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Impacts of extreme precipitation and seasonal changes in precipitation on plants

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Abstract

The hydrological cycle is predicted to become more intense in future climates, with both larger precipitation events and longer times between events. Redistribution of precipitation may occur both within and across seasons, and the resulting wide fluctuations in soil water content may dramatically affect plants. Though these responses remain poorly understood, recent research in this emerging field suggests the effects of redistributed precipitation may differ from predictions based on previous drought studies. We review available studies on both *extreme precipitation* (redistribution within seasons) and *seasonal changes in precipitation* (redistribution across seasons) on grasslands and forests.

Extreme precipitation differentially affected Aboveground Net Primary Productivity (ANPP), depending on whether extreme precipitation led to increased or decreased soil water content (SWC), which differed based on the current precipitation at the site. Specifically, studies to date reported that extreme precipitation decreased ANPP in mesic sites, but, conversely, increased ANPP in xeric sites, suggesting that plant available water is a key factor driving responses to extreme precipitation. Similarly, the effects of seasonal changes in precipitation on ANPP, phenology, and leaf and fruit development varied with the effect on SWC. *Reductions* in spring or summer generally had negative effects on plants, associated with reduced SWC, while subsequent reductions in autumn or winter had little effect on SWC or plants. Similarly, *increased* summer precipitation had a more dramatic impact on plants than winter increases in precipitation.

The patterns of response suggest xeric biomes may respond positively to extreme precipitation, while comparatively mesic biomes may be more likely to be negatively affected. And, seasonal changes in precipitation during warm or dry seasons may have larger effects than changes during cool or wet seasons. Accordingly, responses to redistributed precipitation will involve a complex interplay between plant available water, plant functional type, soil type and resultant influences on plant phenology, growth and

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water relations. These results highlight the need for experiments across a range of plant functional types, critical for predicting future vegetation responses to future climates.

1 Introduction

Two critical priorities under future climates are managing water resources and understanding the impacts of climate change on vegetation. Climate change may dramatically alter water resources through changes in the timing of precipitation (Christensen et al., 2007; IPCC, 2011; Smith, 2011). Increasing evidence suggests that variability and extremes in precipitation are more important drivers of ecosystem processes than mean conditions (Heisler-White et al., 2008, 2009; Smith, 2011; Reyer et al., 2012; Thompson et al., 2013). In particular, both the size and timing of rain events are strong drivers of ecological processes (Schwinning and Sala, 2004; Zeppel et al., 2008a). As a result, responses to changes in the distribution of precipitation over time are likely to differ from responses to individual drought events (Luo et al., 2011). While the effects of drought have been extensively studied (Breshears et al., 2009; Allen et al., 2010), the effects of altered timing of precipitation on plants remain largely unknown (Misson et al., 2011; Volder et al., 2013).

In addition to direct effects on plant growth and mortality rates, altered timing of precipitation may have significant effects on local climatic conditions. This is because local ecosystems such as forests can have a strong influence on temperature, precipitation and albedo (Bonan, 2008). For example, reductions in plant growth and increases in mortality often affect complex links among soil biochemistry, land-surface interactions, carbon and water fluxes, which may alter stream-flow and increase evapotranspiration (Keith et al., 2009; Adams et al., 2011). This creates land-surface feedbacks among vegetation, hydrology and climates (Adams et al., 2011).

To address these issues we need an understanding of the influence of redistributed timing of precipitation on processes across a range of plant functional types, such as shallow- and deep-rooted plants (Fay et al., 2008; Beier et al., 2012). Previous reviews

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have highlighted the striking gap in understanding how plants respond to extreme and altered seasonality of precipitation (Beier et al., 2012; Reyer et al., 2012). Here, we describe the experimental, observational and modeled results of plant responses to altered seasonality of precipitation and extreme precipitation, addressing a key research gap.

Our primary objective is to review the current knowledge on the effects of altered timing of precipitation on grassland and forest ecosystems, ranging from semi-arid grasslands and savannas, Mediterranean and temperate forests to tundra and boreal ecosystems. We examine effects of redistributed precipitation on plant processes, including stomatal conductance, leaf water potential, and Above-ground Net Primary Productivity (ANPP) and soil fluxes. Finally, we assess (1) how do plants respond to changed seasonality of precipitation, (2) under what circumstances does extreme precipitation lead to increased ANPP, and when does it lead to lower ANPP and (3) are plants in those circumstances water-limited to begin with?

Here, we use the following terms (Fig. 1): “Altered” or “redistributed” precipitation includes both “seasonal redistribution” and “extreme precipitation”. “Extreme” means both the amount of and the time between rain events are increased, while the total quantity of water remains constant (see Smith, 2011). “Seasonal redistribution” means reduced precipitation for an entire month or season, with increased precipitation at a later month or season (see Volder et al. 2013).

