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Recovery dynamics and invasibility of herbaceous plant communities after exposure to experimental climate extremes

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Abstract

Do climatic extremes increase the invasibility of plant communities, for example through the creation of gaps and the associated local surplus of available resources? To address this question, small experimental communities consisting of three forb species were first subjected to extreme drought and/or heat treatments in different seasons and species mortality and end-of-season biomass were examined. Then, the establishment of new species and their effects on the productivity of the community were recorded in two subsequent years without additional treatments.

The immediate response to the experimentally induced extremes was similar in all three originally planted species, with drought treatments in summer and autumn, especially when combined with heat, inducing the greatest plant mortality. Recovery in terms of end-of-season aboveground biomass was species-specific however. The dominant species, the N-fixer *Trifolium repens*, recovered poorly from the drought and drought+heat treatments. Differences in community biomass between treatments and to the controls were no longer significant in the next year. Graminoid species, especially, successfully invaded the communities, possibly because of functional dissimilarity with the species already present. Invasibility in the year following the extreme events was increased in communities that had been exposed to both a heat wave and a drought, but the number of newly established species did not increase community productivity. The identities of invading species varied distinctly, but had no clear relation with the extreme events the communities had been exposed too.

The induced climate extremes greatly affected the survival and productivity of the species and influenced the invasibility of the plant communities. However, none of the community properties seemed to be affected in the longer run, as the induced responses faded out after one or two years.

Zusammenfassung

Erhöhen extreme klimatische Bedingungen die Invasibilität von Pflanzengemeinschaften, beispielsweise indem Lücken und damit verbunden ein lokaler Überschuss an verfügbaren Ressourcen geschaffen werden? Um diese Fragestellung anzugehen, untersuchten wir kleine experimentelle Gemeinschaften, die aus drei Krautarten bestanden. Diese Gemeinschaften wurden in verschiedenen Jahreszeiten extremen Trockenheits- und/oder Wärmebehandlungen (= T-, W- bzw. T + W-Behandlung) ausgesetzt, und die Mortalität der Arten und ihre Biomasse am Ende der Vegetationsperiode wurden bestimmt. Danach wurden die Ansiedlung neuer Arten und deren Effekte auf die Produktivität der Gemeinschaft in zwei Folgejahren ohne weitere Behandlungen erfasst. Die unmittelbare Reaktion auf die experimentellen Extrembedingungen war bei den untersuchten Arten

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ähnlich, wobei Trockenheit in Sommer oder Herbst, insbesondere in Kombination mit Temperaturerhöhung, die höchste Pflanzenmortalität verursachte. Die Regeneration, gemessen als oberirdische Biomasse zu Saisonende, war je nach Art unterschiedlich. Die dominante Art,.der N-Fixierer *Trifolium repens*, erholte sich kaum von den T- bzw. T + W-Behandlungen. Die Unterschiede in der Biomasse der Gemeinschaften in unterschiedlichen Behandlungen waren im nächsten Jahr nicht mehr signifikant. Insbesondere Grasartige wanderten in die Gemeinschaften ein, möglicherweise wegen der funktionellen Unähnlichkeit zu den bereits vorhandenen Arten. Die Invasibilität im auf die experimentellen Eingriffe folgenden Jahr war in Gemeinschaften mit T + W-Behandlung erhöht, aber die Zahl der neu angesiedelten Arten erhöhte nicht die Produktivität der Gemeinschaft. Die Identität der einwandernden Arten war sehr unterschiedlich, zeigten aber keine klare Reaktion auf die jeweiligen Behandlungen. Die experimentellen Extrembedingungen beeinflussten erheblich das Überleben und die Produktivität der Arten sowie die Invasibilität der Gemeinschaften. Indessen schien aber keine der Gemeinschaften nachhaltig beeinflusst zu werden, da die Reaktionen nach einem oder zwei Jahren schwächer wurden.

Keywords: Biomass; Colonization; Drought; Experiment; Gap; Heat wave; Legacy effects; Plant ecology

Introduction

Extreme climate events have become a key issue in global change research, in view of their increasing frequency and intensity and their potential impact on ecosystems (IPCC 2012). In plant communities, intense drought and heat events can cause major disturbance, including loss of productivity (Ciais et al., 2005; Boeck, Dreesen, Janssens, & Nijs, 2011) and increased die-off (Breshears et al., 2005; Kreyling, Wenigmann, Beierkuhnlein, & Jentsch, 2008b). Lagged responses include higher mortality, slow recovery or increased sensitivity to pests or future events (Arnone et al., 2008; Reichstein et al., 2013). This might even turn CO_2 sinks into sources, creating a positive feedback for climate warming (Reichstein et al., 2013). An additional effect of extreme events is that they may render communities more sensitive to invasion by new species since disturbance, by creating gaps in the original community, is a major driver of invasibility (Burke & Grime, 1996). This imposes additional pressures on the persistence of plant communities besides the direct effect of the events themselves.

According to the fluctuating resource availability theory (Davis, Grime, & Thompson, 2000), a community becomes more susceptible to invasion when the amount of unused resources is increased. This occurs when resource uptake by the resident community is diminished (e.g., following plant mortality) or when an increase in resources exceeds the sequestration rate of the resident plants (e.g., following improved water supply or eutrophication) (Davis et al., 2000). Several studies have indeed reported enhanced invasibility after disturbance events, including droughts (Belote, Jones, Hood, & Wender, 2008; Jiménez et al., 2011; Kreyling, Beierkuhnlein, Ellis, & Jentsch, 2008a). However, invasibility could also be reduced by disturbance if the events create suboptimal conditions, allowing only few, disturbance-tolerant species to colonize and establish (Davis, Thompson, & Grime, 2005). Several studies have suggested that communities containing more species would generally lower invasibility as more niches are occupied and the amount of unused resources is decreased (e.g., Dukes, 2001; Frankow-Lindberg, 2012; van Ruijven, De Deyn, & Berendse, 2003). This relationship is not ubiquitous and is also related to scale (Fridley et al., 2007). Even so, disturbance can influence the diversity of communities through mortality, diversity can affect invasibility and invasibility can in turn determine diversity through newly incoming species, suggesting that diversity, disturbance (i.e. changes in available resources) and invasibility all co-vary (Clark & Johnston, 2011).

The species that enter the community after an extreme climatic event can influence carbon, water and nutrient cycling through species-specific impacts on productivity, above- and belowground nitrogen storage, etc. For example, grasses invading a semiarid shrubland have been found to increase carbon and nitrogen storage while the opposite was found for woody plants invading wet grasslands (Jackson, Banner, Jobbagy, Pockman, & Wall, 2002; Wolkovich, Lipson, Virginia, Cottingham, & Bolger, 2010). Meta-analysis of plant invasion studies revealed that invading woody and N-fixing species usually had a greater impact on carbon and nitrogen cycles than those by herbaceous and non-N-fixing species (Liao et al., 2008). Knowledge on how extreme events would affect community composition after an extreme event is therefore relevant when assessing elemental cycles of ecosystems over longer periods. Which species invade communities would not only depend on the amount of unused resources and gaps, but also on the characteristics of species that were already present. It is often speculated that species that are functionally different from resident species have a higher invasion success (see the meta-analysis of Price & Pärtel, 2012). The fact that no graminoid species were originally present in our communities enables us to test this assumption.

In this study, we subjected constructed plant communities consisting of three common herbaceous species to experimentally induced drought and/or heat events in different seasons. In the following two years, other species were allowed to invade the plant communities. We hypothesized that (i) the climate extremes would cause different amounts of