

Increased Soil Frost Versus Summer Drought as Drivers of Plant Biomass Responses to Reduced Precipitation: Results from a Globally Coordinated Field Experiment

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ABSTRACT

Reduced precipitation treatments often are used in field experiments to explore the effects of drought on plant productivity and species composition. However, in seasonally snow-covered regions re-

duced precipitation also reduces snow cover, which can increase soil frost depth, decrease minimum soil temperatures and increase soil freeze–thaw cycles. Therefore, in addition to the effects of reduced precipitation on plants via drought, freezing damage to overwintering plant tissues at or below the soil surface could further affect plant productivity and relative species abundances during the growing season. We examined the effects of both reduced rainfall (via rain-out shelters) and reduced snow cover (via snow removal) at 13 sites globally

Received 7 November 2017; accepted 4 February 2018;
published online 21 February 2018

Author Contributions: HALH conceived of and designed the study and analyzed the data; all authors performed research and wrote the paper.

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(primarily grasslands) within the framework of the International Drought Experiment, a coordinated distributed experiment. Plant cover was estimated at the species level, and aboveground biomass was quantified at the functional group level. Among sites, we observed a negative correlation between the snow removal effect on minimum soil temperature and plant biomass production the next growing season. Three sites exhibited significant rain-out shelter effects on plant productivity, but there was no correlation among sites between the rain-out shelter effect on minimum soil moisture

and plant biomass. There was no interaction between snow removal and rain-out shelters for plant biomass, although these two factors only exhibited significant effects simultaneously for a single site. Overall, our results reveal that reduced snowfall, when it decreases minimum soil temperatures, can be an important component of the total effect of reduced precipitation on plant productivity.

Key words: climate; drought; International Drought Experiment; frost; productivity; rain; snow cover; winter.

INTRODUCTION

Drought is among the most influential plant stresses globally, and it is anticipated to increase in some regions over the next century as a result of climate change (Sheffield and Wood 2008; Dai 2011, 2013). Climate warming can contribute to drought by increasing evaporative demands/potential evapotranspiration rates, and at the regional level, periods of reduced precipitation can be a particularly strong driver of drought conditions (Trenberth and others 2014). Numerous field experiments have been conducted at the plot level within sites to examine the effects of reduced precipitation on plant communities via the use of rain-out shelters (*sensu* Svejcar and others 1999; Yahdjian and Sala 2002). Although severe drought inevitably decreases plant productivity (Breshears and others 2005; Ciais and others 2005; Allen and others 2010), reduced precipitation per se typically has site-specific and at times apparently idiosyncratic results, due in part to differences in plant community composition, soil type and treatment intensity (Skinner and others 2004; English and others 2005; Carlyle and others 2014). Rain-out shelter effects also can be highly contingent on the ambient weather conditions over the course of study (Kreyling and others 2017).

A recent meta-analysis demonstrated that aboveground plant productivity is generally more sensitive to increases in precipitation than to reductions, with little variation in the effects of reductions across large-scale precipitation and temperature gradients (Wilcox and others 2017). Although meta-analyses can be useful for synthesizing information and identifying broad patterns across multiple sites, they are limited by often having to integrate data collected using different methods, and in cases where they rely primarily on published data they can be biased against the inclusion of null results

(Hillebrand and Cardinale 2010; Whittaker 2010; Harrison 2011). To address these concerns, it has been suggested that globally coordinated distributed experiments should be organized to address major questions in ecology (Fraser and others 2013). This approach has been successfully implemented to examine, for example, climate warming in the Arctic (ITEX; (Henry and Molau 1997), the effects of nutrient enrichment and grazing (NutNet; (Borer and others 2014) and plant diversity–productivity relationships (HerbDivNet; (Fraser and others 2014). More recently, the International Drought Experiment (IDE) has been initiated to examine drought effects across a range of sites globally using rain-out shelters (Knapp and others 2017).

In seasonally snow-covered regions, reduced precipitation also can reduce snow cover. The latter can lead to increased soil frost depth, decreased minimum soil temperatures and an increase in the frequency of soil freeze–thaw cycles, even when it is coupled with increases in mean annual air temperatures (Henry 2008), resulting in the apparent paradox of colder soils in a warmer world (Groffman and others 2001). Therefore, in addition to the effects of reduced precipitation on plant productivity via drought, reduced snow cover resulting from decreased winter precipitation can increase freezing damage to overwintering plant tissues at or below the soil surface (Tierney and others 2001; Gaul and others 2008; Comerford and others 2013; Campbell and others 2014), further affecting plant productivity and relative species abundances (Kreyling and others 2012a; Vankoughnett and Henry 2014). In addition to plant freezing damage, plants can respond to freezing indirectly via changes in soil microorganisms and nutrient availability (Henry 2007; Blankinship and Hart 2012), soil aggregates (Freppaz and others 2008) or soil fauna (Templer and others 2012). Decreased snow cover also can affect plant growth during the subsequent

growing season by altering soil water dynamics (Iwata and others 2010) and spring phenology (Dunne and others 2003; Huelber and others 2006; Wipf and others 2006; Venn and Morgan 2007; Natali and others 2012).