1.1 Past and projected changes in the timing of precipitation

The hydrological cycle has been intensifying (Huntington, 2006), and is projected to continue to intensify with both the size of and time between rain events increasing over the past century (Christensen et al., 2007; IPCC, 2011). Specifically, climate change is predicted to alter the timing, from one season or period to another, and event size of precipitation, fewer, large, rather than many smaller rain events (Pitman and Perkins, 2008; CSIRO, 2011; IPCC, 2011). Changes in seasonal precipitation patterns are expected to exhibit substantial regional and temporal variation (Christensen et al., 2007).

Projections for future climate scenarios are that *many regions* will experience more intense, extreme precipitation (Christensen et al., 2007; Smith, 2011), whereas *some regions* are projected to receive seasonal shifts, including Africa (Hely et al., 2006) oak savannas (Volder et al., 2013) and prairies of USA (Chimner et al., 2010), southern Australia (CSIRO, 2011) and Mediterranean regions (Misson et al., 2011) including semi-arid Spain (Miranda et al., 2009a). Southern France and south-east Australia may experience decreased precipitation in spring and increases in autumn (CSIRO, 2011; Misson et al., 2011). United States mixed grass prairies are projected to receive wetter winters, and drier summers (Chimner et al., 2010), whereas oak savannas are projected to experience drier summers and wetter spring and autumn (Volder et al., 2013). Semi-arid Spain is projected to receive wetter winters, and drier spring and autumn periods (Miranda et al., 2009a), leading to potential changes in soil and plant processes.

The most direct result of redistributed precipitation is altered soil water content (SWC), with less plant-available water in some periods and more in other periods which is highly dependant upon soil type. Increased pulses of rain have strong impacts on plants in water-limited regions (Zeppel et al., 2008a; Resco et al., 2009), and may increase deep-drainage in water-abundant regions. These changes in SWC are likely to be exacerbated by predicted rising temperatures and intensified heat waves (Smith, 2011), increasing evaporation and transpiration. Therefore, plant responses to future climates are likely to reflect much larger fluctuations in SWC than historically experienced (Knapp et al., 2002; Weltzin et al., 2003) highlighing the urgent need to understand plant responses to extreme and seasonal changes in rainfall events (Smith, 2011).

1.2 How might plants respond?

Variation in soil water content (SWC) and soil type often have a substantial effect on plant and soil processes (Fig. 3) (Brzostek et al., 2012). Increasingly large fluctuations in SWC following redistributed precipitation also drive physiological responses,

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community structure and the distribution of plant functional types (Volder et al., 2013). *Extreme* precipitation may influence plant water relations, hydraulic architecture, and ANPP (Reyer et al., 2012), whereas changing *seasonal* precipitation may also influence phenology, including fruit, leaf and early/late wood development, as well as tiller development of grasses (Volder et al., 2010; Misson et al., 2011).

There is a hierarchy of ecological responses to rain events, ranging from hours to decades (Schwinning and Sala, 2004). When changes in precipitation are comparatively small, plants show a limited response (Gerten et al., 2008; Miranda et al., 2009a). However, under future climates, the variability in SWC that plants experience is likely to rapidly increase beyond current limits (Smith, 2011). The current framework on the effects of altered timing of precipitation suggests that extreme precipitation would lead to increased run-off and deep drainage, shallow soil becoming drier, and reduced plant growth when water is already limiting, or water-logged (Knapp et al., 2008). We test this framework against experimental and modeled data.

1.3 Factors regulating the effects of redistributed precipitation

The influence that redistributed precipitation will have on plant processes is likely to depend upon soil properties, micro-climate, plant functional type, and the nature of the change in timing. Soil water content is driven in part by soil type, soil depth and density. Micro-climatic factors that influence evapotranspiration also determine whether changes in timing have a large impact (Fay et al., 2008; Zeppel et al., 2008b). Further, current mean annual precipitation (MAP), as well as the site aridity index, the ratio of MAP to Potential Evapotranspiration, which influences whether the site is xeric, mesic or hydric, will be a key factor determining whether plant growth increases or declines (Knapp et al., 2008; Heisler-White et al., 2009). Added effects of heat stress, rising mean temperatures, elevated CO_2, vapour pressure deficit (D), and the current season when most precipitation falls, are also likely to influence plant responses to altered precipitation (Volder et al., 2010).

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Plant functional type could also affect the response to changes in timing. Shallow-rooted vs. deep-rooted plants; deciduous vs. evergreen plants; and seedlings, and mature trees vs. mid-life trees may respond differently to altered precipitation (Knapp et al., 2008; Zeppel et al., 2011). More broadly, responses of ANPP to precipitation are likely to vary among biomes (Huxman et al., 2004). In order to identify which variables mediate these effects, and to what extent, we now discuss results of precipitation timing experiments.

