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Impact of climate extremes modulated by species characteristics and richness



in Plant Ecology

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ABSTRACT

Drought and heat extremes can inflict substantial damage on plant communities, but the influences of species characteristics and richness on a community's ability to cope with these events are poorly understood.

In this study, we investigate the effects of species characteristics (drought tolerance and functional group) at different richness levels on (1) the ability to maintain green leaf area during a drought (and heat) extreme (resistance) and recover thereafter (resilience) and (2) the capacity of community biomass to recover by the end of the growing season. Our communities consist of drought-resistant and drought-sensitive grasses and nitrogen-fixing legumes (N-fixers) according to Ellenberg's humidity index, planted in different richness levels (1, 2 and 6 species) with 50% grasses and 50% N-fixers per community. This resulted in 28 different plant communities, repeated under six rain-out shelters, with each climate treatment (control, drought or drought with an additional heatwave) allocated to two main plots.

Grasses associated with drier habitats (assumed resistant) tolerated extremes better than grasses from wetter habitats (assumed sensitive), and grasses were generally more resistant and resilient against climate extremes than N-fixers. Species richness did not influence the green fraction in grasses, while N-fixers senesced more in diverse communities. In contrast, after recovery the N-fixers' biomass was independent of richness, while grasses produced more biomass in species-rich communities, probably due to positive effects of nitrogen fixation. Surprisingly, all these richness effects on stability were similar for resistant and sensitive species.

We demonstrated that understanding community responses to climate extremes requires a simultaneous focus on species characteristics and interspecific interactions (richness). Trends at the community level are determined by functional groups and response groups which influence each other. To obtain generalised universal patters, more insight at this level of complexity is needed.

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1. Introduction

Changes in the global climate are not only altering the average characteristics of climate systems, but also the frequency, intensity, spatial extent, duration and timing of climate extremes (IPCC, 2013; Herring et al., 2014). A climate extreme occurs when the value of a weather or climate variable such as temperature or precipitation exceeds (or falls below) a threshold value near the upper (or lower) end of the range of observed values of the variable (IPCC, 2013). These discrete events often have a disproportionate impact on ecosystems relative to the temporal scale over which they occur.

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http://dx.doi.org/10.1016/j.ppees.2016.12.007 1433-8319/© 2016 Elsevier GmbH. All rights reserved. Reichstein et al. (2013) state that climate extremes can decrease regional ecosystem carbon stocks and therefore reinforce climate change. Despite an increased interest in the ecological impact of climate extremes, many questions remain unanswered especially regarding the significance of individual species characteristics and the importance of biodiversity in mediating the responses (Smith, 2011; Vogel et al., 2012; Bailey and van de Pol, 2016).

Climate models project that summer droughts and heat waves in European grasslands will become longer and more frequent (IPCC, 2007; Evans et al., 2011). Reduced water uptake by roots during drought extremes triggers a cascade of signalling plant hormones (such as abscisic acid, auxin, cytokinins, ethylene, etc.), resulting in stomatal closure and growth inhibition so that further water loss is abated (Chaves et al., 2003; Wahid et al., 2007; Liu et al., 2012; Lipiec et al., 2013; Hasanuzzaman et al., 2013). As such, drought also induces heat stress since lower latent heat dissipation through transpiration increases tissue temperatures (De Boeck et al., 2010). The connection between the water and energy balance also works the other way round: heat results in warmer leaves and higher atmospheric water demand, which will accelerate drought, especially when leaf area is high. Accordingly, heat and drought can reinforce each other (De Boeck and Verbeeck, 2011; Liu et al., 2012; Lipiec et al., 2013; De Boeck et al., 2016), leading to reduced plant productivity and reproduction, early senescence and eventually death (Chaves et al., 2003; Wahid et al., 2007; Lipiec et al., 2013). Since naturally occurring climate extremes thus often feature combined stressors, it is important to examine their effects on plants and plant communities in conjunction. However, whether a climatic extreme induces an extreme ecological response (Smith, 2011) depends on the system's ability to withstand and/or recover from stress as well as on the degree of acclimation of the organisms, and will thus be species- and ecosystem-specific (Diez et al., 2012).

Species-specific characteristics can have a profound impact on a plant's ability to cope with climate extremes. Some species withstand stress without loss of function (resistance), while others are able to recover rapidly after stress (resilience) (Virginia and Wall, 2001; Van Peer et al., 2004; Lake, 2012). The stability of an ecosystem is determined by the traits of the dominant plant species (MacGillivray and Grime, 1995; Díaz and Cabido, 2001) or the presence of some specific species such as nitrogen-fixing legumes that can facilitate neighbour plants for some types of extremes (Pfisterer and Schmid, 2002; Arfin Kahn et al., 2014; Hoekstra et al., 2015; Hernandez and Picon-Cochard, 2016). In general, productive species with a high growth rate (e.g. grasses) have low resistance and high resilience, while slow growers with long-lived organs and low rates of nutrient turnover (e.g. trees) have high resistance and low resilience, indicating a trade-off (MacGillivray and Grime, 1995; Díaz and Cabido, 2001). Therefore, productive species, like many grasses, are expected to recover quickly after a climate extreme, especially in the presence of nitrogen-fixing legumes.