Although plant frost and drought stress typically occur in different seasons, plant stress tolerance can be modified by prior exposure to a different stress over the time scale of months (Kreyling and others 2012b, c; Kong and Henry 2016), due to the phenomenon described as stress memory or cross-acclimation (Walter and others 2013). The latter may be explained by the accumulation of protective compounds or transcription factors that upregulate genes that confer stress tolerance (Bruce and others 2007; Walter and others 2013). Moreover, in the case of prior frost effects on drought stress, when frost damage reduces plant biomass it can result in decreased transpirational water losses during the subsequent growing season.

We examined the effects of both reduced rainfall (via rain-out shelters) and decreased snow cover (via snow removal) on plant cover and above-ground biomass at 13 sites globally within the framework of the International Drought Experiment, a coordinated distributed experiment (Knapp and others 2017). Snow was removed opportunistically from the beginning until the middle of winter to increase soil freezing, and snow removal stopped before the end of winter to minimize its effects on spring melt water and spring phenology. Following snowmelt, half of the snow removal and ambient snow plots were covered with rain-out shelters designed to reduce rain throughput at each location by an amount equivalent to a one-in-one hundred year drought, and the other half were left as ambient rain controls. Our primary goal was to assess, across a range of sites, the extent to which increased frost caused by reduced snow cover might be an important component of the effects of reduced precipitation on plant biomass compared to summer drought. We predicted that snow removal would decrease biomass to the greatest extent in the coldest sites. We also were interested in examining the extent to which the frost and drought effects might interact, with the prediction that prior exposure to frost would decrease the negative effects of drought on plant biomass.

METHODS

Study Sites

Thirteen sites globally (from North America, Europe, Asia and Australia) participated in the exper-

iment (Table 1, Figure 1), and these were primarily characterized by grassland/old field vegetation, although a heathland site and the understory of a riparian forest site also were included. Mean January temperatures ranged from -22 to 2°C , and mean annual precipitation ranged from 200 to 1405 mm (Table 1). Mean annual snowfall ranged from 5 to 194 cm. For each site, the treatments and data collection were conducted over a single year (2014–2015 for Bayreuth, ESW, Hardware Ranch, Kernen and Lac du Bois, 2015–2016 for Changling, Golestan, Hiddensee, Freiburg, Ordesa, Pineta and Richland, and 2016–2017 for Bogong).

Snow Removal and Rain-Out Shelter Treatments

Within sites, a minimum of six $3\text{ m} \times 3\text{ m}$ plots were delineated (Bogong, Freiburg and Changling used eight plots, Bayreuth used 10 plots, and Hiddensee used 12 plots), with two $1\text{ m} \times 1\text{ m}$ subplots within the center of each plot; the rain-out shelter and snow removal treatments were administered in a split-plot design with snow removal (subplots) nested in rain-out sheltering (whole plots; Figure 2). The $3\text{ m} \times 3\text{ m}$ plot size was determined based on the plot size requirements of the International Drought Experiment (Knapp and others 2017). Within each plot, one subplot was assigned randomly to snow removal, and the other left as a control to experience ambient snow cover. To minimize disturbance to the soil and plant litter layer, plastic netting (with 1 cm gaps in the mesh) was placed over both the snow removal and ambient snow subplots before the first snowfall. In addition, soil temperature sensors were placed 2 cm below the soil surface in the center of each snow removal and snow control plot. To increase soil frost, snow was removed opportunistically (typically following major snowfall events) with shovels and brooms down to the level of the plastic mesh. However, snow was allowed to accumulate in the snow removal subplots in late winter to minimize the treatment effects on growing season soil moisture and spring phenology. The Freiburg site received negligible snow cover and thus did not participate in the snow removal component.

After the final snowmelt, rain-out shelters were installed over half of the plots at each site; each rain-out shelter consisted of a metal or wooden frame with angled troughs made of transparent plastic to reduce each rainfall event passively by a fixed percentage (*sensu* (Yahdjian and Sala 2002)). The percent reduction in rain was calculated independently for each site (Table 1) to achieve a

Table 1. Site Characteristics

Site*	Habitat	Latitude	Longitude	Elevation (m)	Mean temper- ature (°C)		Mean annual snowfall (cm)	Mean annual precipitation (mm)	Growing season rain (% of climate normal)	Rain blocked (%)
					January	July				
					Hardware Ranch (USA)	41.6				
Changling (CN)	44.8	123.8	160	18.2	25.1	24	388	79	70	
Kernen (CA)	52.2	- 106.5	512	15.5	18.5	91	354	8	47.5	
Richland (USA)	43.3	- 90.4	222	8.8	21.5	102	938	87	50	
ESW (CA)	43.2	- 81.3	325	5.6	20.8	194	1012	95	45	
Bayreuth (DE)	49.9	11.6	365	1	17.1	-	756	62	40	
Lac du Bois (CA)	50.8	- 120.4	580-900	- 0.7	23.1	64	200	97	50	
Bogong (AU)	- 36.9	147.3	1765	13.2	- 0.9	-	1274	-	40	
Freiburg (DE)	48	7.8	238	1	18.8	5	940	-	40	
Pineta (ES)	42.7	0.1	1239	1.4	16.1	-	1053	-	33	
Ordessa (ES)	42.6	- 0.1	1363	1.5	16.3	-	1027	-	20	
Hiddensee (DE)	54.6	13.1	3	2.3	14.2	9	541	92	40	
Golestan (IR)	37.3	56.1	1845	3	27	100	500	-	-	

*Country codes: AU Australia, CA Canada, CN China, DE Germany, ES Spain, IR Islamic Republic of Iran, USA United States of America.

statistically extreme deviation in annual precipitation relative to long-term records (that is, equivalent to that which has occurred 1% of the time historically based on annual precipitation amounts—either long-term climatological data or interpolated data—for the past 100 years for each site; Knapp and others 2017). Therefore, although the percentage reduction varied among sites, the statistical extremity of drought was comparable across sites. Throughout the growing season, soil moisture from 0 to 15 cm depth was determined at regular intervals for the plots at each site either using moisture sensors or gravimetrically. Neither the Bogong or Golestan sites collected soil moisture data, and nor were rain-out shelters permitted at the latter site.