2 Results of precipitation timing experiments

Many field experiments have imposed drought (Hanson et al., 2003; Wullschleger and Hanson, 2006; Beier et al., 2012) or described the impact of pulses of precipitation (Fravolini et al., 2005; Potts et al., 2006; Zeppel et al., 2008a; Resco et al., 2009). Here, we focus on seasonal changes in precipitation and extreme precipitation. Altered seasonality of precipitation may be implemented, for example, by delivering 80 % of annual precipitation in spring or winter, while retaining the same annual volume (Bates et al., 2006) (Table 1). Alternatively, extreme precipitation regimes have been imposed by adding fewer but larger precipitation events, while maintaining the same total volume of water added (Harper et al., 2005) (Table 2).

2.1 Seasonal changes in precipitation

Impacts of seasonal changes in precipitation have been reported in boreal forests (Gaul et al., 2008), arctic tundra (Schimel et al., 2004), tropical rainforests in the Amazon (Nepstad et al., 2002; Brando et al., 2006, 2008) oak savannas (Volder et al., 2010, 2013) and Mediterranean regions, such as Spain (Miranda et al., 2009b). Although grasslands, savannas and Mediterranean forests differ markedly in the timing of ambient precipitation and the length of growing season, experiments suggest patterns can be found in responses to seasonal changes in precipitation, such as strong changes in

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water stress and productivity in warm or dry seasons, and not in cool or wet seasons. Below, we briefly outline the major experiments in these systems.

2.1.1 Seasonal changes in boreal and sub-alpine regions

Manipulation of precipitation in semi-arid regions using ROS and snow fences has led to alterations in biomass (Chimner et al., 2010; Thomey et al., 2011), the amount and timing of nutrient cycling (Schimel et al., 2004), and mortality and community composition (Schwinning et al., 2005a, b). In the cold desert grasslands in the Colorado Plateau (USA), with a mean annual precipitation (MAP) of 218 mm, plant water relations and growth of all three measured species were more sensitive to summer drought than winter drought (Schwinning et al., 2005a, b).

2.1.2 Seasonal changes in grasslands

Seasonal redistribution experiments in grasslands have led to changes in ANPP, with results indicating that the response of ANPP depends on which seasons receive additional water and which seasons receive less water. The seasonality of precipitation was altered in grasslands in Oregon, USA over seven years, moving 80 % of annual precipitation to winter or spring (Bates et al., 2006). When precipitation was moved to winter, SWC and biomass did not change. In contrast, when precipitation was moved to spring, productivity reduced. Further, many of the biomass reductions did not occur until the fourth year of treatment. Apparently in spring, increased evaporation offset the increased amount of water, such that SWC did not increase enough to stimulate growth (Bates et al., 2006). Similarly, in a limestone grassland in England, 20 % increases in summer precipitation increased summer growth, whereas increased autumn and winter precipitation had no effect on growth (Morecroft et al., 2004). Note that increases in spring precipitation lead to growth *reductions* in Oregon, whereas increases in summer precipitation in England, lead to *increases* in growth. This may be because potential

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evapotranspiration was higher than water addition due to the warmer air in Oregon, compared with England.

A study from semi-arid plant communities in Spain conducted glasshouse experiments, using drought and seasonal precipitation redistribution treatments. The altered seasonality treatment reduced both spring and autumn by 15 % and increased winter precipitation by 30 %. Accentuated seasonality decreased mean individual ANPP by 30 %, and did not alter flowering phenology (Miranda et al., 2009a). The absence of a flowering response contrasts with the Mediterranean woodland, where changing seasonal precipitation resulted in differences in phenology (Misson et al., 2011). These contrasting results are likely to be a consequence of the different treatments applied, species measured, or biomes of origin, and highlight the importance of comparing different biomes (Beier et al., 2012).

2.1.3 Seasonal changes in Mediterranean forest

In the Mediterranean *Quercus ilex* forest, Montpelier, France, phenological responses of trees to seasonal drought were tested using rainout shelters (Misson et al., 2011). Exclusion of 97 % of autumn precipitation did not significantly alter leaf, flower or fruit development. However, exclusion of 87 % of spring precipitation resulted in water stress during important phases of leaf and fruit development. Only half of the sampled trees in the spring treatment reached the stage of functionally mature leaves, with the others abandoning leaf development at earlier stages. Further, only one of six female trees reached complete fruit maturation, though male flowers were unaffected, likely due to the higher resource requirements for female flowers and earlier leaf development, before highest water stress, compared with male flowers (Misson et al., 2011). These results indicate that the quantity of spring precipitation is more important than total annual precipitation for this system, with significant implications for vegetation predicted to receive reductions in precipitation in spring, such as Spain, France, and south-east Australia.

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2.1.4 Seasonal changes in savanna

An oak savanna in southern USA received six-years of precipitation redistribution, with 40 % of summer precipitation redistributed to spring and autumn, intensifying the summer drought (Volder et al., 2013). Soil water content, photosynthesis and relative growth rates declined under seasonally redistributed precipitation, and tiller reproduction in grasses was delayed. However, redistributed precipitation had no effect on mortality. Results suggest that species composition of these oak savannas will alter in a climate where precipitation shifts from summer to spring and autumn (Volder et al., 2010).

