never affected by previous events, and differences in plant mortality that were visible at the end of the growing season (in scenarios IV and II, see Fig. 2a, b) were attributable uniquely to the first extremes. When expressed as leaf survival, however, resistance to the second extreme was negatively affected by previous events, but only for DH and under the scenario with the shortest recovery period (scenario II, Fig. 3b; $\chi^2 = 7.55$, $P = 0.006$). Previous exposures with a longer recovery period (scenarios IV and III) did not change the resistance of leaf survival to the second extreme.

3.3 Leaf colour

During the induced H and DH extremes, the plants became greener than those in the C and D treatments (which leaned more to towards yellow-green), as indicated by the higher hue values in Fig. 2c. This was the case in all scenarios. Only in October, just

before the biomass harvest, the colour difference between the treatments faded out in scenarios III and II. These findings suggest that, despite the greater leaf and/or plant mortality, the remaining leaves in these treatments contained more chlorophyll.

3.4 End-of-season biomass and nitrogen stock

Relative to the control treatment, the two heated treatments (H and DH) increased the aboveground biomass by the end of the growing season in all scenarios with two recurrent extremes (Fig. 4a; $F = 24.78$, $P < 0.0001$; $F = 13.36$, $P = 0.0006$ and $F = 11.81$, $P = 0.001$ for scenarios IV, III and II, respectively). There were no differences between the three scenarios with recurring climate extremes themselves. In the plant assemblages exposed only to the single extreme (scenario I), an increased aboveground biomass was likewise observed but only in DH ($F = 2.84$, $P = 0.045$). While the belowground and the total (aboveground + belowground) biomass were similar in all treatments, biomass partitioning towards the aboveground parts was enhanced (as indicated by the lower root-to-shoot ratios in Fig. 5) in the DH treatments of scenarios IV and II ($F = 5.13$, $P = 0.003$ and $F = 4.81$, $P = 0.01$). The DH treatment of scenario III and the H treatments of all scenarios showed a similar (albeit statistically nonsignificant) trend. In agreement with the biomass data, the total nitrogen stock and root nitrogen stock did not differ between treatments. The aboveground parts, however, showed a higher nitrogen stock in the DH treatment of scenario III ($F = 3.50$, $P = 0.02$), and this trend was visible in the DH treatments of the other scenarios as well (Fig. 4b).

4 Discussion

4.1 Effects of single extremes

In contrast to our expectations, drought-only extremes (i.e. drought not combined with heat) did not influence end-of-season biomass or plant survival, and had only limited

effects on leaf survival. The number of days without water input and timing of our preceding extremes were the same or close to that applied in the summer drought extreme by De Boeck et al. (2011), which was carried out with the same experimental set-up. Unlike this study, De Boeck and colleagues observed a strong negative impact of the

5 drought extreme on end-of-season biomass. The fact that the same drought duration can lead to very different productivity responses is highly intriguing. As there were no noteworthy differences in air temperature between both experiments that could induce substantial differences in vapour pressure deficit or soil drying, we believe that this difference is mainly attributable to the different plant combinations used. The plant

10 assemblages exposed to climate extremes by De Boeck et al. (2011) were similar to the ones used here, except that we did not include *Trifolium repens* L. Apparently, this one species created a substantial difference in the drought response of the assemblage. Without the fast growing legume *T. repens*, all assemblages produced much less biomass (more than eight times less), and, as a consequence, likely consumed

15 much less water. We therefore assume that a greater water consumption in the study by De Boeck and colleagues explains the much higher vulnerability to drought. This explanation is in line with other experiments that observed a stronger negative effect of drought on plant communities containing greater nitrogen stocks, either through the presence of legumes (Pfisterer and Schmid, 2002; Kreyling et al., 2008) or through

20 manually added nitrogen (Gordon et al., 1999; Keller, 2005), as these communities were more productive. Furthermore, other studies have also related ecosystem productivity to drought sensitivity (van Ruijven and Berendse, 2010; Van Peer et al., 2001; Van Peer et al., 2004; Wang et al., 2007). This implies that plant community composition and/or ecosystem fertility are essential in the response of a community to drought

25 extremes.