Plant Cover and Biomass

In the summer, percent aboveground cover was estimated separately for each species rooted within each snow removal and ambient snow subplot using a modified Daubenmire method (1959; Bonham and others 2004), in which cover is estimated to the nearest 1% for each species rooted within the plot. Percent cover also was estimated for woody overstory, litter, bare soil, animal diggings/disturbance, and rocks if present. Within-season sampling frequency was adjusted for individual sites based on the phenology of the component species to capture the maximum cover of each species. At the timing of peak biomass, rooted aboveground biomass was harvested from the plots and sorted by species and separated into the following six categories: (1) previous year's dead, and

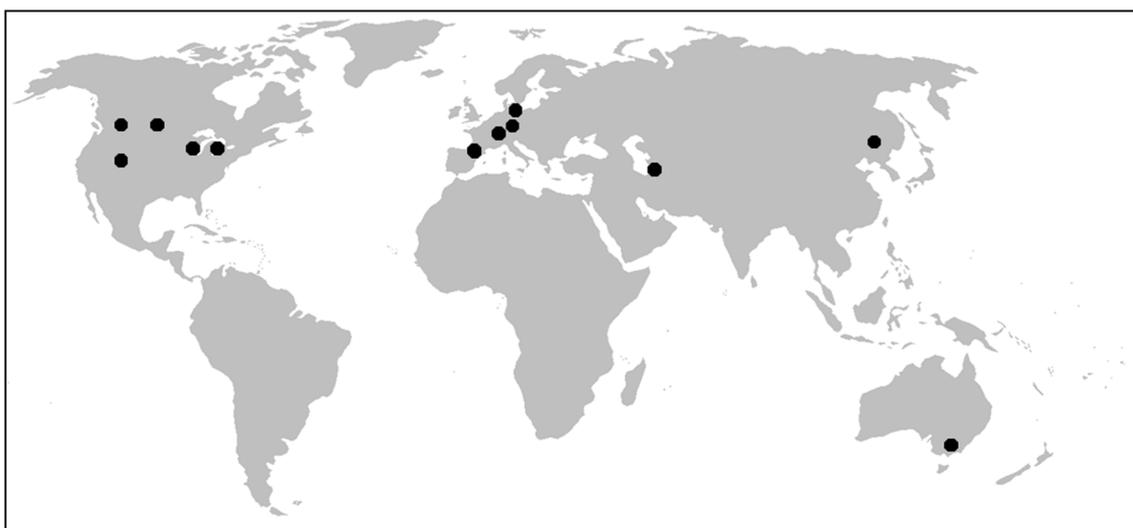


Figure 1. Study site locations (black points) World map adapted from https://commons.wikimedia.org/wiki/Maps_of_the_world#/media/File:BlankMap-World-noborders.png, PublicDomain.

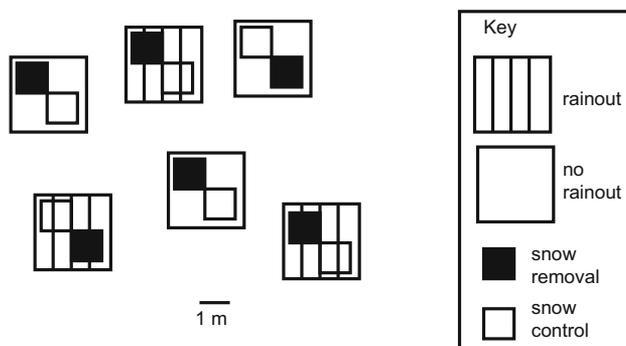


Figure 2. Experimental design for a site with three rain-out shelters and three ambient rain plots. The snow removal subplots were nested randomly within the rain-out shelter and ambient rain plots.

current year's: (2) bryophytes, (3) graminoids (grasses, sedges, rushes), (4) legumes, (5) non-leguminous forbs, (6) woody growth. The Lac du Bois (CA) site only could contribute total aboveground biomass data (that is, not sorted by functional group), the Bogong (AU) site only could contribute aboveground biomass data (sorted by functional group), and the Golestan (IR) site only could contribute plant cover data. All biomass was dried at 60°C for a minimum of 48 h prior to weighing to the nearest 0.01 g. For seven sites (Bayreuth DE), Changling (CN), ESW (CA), Hardware Ranch (USA), Ordesa (ES), Pineta (ES) and Richland (USA), standing root mass was measured at the timing of the aboveground biomass harvest from at least two 2 cm diameter by 15-cm-deep soil cores collected from each subplot.