Besides species-specific characteristics, species richness can determine ecosystem stability, with species-rich communities generally being more stable than species-poor ones (Elton, 1958; Bloor and Bardgett, 2012; Roscher et al., 2013). Multi-species communities are hypothesized to have an 'insured' stability due to the higher probability of containing (for example) drought-adapted species that can buffer ecosystem functioning (Yachi and Loreau, 1999). Moreover, species richness is an important factor regulating the productivity of an ecosystem. Firstly, complementarity (including facilitation) in space and time enables more diverse communities to take up more resources compared to less diverse communities, resulting in higher productivity (Hooper, 1998; Nijs and Impens, 2000; Hooper et al., 2005). In addition, species-rich communities have a higher probability (selection or sampling effect) that one or more productive species become dominant (Hooper et al., 2005). Despite these well-defined mechanisms, the complex interplay between biodiversity, ecosystem stability and productivity yields varying results (e.g. Isbell et al., 2015 [positive richness effects on productivity and stability]; Lanta et al., 2012 [positive richness effects on productivity, negative richness effects on stability]; Van Ruijven and Berendse, 2005 [richness effect on resilience, but not on resistance]). Studies that systematically vary both species attributes and community structure may contribute to elucidating this interplay, but to our knowledge, species-specific drought tolerance was never included in experimental studies on diversity and climate extremes.

In this study, we explore effects of species characteristics (drought tolerance and functional group) and species richness on the impact of extreme drought only and extreme drought with an additional heat wave. We investigate the responses of droughtresistant, drought-sensitive and mixed plant communities (species selected according to Ellenberg's humidity index; Ellenberg et al.,

1991), composed of one, two or six species with an equal amount of grasses and nitrogen-fixing legumes (hereafter called N-fixers) during and after the imposed extremes. Specifically, effects of these controlled species characteristics (assumed resistant or sensitive, grass vs. N-fixer) at different richness levels are assessed on (1) the capacity to maintain green leaf area during a climate extreme (resistance) and recover thereafter (resilience) and (2) the capacity of community biomass to recover by the end of the growing season. We hypothesize that species associated with on average drier soil conditions will be more able to keep plant tissue alive during extreme events compared to species that are found more frequently in wetter habitats. On the other hand, dry-habitat species should be less resilient based on their generally lower growth rates. Richness effects on resistance are expected to differ for species assumed resistant and sensitive because differences in productivity between these groups affect water use during drought. N-fixing species are predicted to facilitate grasses especially during recovery after extremes.

2. Materials and methods

2.1. Experimental design

For this experiment we selected 12 species that occur in Belgian grasslands (Table 1): three drought-sensitive grasses (SG), three drought-resistant grasses (RG), three drought-sensitive Nfixers (SN) and three drought-resistant N-fixers (RN). The drought tolerance level of these species was determined with Ellenberg's humidity index (Ellenberg et al., 1991), since this is the most objective value for drought resistance available for all plants used in the experiment. The humidity index gives a value between one and twelve indicating the soil moisture conditions in which a plant prefers to grow (1: very dry - 12: underwater). On April 5 and 6 2012 (DOY 96 and 97), seeds were sown in quickpots containing sandy soil (78% sand, 19% loam, 3.0% clay, pH 5.5, 260 g m⁻³ P, $110 \,\mathrm{g}\,\mathrm{m}^{-3}$ K, 97 $\mathrm{g}\,\mathrm{m}^{-3}$ Mg, 1300 $\mathrm{g}\,\mathrm{m}^{-3}$ Ca, 1.4 $\mathrm{g}\,\mathrm{m}^{-3}$ Na), with a volumetric water content of $0.201 \text{ m}^3 \text{ m}^{-3}$ (pF 2) at field capacity, $0.052 \text{ m}^3 \text{ m}^{-3}$ (pF 3.3) at the point of reduced water availability and $0.030\,m^3\,m^{-3}$ (pF 4.2) at wilting point (Bodemkundige Dienst van België, Leuven, Belgium). Between May 22 (DOY 143) and June 6 (DOY 158) 2012, the seedlings were transplanted into experimental containers (PVC tubes: Ø 40 cm, 50 cm deep) with the same soil. All transplanted seedlings were of comparable size per species and survival was more than 95%, with immediate replacement of individuals that died after transplanting. The containers were buried to keep the soil temperature in the communities near natural conditions, and a closed lid at the bottom prevented water inflow from the surroundings. Each community consisted of 42 individuals, planted in a hexagonal grid with 4 cm interspace.

Experimental communities were either monocultures (S1, 42 individuals per species), or communities with two (S2, 21 individuals per species) or six (S6, 7 individuals per species) species composed of 50% grasses and 50% N-fixers. In addition, all species from the same functional group had the same drought tolerance according to Ellenberg et al. (1991). This resulted in S2 and S6 communities that could be classified as either drought-sensitive (50% sensitive grasses and 50% sensitive N-fixers), drought-resistant (50% resistant grasses and 50% resistant N-fixers) or mixed (50% sensitive grasses and 50% resistant N-fixers or vice versa). Combining the species in this way resulted in twelve different monocultures, twelve different S2 and four different S6 combinations (Table 2). The arrangement of the different species within the hexagonal grid can be found in supplementary file 1. The communities were set up in six main plots of which two (main plots 4 and 6) served as controls (C), two (main plots 1 and 3) were exposed to

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