We did not expect negative effects of heat-only extremes, as plants would be able to cool themselves when supplied with ample water. Our experiment indeed revealed no detrimental influence of heat (except very occasionally in scenario IV, see Fig. 2), and – in contrast – even an increased aboveground biomass. When heat was combined

with drought, leaf and plant survival declined strongly, yet aboveground biomass at the end of the season was likewise greater. The heated and especially the combined treatments leaned towards a lower root-to-shoot ratio than the non-heated treatments (C and D). This shift in biomass and also nitrogen allocation from roots to shoots in the heated treatments suggests a reduced investment in the search for nutrients or a lower seasonal retranslocation of nitrogen from already senescing leaves to storage organs (Heckathorn and Delucia, 1996). The heated treatments may thus have had more easy access to soil nutrients, through accelerated nutrient mineralization under heating (Emmett et al., 2004; Rustad et al., 2001), or through decreased nutrient competition as a consequence of mortality of neighbouring plants. Higher oxygen levels in the drier soils of DH compared to H may have further stimulated mineralization. This may explain why treatment H and especially DH tended to maintain relatively more biomass and nitrogen in the aboveground parts compared to C and D. This hypothesis is supported by the leaf colour data, where greener leaves in the DH treatment indicated more nitrogen and thus photosynthetically more active leaves (Larcher, 2003).

Our results show varying impacts of the preceding single extremes on plant and leaf survival depending on the scenario, in spite of the similarity in soil water content and daily maximal temperature. The first extreme of scenario III did not induce any plant mortality, contrasting the first extremes of scenarios IV and II were plant mortality reached 58 and 30 %, respectively. The sensitivity of plants thus varied within the time span of a few weeks. Possibly the phenological stage of the plants determined their vulnerability (amount of leaf area and thus evaporating surface, or investment in reproductive organs) (Cakir, 2004; Craine et al., 2012; Ge et al., 2012). However, these differences in mortality were not present anymore in the end-of-season biomass, indicating that remaining plants profited from decreased competition for resources.

4.2 Single versus recurrent extremes and effect of recovery time

When facing recurrent extremes, the state of the system when entering the second event will be a factor determining the outcome. This state is determined by the sys-

tem's resistance and resilience to the first event, and the elapsed time since that first event. Slow-growing, long-lived systems that are not very resilient (e.g. forests) will face a slow recovery, and may be more likely to experience the cumulative impact of multiple extremes in the course of their lifespan. Grasslands however, generally exhibit fast recovery (Brilli et al., 2011; Walter et al., 2011; Zavalloni et al., 2008), which we also observed in this study. The recovery period between recurrent extreme events in grasslands would therefore be most important in the case of relatively short interval periods, as recovery would then still be incomplete. Our results indeed show that leaf mortality at the end of the second extreme, which was limited to the combined treatment, was induced only when the recovery period was 14 days. Strikingly, this occurred in spite of apparent complete recovery in living leaves before the initiation of that second event. The fact that a reduced resistance caused by the first event was still present but no longer detectable in the form of leaf mortality, indicates that physiological or molecular processes were still affected. However, this phenomenon did not persist very long, as the scenarios with a longer interval period did not show such a reduced resistance. Unfortunately, the alternative hypothesis of a possible improved resistance induced by a preceding extreme with a longer interval, could not be tested, as the second extreme alone did not trigger mortality responses.

Our assemblages were constructed and consisted of only three species, so a comparison with more species-rich communities is of interest. Some experiments have indeed found that community resilience increases with species richness (DeClerck et al., 2006; van Ruijven and Berendse, 2010), in line with the 'insurance hypothesis' which states that more diverse systems are more resilient (and resistant) to environmental perturbations (Yachi and Loreau, 1999; Kahmen et al., 2005; Tilman et al., 2006). This is explained by a greater probability of including species that will increase their performance and compensate for declining species in response to a particular perturbation. Van Peer et al. (2001; 2004) likewise observed greater resilience in species-richer assemblages after a combined drought and heat extreme, owing to greater mortality and thus decreased resource competition during regrowth. However, several experiments