Statistical Analyses

To assess the treatment effects on soil temperature and soil moisture, the responses of minimum annual temperature, number of freeze–thaw cycles and minimum annual soil water content were analyzed. Total aboveground biomass was analyzed for the date from each site that featured the highest biomass values, and these analyses were followed by analyses of treatment effects on the total aboveground biomass for each functional group. For plant cover, the maximum growing season value for each species in each plot was first determined, and then summed for each plot. The biomass data were \log_{10} -transformed, and the percent cover data were square root-transformed, to meet the assumption of normality for the subsequent statistical analyses.

Dependent variable responses to the snow removal and rain-out shelter treatments, along with their interaction, were analyzed in a nested fashion: first among the replicate plots within each site, then among sites. For within-site analyses, the responses were assessed using split-plot analysis of variance (ANOVA), with the understanding that these analyses might be limited by low statistical power (that is, the focus of coordinated distributed experiments is on maximizing the number of replicate sites, whereas the workload at each site is minimized to encourage widespread participation). Therefore, marginally significant trends in the data (that is, $P < 0.1$) were noted. For the among site analyses, two-way ANOVA with site included in the model as a random factor revealed no significant interactions between the snow removal and rain-out shelter effects for the plant response variables. Follow-up analyses were therefore per-

formed on the snow removal and rain-out shelter effects separately. Specifically, the log response ratios of the biomass responses for each site were regressed against the treatment effects on minimum soil temperature, number of soil freeze–thaw cycles (that is, transitions to below 0°C then back again), minimum soil water content and the percentage of rain blocked by the rain-out shelters. All statistical analyses were performed using JMP[®] 13 software (SAS Institute Inc., Cary, NC).

RESULTS

Treatment Effects on Soil Temperature and Soil Moisture

Snow removal decreased minimum soil temperature among sites ($P < 0.001$), but there was an interaction between snow removal and site ($P < 0.001$) resulting from some sites showing a strong effect, and others no effect (Table 2). There also was an interaction ($P = 0.002$) between snow removal and site for the number of soil freeze–thaw cycles, with some sites exhibiting an increase and others a decrease (Table 2). The rain-out shelters reduced minimum soil water content among sites ($P = 0.041$; Table 2), and there was no significant effect of snow removal on post-snow-melt soil water content ($P = 0.87$).

Plant Biomass and Cover Responses

Within sites, there were no interactions between snow removal and rain-out shelter effects for aboveground biomass or cover. Therefore, the snow removal data displayed in the figures were pooled over the rain-out shelter treatments, and vice versa. Snow removal reduced aboveground biomass for ESW ($P = 0.027$) and Lac du Bois ($P = 0.020$), and there was a marginally significant aboveground biomass reduction for Changling ($P = 0.0745$; Figure 3A). These effects were driven by decreases in legumes (ESW; $P = 0.017$) and grasses (Changling; $P = 0.020$). Snow removal also reduced total percent cover for Changling ($P = 0.020$) and Golestan ($P = 0.007$; Figure 3B), with the effects driven by decreases in grasses ($P = 0.02$ and $P = 0.034$, respectively). Rain-out shelters reduced aboveground biomass for Kernen ($P = 0.007$), Changling ($P = 0.002$) and Freiburg ($P = 0.04$; Figure 4A). These effects were driven by decreases in grasses (Kernen, $P = 0.004$; Changling, $P = 0.02$) and forbs (Freiburg, $P = 0.031$). Rain-out shelters also resulted in a moderately significant increase in aboveground biomass for Lac du Bois

Table 2. Mean and Standard Error of Minimum Winter Soil Temperature and Number of Soil Freeze–Thaw Cycles (Ambient vs. Snow Removal Plots) and Minimum Growing Season Soil Moisture (Ambient vs. Rain-Out Shelter Plots)

Site	Minimum soil temperature (°C)				Number of freeze–thaw cycles				Minimum soil moisture (°C)			
	Ambient snow		Snow removal		Ambient snow		Snow removal		Ambient rain		Rainout shelter	
	Mean	(s.e.)	Mean	(s.e.)	Mean	(s.e.)	Mean	(s.e.)	Mean	(s.e.)	Mean	(s.e.)
Hardware Ranch (USA)	– 5.4	(0.4)	– 7.8	(0.3)	40	(6)	45	(9)	8.4	(0.9)	7.4	(0.2)
Changling (CN)	– 12.1	(0.7)	– 15.3	(0.2)	14	(2)	15	(2)	8.7	(3.3)	10.1	(3.1)
Kernen (CA)	– 12.1	(0.4)	– 12.2	(0.4)	16	(4)	10	(6)	7.5	(2.1)	5.4	(1.8)
Richland (USA)	– 1.8	(0.2)	– 6.6	(0.9)	18	(3)	27	(11)	17.7	(1.8)	16	(2.9)
ESW (CA)	– 3	(0.2)	– 11.7	(0.8)	32	(7)	24	(2)	17.7	(0.5)	12.4	(0.8)
Bayreuth (DE)	– 2.2	–	– 2.3	–	21	–	10	–	16.8	(2.5)	13.4	(1.2)
Lac du Bois (CA)	– 1.9	(0.2)	– 5.5	(0.3)	–	–	–	–	5.5	(2.8)	3.8	(4.2)
Bogong (AU)	0.0	(0.1)	– 0.4	(0.1)	0	(0)	1	(0)	–	–	–	–
Freiburg (DE)	–	–	–	–	–	–	–	–	7.6	(1.3)	5.3	(1.7)
Pineta (ES)	– 1.9	(0.2)	– 2.4	(0.2)	20	(4)	52	(5)	38	(1.8)	38.2	(1.4)
Ordesa (ES)	– 2.9	(0.3)	– 2.8	(0.2)	27	(0)	33	(10)	10.4	(0.7)	10	(0.3)
Hiddensee (DE)	– 1.2	(0.3)	– 0.9	(0.2)	3.4	(0.6)	2.5	(0.5)	8.1	(0.7)	7.1	(0.6)
Golestan (IR)	– 1.3	(0.8)	– 3	(1.0)	8	(6)	7	(2)	–	–	–	–

Significant ANOVA treatment effects: minimum soil temperature–site ($P < 0.001$), sitesnow removal ($P < 0.001$); number of freeze–thaw cycles–sitesnow removal ($P = 0.002$); minimum soil moisture–rain-out shelter ($P = 0.041$).