2.2 Extreme precipitation

A suite of precipitation manipulation experiments have been conducted within a mesic grassland at the Konza Prairie Biological station (Kansas, USA) (Knapp et al., 2001; Fay et al., 2002; Harper et al., 2005; Fay et al., 2008; Heisler and Knapp, 2008). One redistribution experiment examined how variation in quantity, event size, and interval between precipitation events influenced SWC, ANPP, respiration, and photosynthesis of tallgrass prairie grasses and forbs (Fay et al., 2008). Increases in event size led to more ANPP, although a threshold was reached, and the effect decreased as the interval between precipitation events increased (see Fig. 2g in Fay et al., 2008). It is clear that increasing water did not always lead to increased ANPP, with a threshold of maximum SWC at 600 mm MAP in Fay et al. (2008). Another study at Konza Prairie Biological station imposed extreme precipitation over four growing seasons (Harper et al., 2005). A 50 % increase in the length of dry intervals while holding the total volume constant, led to 19 % reductions in soil water content, and 9 % reductions in ANPP (Harper et al., 2005).

A comprehensive set of extreme precipitation experiments measured ANPP across a precipitation gradient in southern USA grasslands. Precipitation was applied as either 12, six or four events, with the same total amount of water applied (Heisler-White et al., 2008). The responses from this xeric, semi-arid steppe were compared with a mixed grass prairie and a mesic tall grass prairie along a 600 km productivity and precipitation gradient (Heisler-White et al., 2009). Responses of ANPP depended on mean soil water content and aridity index (MAP/potential evapotranspiration) for each grassland type. At the two more xeric (water-limited, aridity index < 1, see Table 3) sites, extreme precipitation caused more time at above-average SWC, increasing ANPP. In contrast, at the more mesic (water-abundant, aridity index > 1) site, extreme precipitation led to extended periods of below-average SWC, reducing ANPP (Heisler-White et al., 2009). This comparison suggests there was a *threshold* of plant available water to extreme precipitation across these studies, and that initial site conditions such as the aridity index, soil type and rooting depth will influence growth responses to altered timing of precipitation.

2.3 Modeling studies

Modeling studies on altered precipitation enable comparisons across ecosystems. Modeling studies generally suggest that shifts in the timing of precipitation alter both plant community composition and NPP (Epstein et al., 1999; Gerten et al., 2008). A study examining the impact of changed seasonality in precipitation using the Dynamic Global Vegetation model, LPJ, in African reported that deciduous and semi-deciduous forests were more sensitive than other plant functional types to changes in the seasonality of precipitation (Hely et al., 2006). Dry sites and periods generally are more affected by shifts in precipitation compared with wet sites and periods (Gerten et al., 2008), as has been found in some empirical studies (Knapp et al., 2002). Similarly, shifts in seasonality that alter the amount of precipitation during the spring may have larger effects on community composition and NPP than shifts in seasonality during other seasons (Wiles et al., 2011). More generally, shifts in precipitation likely will affect NPP in water-limited systems because of the close link between NPP and precipitation in these systems (Gerten et al., 2008). However, the effect of shifts in precipitation may reflect the length of the dry period (Gerten et al., 2008), and interactions with other climate change variables, including CO_2 and temperature (Luo et al., 2008).

3 Synthesis

3.1 Synthesis on seasonal changes

Redistributing the seasonality of precipitation not only influences water stress and biomass, but phenological changes such as fruiting of male and female plants (Misson et al., 2011), and tiller production (Volder et al., 2013). Redistributed precipitation resulting in *reduction*s in spring or summer precipitation often led to water stress, and was associated with reduced biomass and altered phenology, while the subsequent increases in autumn or winter precipitation had little or no effect on plant processes. Similarly, *increased* summer precipitation had a larger effect on SWC and biomass than winter increases. In summary, changed precipitation in spring and summer had a more dramatic impact on vegetation than changes in autumn and winter, reflecting larger effects of redistributed rainfall on SWC during warm or dry months compared with cool or wet months. It is noteworthy that the majority of studies that altered seasonal precipitation were conducted in grasslands, with few studies on trees.

3.2 Synthesis on extreme precipitation

The response to extreme precipitation differed in xeric (water-limited) and comparatively mesic (water-abundant) sites. Studies to date suggest that xeric ecosystems generally were associated with positive responses of ANPP to extreme precipitation, while comparatively mesic ecosystems were associated with negative responses of ANPP. This pattern was supported by rainout shelter, observational and modeling studies. In general, within ecosystems which were not water-limited (> 600 mm MAP, or an aridity index > 1.0, see Fig. 3), (Harper et al., 2005; Fay et al., 2011) extreme precipitation led to a *reduction* in mean soil water content, followed by a reduction in growth or

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ANPP (Fig. 2). In contrast, below 600 mm or an aridity index of < 1, soil water content and ANPP increased. A landscape scale study using remote sensing to quantify a threshold on plant responses to drought in the south-west USA (Clifford et al., 2013; Hicke and Zeppel, 2013). Clifford et al. (2013) observed high die-off and mortality rates at sites below 600 MAP, whereas there were no observations of mortality above the threshold, presumably due to an absence of water limitation. Finally, many ecosystems convert from grassland/savanna to more dense forests as MAP increases above potential evapotranspiration, when the aridity index exceeds 1, meaning the effects of extreme precipitation may also coincide with changes in ecosystem type.