have observed no or the opposite effect of species richness on resilience to perturbations (Pfisterer and Schmid, 2002; Elmqvist et al., 2003; Wardle et al., 2000; Zavalloni et al., 2009). These observations lead to the idea that the functional diversity of a community, in particular its "response diversity" (Elmqvist et al., 2003), is a critical determinant of the resilience of a system (Chillo et al., 2011; Hooper et al., 2005), with 'response diversity' being the diversity of responses among species that otherwise have a similar function in the system (thus belonging to the same functional group). Functional groups with a lower response diversity would diminish the resilience since less compensatory effects among species can occur (Chillo et al., 2011; Elmqvist et al., 2003). Other experiments rather suggest that the traits of dominant species are more important in determining community recovery (Gilgen et al., 2010; Mokany et al., 2008; van Ruijven and Berendse, 2010). Our results lean towards this theory, as the absence of a nitrogen fixer seemed to define the community response. Yet, the relation between (functional) diversity, productivity, and resilience still requires further study in order to make projections on how ecosystems will react to multiple extremes more reliable.

5 Conclusions

Our results show that, when experimental temperate herbaceous assemblages were exposed to recurrent extreme events, the effect of a preceding event disappeared fairly quickly. The resistance to subsequent events in terms of leaf survival was reduced when the recovery period was relatively short (14 days for the assemblages studied here), but not when it was longer. Especially combinations of extreme heat and drought suffered from loss of resistance, and the memory effects of previous events occurred even though recovery seemed complete and no more leaf damage was detectable. End-of-season biomass was independent of the recovery period and of the number of applied events, despite substantial plant loss in some of the treatments. In the assemblages exposed to the heated and combined heat and drought extremes, aboveground

biomass was even increased, indicating that indirect effects of heating compensated for the short-term negative effects.

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Table 1. Overview of different scenarios and treatments with number of replicate experimental plant assemblages per treatment, length of the drought events and the average daily maximal temperatures during the heat waves. C = control, D = drought, H = heat, DH = drought + heat. * = highest average daily T_{max} at the height of the canopy observed in the control plots during the entire period (DOY 153–225) preceding the second event.