($P = 0.08$; Figure 4A). For total percent cover, there was a moderately significant increase under rain-out shelters for Lac du Bois ($P = 0.078$; Figure 4B), driven by a significant increase in legumes ($P = 0.048$). Rain-out shelters also resulted in a decrease in forb cover for ESW ($P = 0.013$). Snow removal resulted in a 19% decrease in total root biomass for Changling ($P = 0.011$), a marginally significant decrease of 31% for Hardware Ranch ($P = 0.068$), and a marginally significant increase of 92% for Richland ($P = 0.051$; data not shown). There also was a marginally significant increase in root biomass of 15% for Changling under rain-out shelters ($P = 0.059$).

Among sites, the log response ratios of the snow removal effects on aboveground biomass were significantly influenced by reduction in minimum soil temperature ($P = 0.017$), and this effect was driven by the strong negative biomass responses of the five sites that experienced the largest decreases in minimum soil temperature (Figure 5A). There was no significant relationship between the log response ratios of the aboveground biomass response to snow removal and the number of soil freeze–thaw cycles ($P = 0.91$), minimum soil temperature ($P = 0.32$), January air temperature ($P = 0.30$) or annual snowfall ($P = 0.27$). The among site rela-

tionship between the log response ratios of the rain-out shelter effects on both aboveground biomass and reduction in minimum soil moisture was not significant ($P = 0.38$; Figure 5B), and likewise, the log response ratios of the rain-out shelter effects were not significantly correlated with the percentage of precipitation blocked among sites ($P = 0.18$). However, there was a marginally significant negative correlation among sites between the absolute magnitudes of the rain-out shelter effects on biomass and mean annual precipitation ($P = 0.07$; that is, the driest sites in Figure 4A featured the largest magnitude responses).

DISCUSSION

Our results revealed that soil frost effects on plant biomass resulting from reduced snow cover indeed can be substantial relative to the effects of reduced spring and summer precipitation. These effects were most apparent for sites that experienced a meaningful reduction in minimum soil temperature in response to snow removal (in this case, 2°C or greater at 2 cm soil depth). The severity of winter temperature on its own was not a reliable predictor of snow removal effects on aboveground biomass, in that there was no snow removal effect