It is crucial to note, however, that soil type (clay, loam or sand), soil depth and rooting depth influence plant available water, regardless of MAP, and further studies are required to test plant responses to extreme precipitation across other plant functional types and other biomes. Little research has been conducted in tropical, tundra and boreal regions on plant responses to altered timing of precipitation. Of the studies from boreal regions to date, only one described the impact of altered precipitation on roots, but not above-ground processes (Gaul et al., 2008). These temperature limited systems may show markedly different responses compared to warmer biomes. We also may expect different responses from shallow- and deep-rooted plants, such as juvenile vs. mature plants. If rain falls in large volumes in short periods, the water may drain away before shallow-rooted plants are able to use it (Fig. 3). However, deep-rooted plants are likely to access deeper stores of water and show more dampened responses than grasses. Alternatively, decreased water availability resulting from extreme precipitation may lead to increased root depth and volume. However, recent studies report that deep-rooted plants do not always tolerate drought-stress better than shallow-rooted plants, indicating further research is required to elucidate the mechanisms explaining these unexpected differences across rooting depths (Morecroft et al., 2004; West et al., 2012).

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4 Key research gaps and unresolved problems

This review indicates key research gaps in understanding the effects of extreme and seasonal changes in precipitation. These include: (1) responses of a broad range of plant functional types, particularly on trees, (2) responses of boreal and temperate forests, (3) effects on below ground processes, and (4) the effects of changes in precipitation in conjunction with heat waves, rising temperatures and increasing [CO_2]. Most research in this field has examined the influence of extreme or seasonal changes in precipitation on grasslands (Knapp et al., 2008; Heisler-White et al., 2009; Fay et al., 2011), with few studies on tree species (Zeppel, 2013). Further, there is a paucity of studies describing the effects of altered precipitation on biomes such as tundra, boreal forests, and temperate forests. Our current understanding of below-ground processes and how these respond to extreme precipitation is lacking, particularly in forests and woodlands, in part due to logistical constraints. Finally, very few studies exist describing plant responses to interactions between altered precipitation and heat waves, and none, to our knowledge, with altered precipitation and elevated [CO_2]. To address these knowledge gaps, future work is needed, testing whether:

1. tree responses to seasonal changes in precipitation are buffered compared to grasses;
2. seedlings and shallow-rooted plants show different responses to altered precipitation than mature or deep-rooted plants, and what causes these differences; and
3. heat waves exacerbate the water stress from extreme precipitation in xeric regions and ameliorate water logging in mesic regions.

5 Conclusions

Extreme precipitation, by definition, leads to wetter (waterlogged) *and* drier conditions, and it is clear that the influence of extreme precipitation on plant growth is not con-

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sistent across ecosystems. Rather, the available data generally suggest biomass either decreased or increased depending on whether the average soil water content decreased or increased respectively. The response of ANPP to extreme precipitation in grasslands was an *increase* in soil water content and ANPP in water-limited sites. In contrast, extreme precipitation led to a *decrease* in a soil water content and ANPP in mesic sites. Data are needed across a range of root depth, soil type and plant age, plant functional types and patterns of seasonal redistribution of precipitation to refine this pattern.

Seasonal changes in precipitation often led to significant water stress, changes in phenology and decreased biomass. *Reduction*s in spring or summer often led to water stress, altered phenology, including reduced fruit and leaf development, as well as reduced biomass, with subsequent reductions in autumn or winter having little effect. Similarly, *increased* summer precipitation had a larger impact on biomass than winter increases. In summary, across forests and grasslands changed precipitation in summer and spring had a larger impact on vegetation than changes in winter and autumn. Thus, in conclusion, studies showed a clear pattern exists. The initial conditions, and whether the site is water-limited or water-abundant, are key factors driving water relations and productivity under extreme precipitation. Similarly, even when total precipitation remains unchanged, seasonal shifts alter water relations and productivity as well as phenology, leaf and fruit development, with more marked changes in summer and spring compared with winter and autumn changes. Considering projections of seasonal redistribution of precipitation, based on these results, we can expect key biological changes including increased water stress and changes in biomass, wood, leaf and fruit development.

This improved understanding of plant and ecosystem responses to extreme precipitation and seasonal changes in precipitation will inform emerging vegetation models and enable better understanding of vegetation, carbon and water resources in future climates.

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Table 1. Responses of vegetation to changed *seasonal* precipitation. Biome, site location, latitude and longitude, experimental reduction in precipitation, Mean Annual Precipitation (MAP), description of whether experimental reduction in precipitation (P) was reduced or redistributed, in addition to the measured response and source reference. Results represent a selection of studies and are not a comprehensive list. Abbreviations: ANPP = above-ground net primary productivity; A_n = photosynthesis; ψ_m = midday leaf water potential (kPa); ψ_{pd} = pre-dawn leaf water potential; g_s = stomatal conductance.