Scenario	Interval (days)	Treatments		nr. of plant assemblages	average daily T_{max} (°C)	drought (days)	average daily T_{max} (°C)	drought (days)
		1st event	2nd event		1st event		2nd event	
		C	C	27	29.3*	0	23.4	0
IV	42	D	D	15	27.9	25	23.4	25
IV	42	H	H	15	32.6	0	30.2	0
IV	42	DH	DH	15	32.6	25	30.2	25
III	25	D	D	15	30.9	19	23.4	25
III	25	H	H	15	34.5	0	30.2	0
III	25	DH	DH	15	34.5	19	30.2	25
II	14	D	D	15	29.1	20	23.4	25
II	14	H	H	15	32.9	0	30.2	0
II	14	DH	DH	15	32.9	20	30.2	25
I	/	C	D	9	29.3*	/	23.4	25
I	/	C	H	9	29.3*	/	30.2	0
I	/	C	DH	9	29.3*	/	30.2	25
Total		13		189				
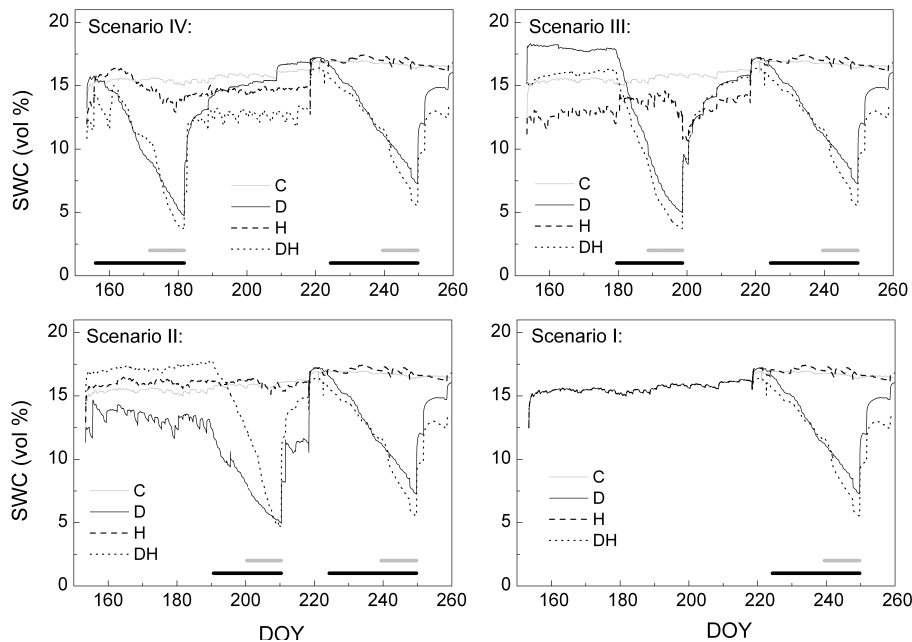
Fig. 1. Volumetric soil water content (SWC) during different scenarios and treatments. C = control, D = drought, H = heat, DH = drought + heat. Bottom lines in each graph indicate timing of the climate events (black line = timing of drought extreme, grey line = timing of heat extreme).
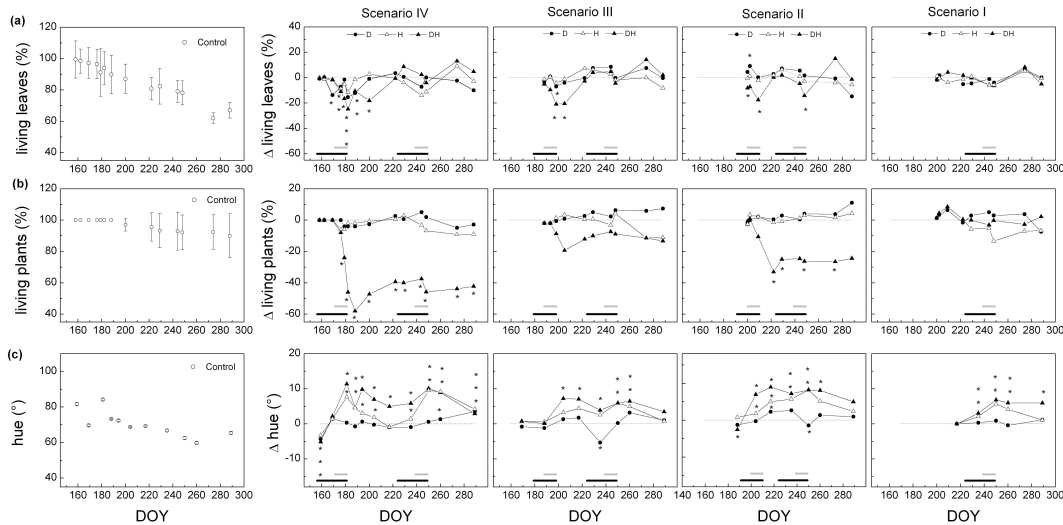
Fig. 2. Course of **(a)** the percentage of living leaves, **(b)** the percentage of living plants and **(c)** hue (°, unique yellow is situated on 60°, unique green on 120°) of the controls (left panel) and the difference between the controls and the treatments during the different scenarios. Standard errors are displayed for the controls but are not shown for the other treatments for improved clarity. D = drought (closed circles), H = heat (open triangles), DH = drought + heat (closed triangles). Bottom lines in each graph indicate timing of the climate events (black line = drought, grey line = heat wave). Asterisks, arranged in the same vertical order as the points, indicate significant differences (*P* <0.05) between treatments and control on that day. DOY = day of year.
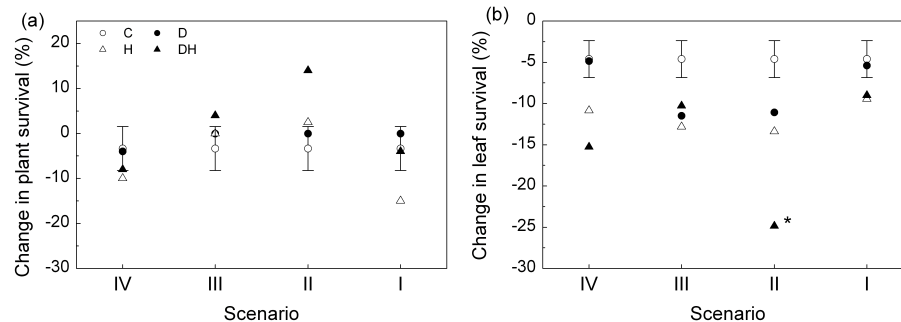
Fig. 3. Influence of the second extreme on **(a)** plant survival and **(b)** leaf survival, per scenario. C = control, D = drought, H = heat, DH = drought + heat. For improved clarity, standard errors are displayed only for the controls. Asterisks next to symbols indicate significant differences (*P*<0.05) between treatment and control.
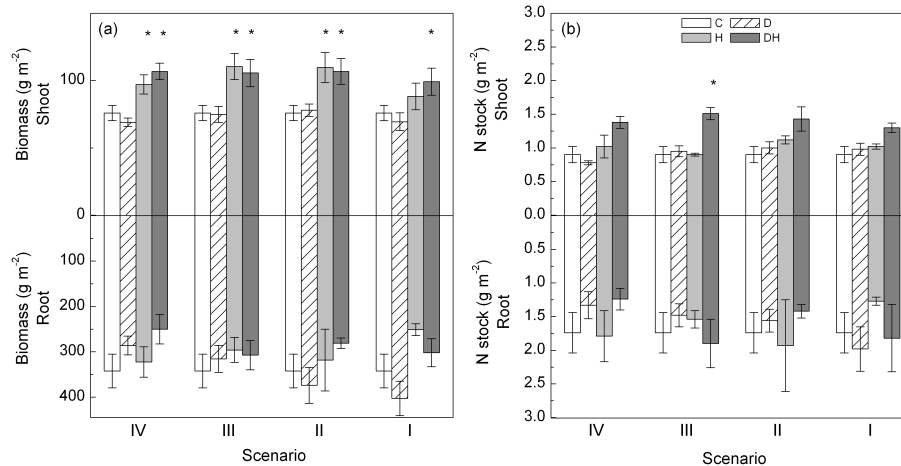
Fig. 4. Mean values and standard errors of **(a)** end-of-season above- and belowground biomass and **(b)** end-of-season above- and belowground nitrogen stock, per scenario and treatment. C = control, D = drought, H = heat, DH = drought + heat. Asterisks indicate significant differences between treatment and control ($P < 0.05$).
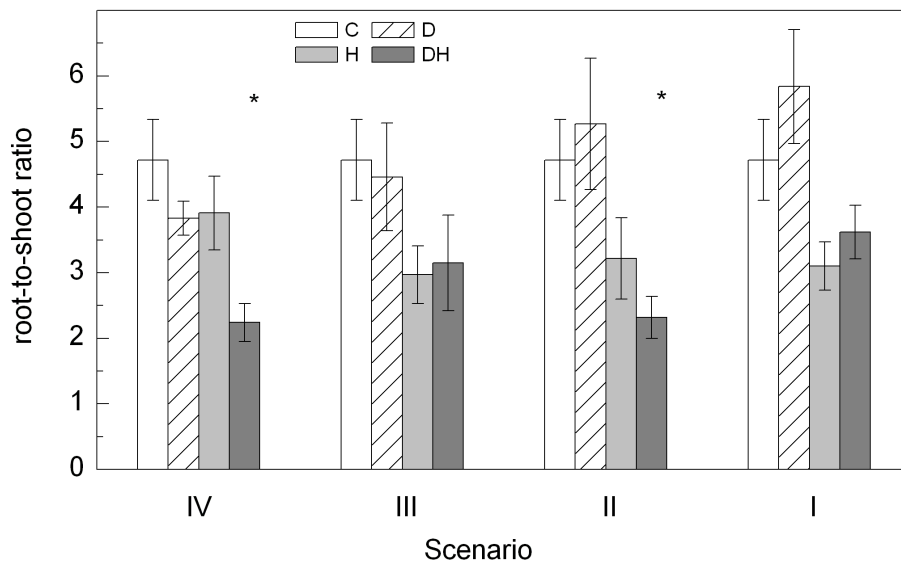
Fig. 5. Root-to-shoot ratios, per scenario and treatment. C = control, D = drought, H = heat, DH = drought + heat. Asterisks indicate significant differences between treatment and control ($P < 0.05$).