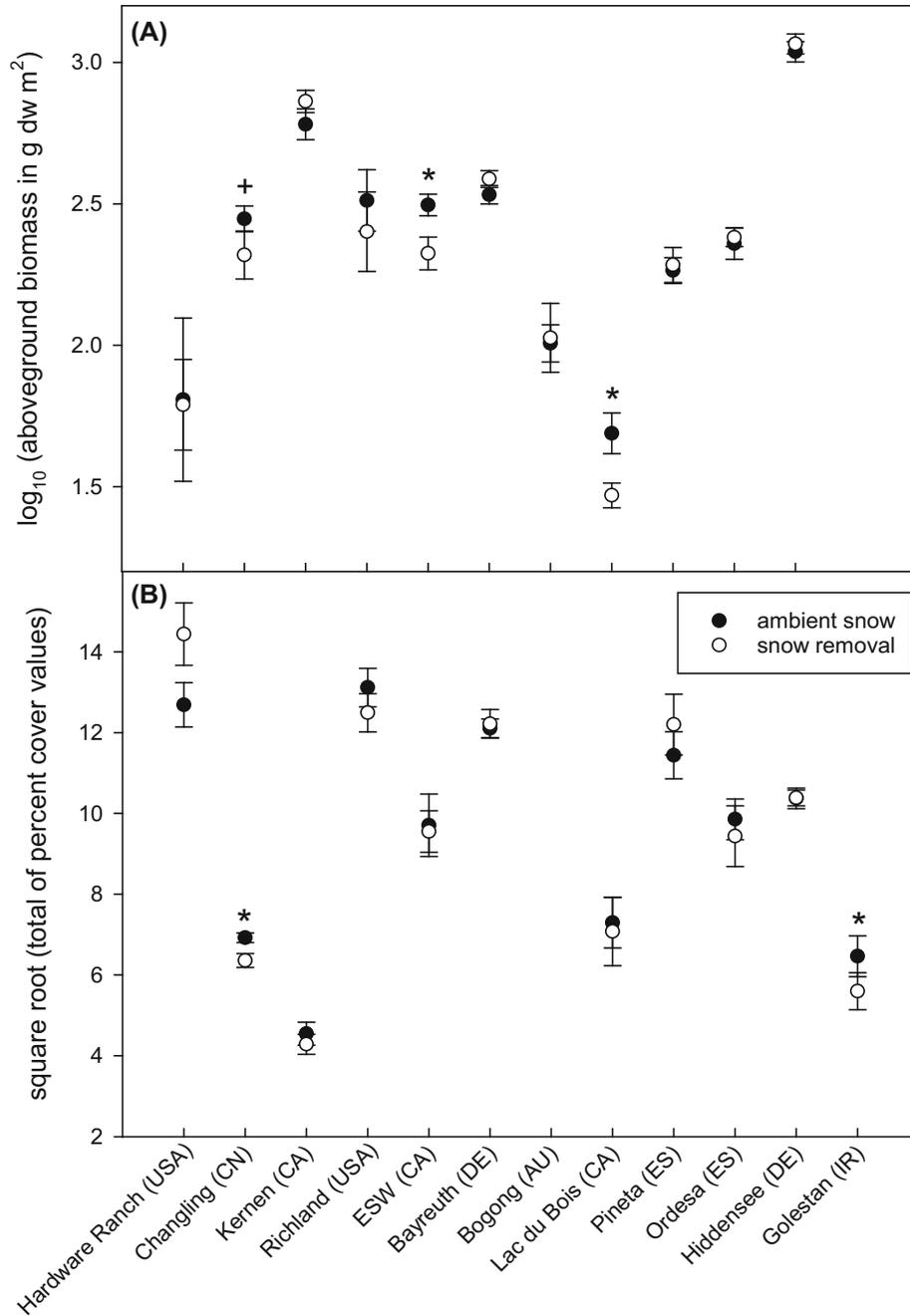


Figure 3. Mean **A** aboveground biomass and **B** total percent cover (that is, total of all species cover values) for the ambient snow and snow removal subplots. Data pooled over the rain-out shelter treatments, and error bars denote standard error. Sites are ordered on the x-axis (left to right) from coldest to warmest mean January air temperature. Asterisks indicate significant differences ($P < 0.05$) within sites, and crosses denote a marginally significant difference ($P < 0.1$).

for Kernen, a relatively cold site, whereas snow removal affected biomass or cover for Lac du Bois and Golestan, respectively, which experience much milder winters in comparison (although Kernen experienced unusually low snow cover in the ambient plots during the study, which may have

diminished its snow removal effect). Similarly, the total number of soil freeze–thaw cycles was not a reliable predictor of snow removal effects on aboveground biomass. The latter was not surprising given that the freeze–thaw cycles for many sites were of low amplitude (that is, dropping only a