Biome	Site	Latitude & Longitude	% reduction in precip	MAP (mm)	Seasonal /Annual reduction	P reduced or redistributed	Growth response	Reference
Grassland	SE Spain	36°49′ N 2°15′ W	75 %, 50 % and altered timing	200	Seasonal and annual	Reduced and distributed	Accentuated seasonality reduced biomass and recruitment	Miranda et al. (2009b)
Cold desert Grasslands	Canyonlands National Park, Utah,	38.1755° N, 109.7202° W	Winter, summer or yearlong drought.	215	Winter and summer	Annual reduced	Summer drought effects on ψ_{pd} higher than the winter drought effects. g_s reduced.	Schwinning et al. (2005a)
Grassland	Great Basin, Oregon, USA	119°43′ W 43°29′ N	1) 80 % falls in winter; 2) 80 % in spring	300	Winter and Spring	Redistributed	Winter comparable to control. Spring treatment, less biomass.	Bates et al. (2006)
Shrub Steppe	Great Basin, Oregon, USA	119°43′ W 43°29′ N	"winter" "spring" or "current"	300	Winter and Spring	Redistributed	Shifts to spring reduced growth	Svejcar et al. (2003)
Arctic tundra	Brooks Range, Alaska.	149°38′ W, 68°38′ N	Increased w snow fence.	318	Winter	Increased	Deeper snow altered amount and timing of plant-available N.	Schimel et al. (2004)
Mixed-grass prairie	Wyoming, USA	n/a	1) +50 % winter 2) +50 % summer 3) −50 % summer	380	Winter and summer	Increased and decreased	1) 50 % biomass increase 2) 44 % increase 3) 18 % decrease	Chimner et al. (2010)
Temperate, savanna	Southeast Arizona, USA	31°29′ N 110°20′ W	±50 % in summer and winter.	602	Winter and summer	Reduced and redistributed	Summer precipitation more important for seeding growth	Weltzin and McPherson (2000)
Mediterranean forest.	Montpelier, Southern France	3°35′45″ E, 43°44′29″ N,	−97 % autumn, −87 % spring	1127	Spring and Autumn	Seasonal reductions	Autumn – no effect. Spring – more negative ψ_m	Misson et al. (2011)
Boreal, Spruce Forest	Southeast Germany	50°08′ N, 11°52′ E	No reduction in annual	1160	Summer	Redistributed	Fine root biomass, production and necromass higher in treatment	Gaul et al. (2008)
Grassland	England grasslands	1°20′ W 51°46′ N	−90 % summer +20 % summer	n/a	Summer and winter	Increased and reduced	Abundance deceased Abundance increased Winter no effect	Morecroft et al. (2004)
Savanna	Oak – savanna	30°34″ N 96°21″ W	−40 % summer + spring and autumn	1018	Summer, Spring and Autumn	Redistributed	Reduced relative growth rate and A_n of trees grown with grasses	Volder et al. (2010); Volder et al. (2013)
Tropical Rainforest	Floresta, Amazon, Brazil	2.897° S, 54.95° W	50 %	~ 2000	Wet season	Reduced	Non-sig. reduction of 12 % of fruit production.	Brando et al. (2006)
Tropical Rainforest	Floresta, Amazon, Brazil	2.897° S, 54.95° W	35–41 % from 2000 to 2004	~ 2000	Wet season	Reduced	Decrease, 12 % first year, 62 % after for ANPP	Brando et al. (2008)
Tropical Rainforest	Floresta, Amazon, Brazil	2.89° S, 54.95° W,	34–40 %	~ 2000	Wet season	Reduced	22 % decrease in ANPP	Nepstad et al. (2002)
Tropical Rainforest	Floresta, Amazon, Brazil	2.89° S, 54.95° W,	34–40 %	~ 2000	Wet season	Reduced	Soil water modeled, water budget estimated	Belk et al. (2008)
Tropical Rainforest	Floresta, Amazon, Brazil	2.89° S, 54.95° W,	60 %	~ 2000	Wet season	Reduced	34 % increase in mortality	Nepstad et al. (2007)

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Table 2. Responses of vegetation to *extreme* precipitation. Biome, site location, latitude and longitude, experimental reduction in precipitation, Mean Annual Precipitation (MAP), description of whether experimental reduction was annual (across the entire year) or during one season, in addition to the measured response and source reference. LTER is "Long Term Ecological Research" site. Results represent a selection of studies and are not a comprehensive list. Abbreviations: ANPP = Above-ground net primary productivity; A_n = photosynthesis; ψ_m = midday leaf water potential (kPa); ψ_{pd} = pre-dawn leaf water potential; g_s = stomatal conductance.