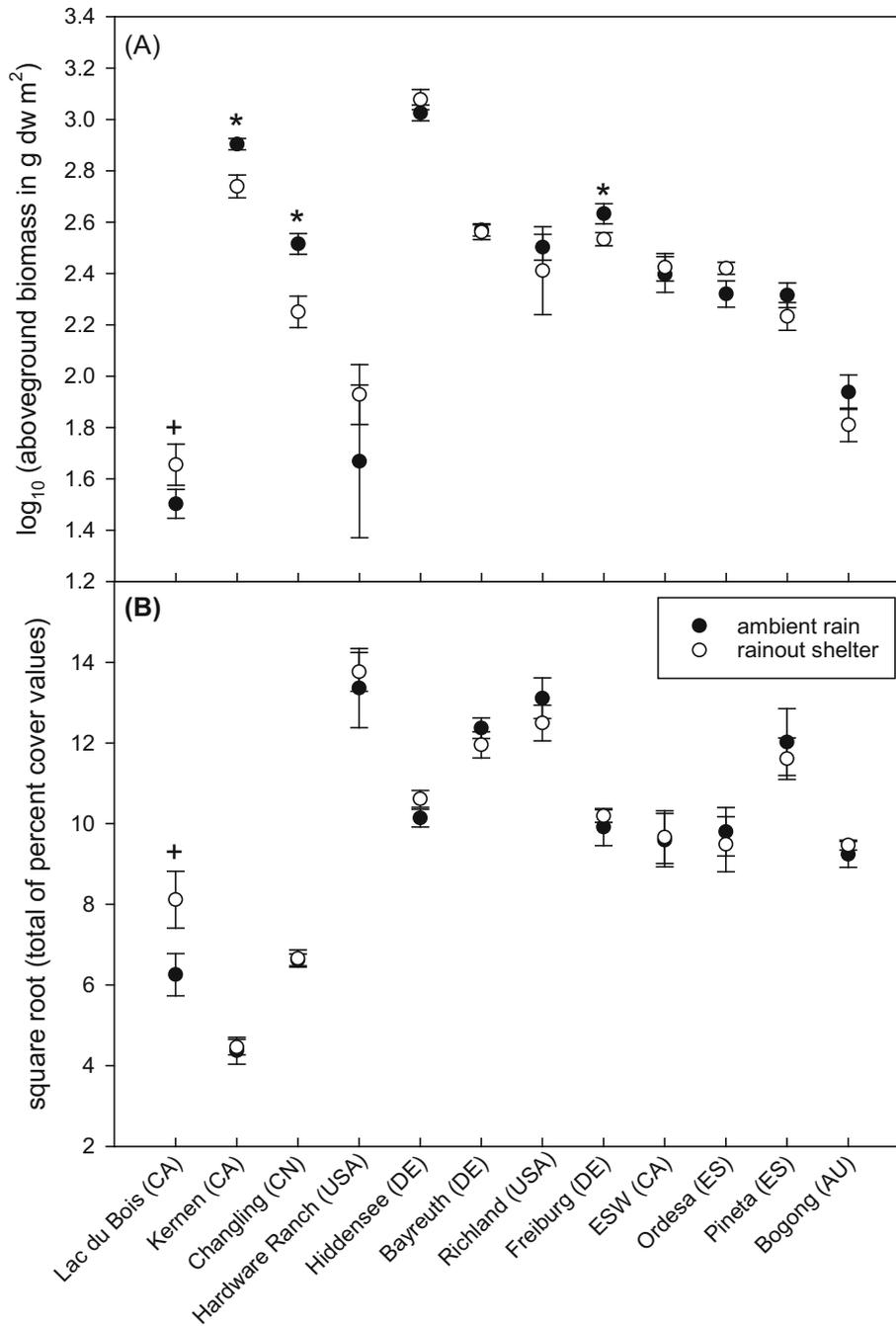


Figure 4. Mean **A** aboveground biomass and **B** total percent cover (that is, total of all species cover values) for the ambient rain and rain-out shelter plots. Data pooled over the snow removal treatments, and error bars denote standard error. Sites are ordered on the x-axis (left to right) from lowest to highest mean annual precipitation. Asterisks indicate significant differences ($P < 0.05$) within sites, and crosses denote a marginally significant difference ($P < 0.1$).

degree or so below freezing), which often produces little damage (Henry 2007); nevertheless, the number of freeze–thaw cycles can be influential when freezing is consistently more intense (Elliott and Henry 2009), and the timing and duration of soil frost also can have important consequences for

plant biomass responses (Malyshev and Henry 2012). With respect to functional groups, legumes can be particularly susceptible to frost (Joseph and Henry 2008), and declines in this functional group largely explained the snow removal effect at one site (ESW), but at other sites, declines in grass

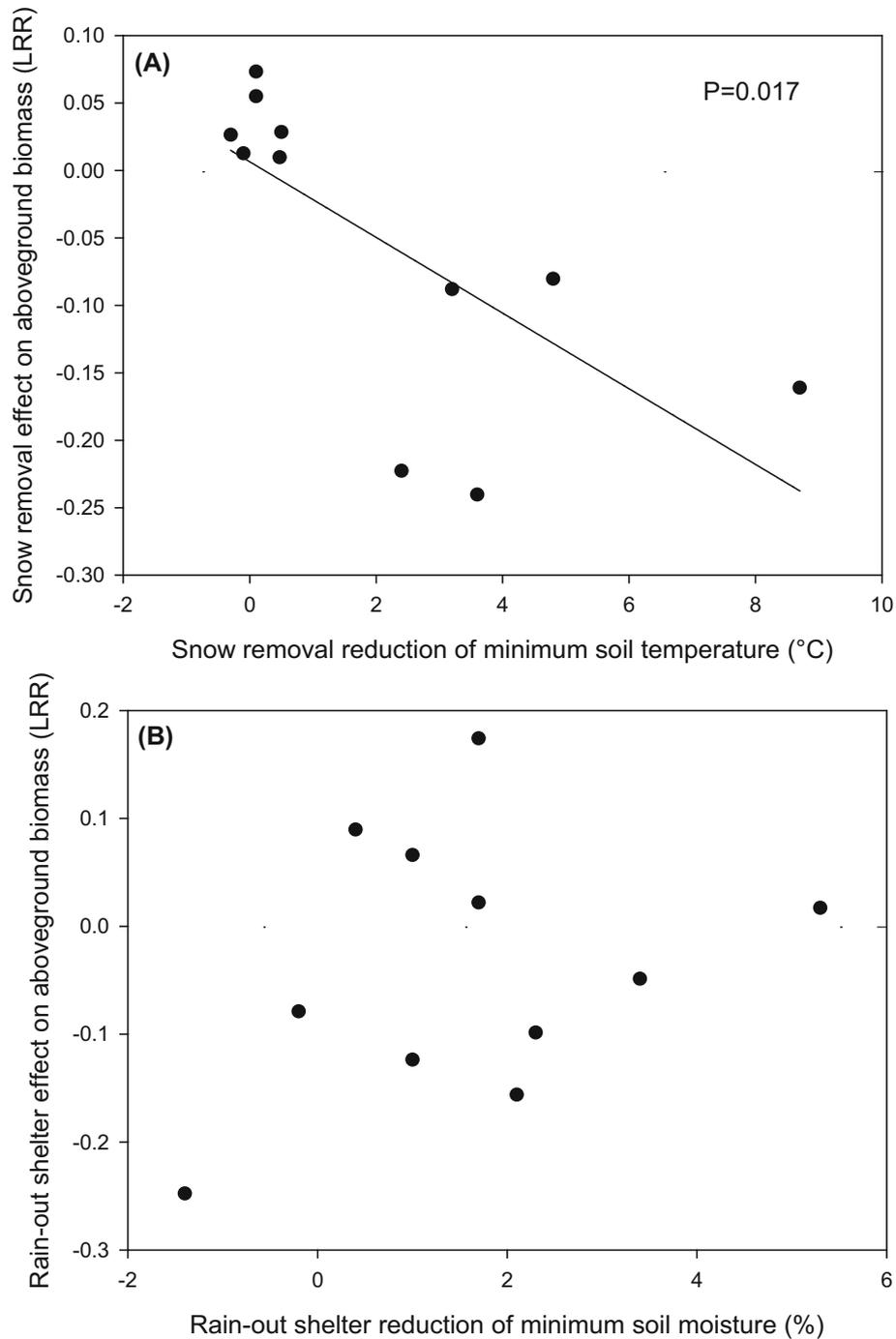


Figure 5. **A** The snow removal effect on aboveground biomass (log response ratio) for each site as a function of the snow removal reduction in minimum soil temperature. **B** The rain-out shelter effect on aboveground biomass (log response ratio) for each site as a function of the rain-out shelter reduction in minimum soil moisture.

biomass and cover were responsible for the total biomass declines in response to snow removal.

Although a substantial percentage of spring and summer precipitation (20–70%, but typically 40%) was blocked by the rain-out shelters, there were only significant reductions in aboveground biomass

for three sites. As discussed previously, the effectiveness of rain-out shelters is contingent on the ambient weather over the course of study (Kreyling and others 2017), and we anticipated minimal rain-out shelter effects may be observed in very dry or very wet years for a given site. For example, rain-

out shelters should have no effect in the absence of rain, whereas a rain-out shelter plot may receive abundant rain in a very wet year; both scenarios might not be expected to produce large treatment effects on plant biomass. We did not observe a clear relationship between rain-out shelter effects on biomass and ambient growing season precipitation (relative to the climate normals), and one site (Kernen) that experienced extremely low rainfall exhibited a significant rain-out shelter effect. Likewise, the effect of the rain-out shelters on minimum soil moisture was a poor predictor of the aboveground biomass responses. However, it has been demonstrated previously that apart from total precipitation, the timing and size of individual rainfall events can play an important role in plant biomass responses (Fay and others 2008; Kulmatiski and Beard 2013). Moreover, the marginally significant negative correlation among sites between the absolute rain-out shelter effect size on biomass and mean annual precipitation indicated that biomass was generally the most responsive to rain-out shelter treatment in the driest sites, although the direction of the biomass response was not consistent. In addition to blocking rain, the rain-out shelter infrastructure blocks solar radiation and can affect plot temperature, but such infrastructure artifacts have been documented to be minimal (for example, no detectable change in solar radiation for 30% rainfall interception, and less than 10% decrease in solar radiation for 80% rainfall interception; Yahdjian and Sala 2002).

The drought treatment in our experiment was limited to 1 year, and greater effects on plant biomass can occur in response to multiple years of drought (Hoover and others 2014). In addition, as addressed above, aboveground plant productivity appears to be more sensitive to increases in precipitation than to reductions (Wilcox and others 2017), and although some northern regions are predicted to experience increased drought over the next century, others are predicted to experience increases in precipitation (IPCC 2014). Therefore, better understanding of the interaction between increased summer and winter precipitation also remains an area of research need in predicting plant climate change responses. Moreover, a better understanding of precipitation responses is required for non-herbaceous systems.

One aspect of the plant responses to decreased precipitation that we were only able to document superficially was the root response. Over half of the sites collected root data, but this was limited to small-volume samples of standing biomass at a fixed depth, whereas changes in rooting depth and

root turnover are often important facets of root responses to drought (Xu and others 2015). The collection of the latter root data can be difficult to implement in a coordinated distributed experiment, given that such experiments are geared toward ease of sampling as a means of promoting widespread participation (Fraser and others 2013). However, the collection of such data in the context of a coordinated distributed experiment would likely be of great value; despite the general finding that relative allocation of biomass to roots increases in response to severe drought, root responses to drought remain highly variable (Eziz and others 2017), and variability among experiments, particularly with respect to relative water availability, may be important in explaining the observed variation among studies (Poorter and others 2012).

Interactions between frost and drought have been observed experimentally at the level of individual plants (Kreyling and others 2012b, c), and the secondary goal of our study was to explore frost-drought interactions at the plant community level. Although none of these interactions were significant, there was only one site (Changling) where both significant frost and drought effects occurred. Given that the main effects of frost and drought were not significant for the remainder of the sites, it remains inconclusive based on our results whether frost-drought interactions may be important at the community level. Nevertheless, one insight gained from our study is that it may be unlikely for both of these stressors to coincide for a given site within the same year. There are of course facets of decreased winter precipitation other than increased soil frost [for example, advanced spring phenology and decreased growing season soil moisture (Wipf and others 2006; Iwata and others 2010; Natali and others 2012)] that could promote interactions between reduced winter and summer precipitation, but as described at the outset, in our study we specifically attempted to isolate the frost effect from these other effects.

Conclusions

Our study demonstrated that frost effects resulting from reduced winter precipitation are a potentially important component of the total annual effect of reduced precipitation on plant biomass, and these effects are not simply restricted to the coldest sites. Although our attempt to examine interactions between frost and drought was impeded by a lack of simultaneous frost and drought effects within sites, the result that many sites did not show significant responses to snow removal or rain-out shelters is in

itself informative in the context of publication bias and meta-analysis; not only would the nonsignificant results in the current study have been difficult to publish on their own, but the coordinated distributed experiment encouraged participation by sites that otherwise would not have attempted snow removal or rain-out shelter experiments (for example, snow manipulation experiments are typically not conducted at warmer sites). Moving forward, the broader inclusion of sites in coordinated field experiments can clearly impart greater generality and improved perspective in climate change research.

ACKNOWLEDGEMENTS

The authors thank Angelika Kübert for assistance with data collection.

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