Biome	Site	Latitude and Longitude	% reduction in precip	MAP (mm)	Seasonal /Annual reduction?	Annual P reduced or redistributed	Growth response	Reference
Grassland	SE Spain	36°49′ N 2°15′ W	75 %, 50 %; and altered timing	200	Seasonal and annual	Reduced and redistributed	50 % reduction reduced productivity, plant cover and diversity	Miranda et al. (2009b)
Semi-arid grassland	Colorado USA	40°49′ N 104°46′ W	None	321	None	Redistributed	Extreme plots: higher ANPP, A_n and less water stress (ψ_m)	Heisler-White et al. (2008)
Semi-arid grassland	LTER, Nunn, Colorado USA	40°49′ N 104°46′ W	None	321	None	Redistributed	Higher mean soil water content and higher ANPP	Heisler-White et al. (2009)
Mixed grass praire	Hays, Kansas, USA	38°53′ N 99°23′ W	None	576	None	Redistributed	Higher mean soil water content and higher ANPP	Heisler-White et al. (2009)
Tall grass prairie	Konza Prairie LTER, Kansas, USA	39°05′ N 96°35′ W	None	835	None	Redistributed	Lower mean soil water content and higher ANPP	Heisler-White et al. (2009)
Grassland	Konza Prairie LTER, Kansas, USA	39.1°N 96.9°W	47–119 %	835	Increases and decreases in timing, size	Reduced and redistributed	Increases in event size lead to more ANPP, respiration and A_n.	Fay et al. (2008)
Grassland	Konza Prairie LTER, Kansas, USA	39°05′ N, 96°35′ W	30 % reduction and altered timing.	835	Seasonal and annual	Reduced and redistributed	Decreased soil fluxes by 13 % and plant productivity by 8 %	Harper et al. (2005)
Grassland	Konza Prairie LTER, Kansas, USA	39°05′ N, 96°35′ W	30 % reduction and altered timing	835	None	Reduced and redistributed	Variation in soil moisture was amplified in plant growth responses.	Fay et al. (2011)

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Table 3. Synthesis of extreme precipitation studies on the soil water content (SWC) and aboveground net primary productivity (ANPP), mean annual precipitation (MAP) and mean annual potential evapotranspiration (E_{pot}) of grasslands, showing that ANPP either increases or decreases in the same direction as SWC. CO is Colorado, KS is Kansas. Ecosystem is defined using the Koppen climate definition (McKnight and Hess, 2000).

Ecosystem and Köppen climate definition	SWC	ANPP	MAP (mm)	E_{pot}(mm)	Aridity Index (MAP/E_{pot})	Reference
Shortgrass prairie: semi-arid	↑15 %	↑77 %	321, CO	> 1000	< 0.32	Heisler-White et al. (2008)
Shortgrass prairie: semi-arid	↑19 %	↑30 %	321, CO	> 1000	< 0.32	Heisler-White et al. (2009)
Mixed grass praire: ecotone between semi-arid and humid subtropical	Increase	↑70 %	576, KS	749	0.77	Heisler-White et al. (2009)
Tallgrass prairie: humid subtropical	↓19 %	↓9 %	835, KS	687	1.21	Harper et al. (2005)
Tallgrass prairie: humid subtropical	↓20 %	↓18 %	835, KS	687	1.21	Heisler-White et al. (2009)
Tallgrass prairie: humid subtropical	↓14 %	↓15 %	835, KS	687	1.21	Fay et al. (2011)

Table 4. Nomencalture.

[CO_2]	CO_2 concentration
ANPP	Above-ground Net Primary Productivity
D	vapour pressure deficit (kPa)
SWC	soil water content

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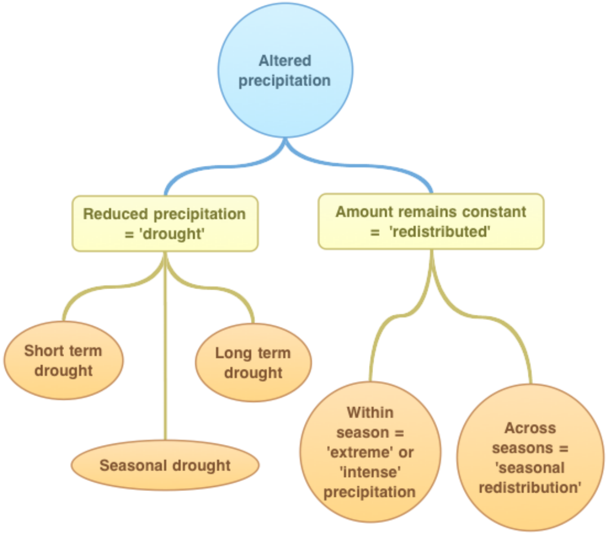

Fig. 1. A schematic diagram explaining different types of altered precipitation. If the amount of precipitation is substantially reduced, this may be defined as "drought". Descriptions of drought should include duration (e.g. short-term, long-term and seasonal drought) and also intensity (slight, moderate or severe) which will depend upon site conditions and species. If the amount of precipitation is not reduced then this may be defined as "redistributed" precipitation, where the total amount of water remains constant but the amount of water and timing between watering events increase. Redistributed precipitation may take place within a season, for example, a rainout shelter within a growing season (Fay et al. 2008), or within glasshouses over a three month period. Redistributed precipitation may also take place across seasons, where water is withheld during one season and supplementally reapplied in the following months/seasons. For further explanation of "extreme" precipitation events, see Smith (2011).

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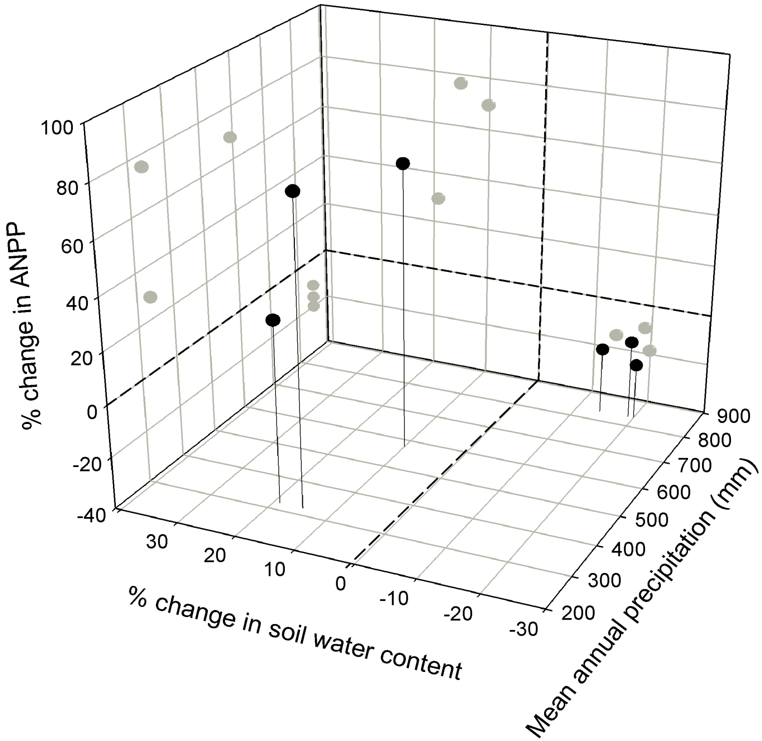

Fig. 2. The effect of extreme precipitation on Above-Ground Net Primary Productivity (ANPP) across a rainfall gradient. The three-dimensional plot shows the relationship between relative changes in soil water content (%), and the percent change in Above-Ground Net Primary Productivity (ANPP, %) due to extreme precipitation, based on the Mean Annual Precipitation (mm) of the site. The black dots represent data points on the x-, y-, and z-axis. The grey dots represent where the data would fall on a two dimensional scatter plot. Dashed lines represent the zero line, where % change in soil water content or ANPP is zero.

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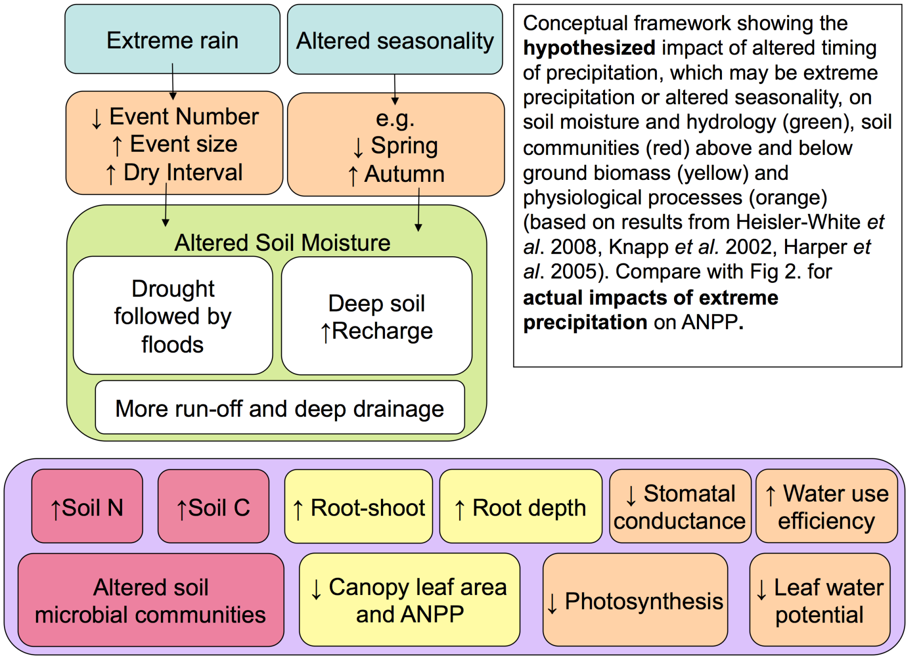

Fig. 3. Conceptual framework showing the possible impacts of extreme and seasonal precipitation on soil and plant processes.

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