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Deepened winter snow cover enhances net ecosystem exchange and stabilizes plant community composition and productivity in a temperate grassland

Running head: Deepened snow stabilizes grassland community

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Abstract

Global warming has greatly altered winter snowfall patterns, and there is a trend towards increasing winter snow in semi-arid regions in China. Winter snowfall is an important source of water during early spring in these water-limited ecosystems, and can also affect nutrient supply. However, we know little about how changes in winter snowfall will affect ecosystem productivity and plant community structure during the growing season. Here, we conducted a five-year winter snow manipulation experiment in a temperate grassland in Inner Mongolia. We measured ecosystem carbon flux from 2014 to 2018 and plant biomass and species composition from 2015 to 2018. We found that soil moisture increased under deepened winter snow in early growing season, particularly in deeper soil layers. Deepened snow increased the net ecosystem exchange of CO_2 (NEE) and reduced intra- and inter-annual variation in NEE. Deepened snow did not affect aboveground plant biomass (AGB) but significantly increased root biomass. This suggested that the enhanced NEE were allocated to the belowground, which improved water acquisition and thus contributed to greater stability in NEE in deep-snow plots. Interestingly, the AGB of grasses in the control plots declined over time, resulting in a shift towards a forb-dominated system. Similar declines in grass AGB were also observed at three other locations in the region over the same time-frame and are attributed to four years of below-average precipitation during the growing season. By contrast, grass AGB was stabilized under deepened winter snow and plant community composition remained unchanged. Hence, our study demonstrates that increased winter snowfall may stabilize arid grassland systems by reducing resource competition, promoting coexistence between plant functional groups, which ultimately mitigates the impacts of chronic drought during the growing season.

INTRODUCTION

Plant productivity, species composition and community stability in arid and semi-arid ecosystems greatly depend on precipitation regimes (Bai, Han, Wu, Chen, & Li, 2004; Cleland et al., 2013;

Knapp et al., 2002; Leffler, Klein, Oberbauer, & Welker, 2016). In the past few decades, mean winter snow depth in northern China has increased significantly, especially in temperate grasslands, which is attributed to greater winter sea-level pressure and cold air surges from northern Siberia (Hartmann, Klein Tank, & Rusticucci, 2014; Huang et al., 2016; Peng, Piao, Ciais, Fang, & Wang, 2010; Tsunematsu et al., 2011). Winter snow can stimulate plant production by increasing soil nutrient and water supply at the beginning of growing season (Grippa et al., 2005; Schimel, Santa, Bilbrough, & Welker, 2004; Semenchuk et al., 2015; Wipf & Rixen, 2010), which is especially critical for plants in temperate grasslands in Inner Mongolia, where plant growth during spring is heavily reliant on snowmelt (Peng et al., 2010; Wang et al., 2017). Hence, changes in winter snow cover are likely to influence plant physiological processes, competition between species and community composition, but our current understanding of plant responses to changes in snow cover is inadequate. To generate general predictions of dryland ecosystem stability under altered precipitation regimes, we first need to determine how plant responses will affect the reordering of species in the community and thus modify competition between functional groups (Cleland et al., 2013; Hautier et al., 2015; Leffler et al., 2016; Liu et al., 2018; Smith, Knapp, & Collns, 2009).

Winter snow can affect the temporal and spatial variation of soil water and nutrients (Dorji et al., 2013; Wang et al., 2017; Yano, Brookshire, Holsinger, & Weaver, 2015). Snowmelt in the spring infiltrates into the soil to different depths (Dorji et al., 2013; Wang et al., 2017). During the early growing season, plants predominantly take up water from spring snowmelt in the upper soil horizons, whereas deep water supplies from snowmelt infiltration are more important for plants during the peak and late growing season in dryland ecosystems, when water becomes less available in upper soil horizons but root growth allows access to deep reserves (Asbjornsen, Shepherd, Helmers, & Mora, 2008). In addition, snow cover creates a thermal insulation effect, resulting in a warmer soil microclimate that enhances microbial activity (Schimel et al., 2004; Schmidt & Lipson, 2004). Microbial dieback during snowmelt releases a substantial amount of nutrients, which are critical to alleviate nutrient limitation of plant growth at the beginning of the growing season (Larsen, Michelsen, Jonasson, Beier, & Grogan, 2012; Li et al., 2016; Schmidt & Lipson, 2004). Hence, snow cover alters the seasonal and vertical distribution of water and nutrients in the soil, which underpins plant biomass allocation and is likely to shape plant community structure.

The temporal and spatial variation of resource availability resulting from winter snow cover regulates plant phenology and biomass allocation (Christiansen, Lafreniere, Henry, & Grogan, 2018; Dorji et al., 2013; Wang et al., 2017). On the one hand, deeper winter snow cover can result in later snowmelt, thus delaying spring green-up and constraining plant growth in the early growing season (Wang et al., 2017). On the other hand, increased water and nutrient supply from snowmelt can facilitate plant development and growth in warmer spring weather (Shen, 2011), which accelerates net ecosystem carbon uptake and plant productivity (Christiansen et al., 2018; Dorji et al., 2013; Wang et al., 2017). Additionally, because rooting depth generally follows water infiltration depth (Fan, Miguez-Macho, Jobbágy, Jackson, & Otero-Casal, 2017), some plants allocate more photosynthetic products to belowground biomass to access deep water supplies from snowmelt, which may be particularly critical to alleviate water-limited plant growth in arid and semi-arid ecosystems (Hasibeder, Fuchslueger, Richter, & Bahn, 2015; Hui & Jackson, 2006; Shipley & Meziane, 2002; Yang et al., 2011).

Changes in plant growth and phenology in response to deeper snow cover could ultimately modify plant community composition and ecosystem function via distinct effects on different species or functional groups. Physiological changes in individual plants determine the response of different species to the current environment change, which can lead to species reordering and shifts in functional groups within the community (Cleland et al., 2013; Leffler et al., 2016; Luo et al., 2011; Smith et al., 2009). Grass and forb species, the two main plant functional groups in temperate grasslands, coexist due to significant niche stratification for optimal resource acquisition in soils (Nippert & Knapp, 2007a; Nippert & Knapp, 2007b). Grasses primarily absorb water from surface soils due to their fibrous roots with high branching intensity (Li, Liu, McCormack, Ma, & Guo, 2017; Nippert & Knapp, 2007b; Roumet, Urcelay, & Diaz, 2006). Consequently, grasses are more responsive to short-term pulses of water availability, but also more sensitive to soil surface drying over longer periods (Nippert & Knapp, 2007b; Sala, Lauenroth, & Golluscio, 1997). Conversely, many forbs can access deeper water reserves through taproots (Nippert & Knapp 2007a) and deep-rooted forbs can benefit from accessing water in deeper soil horizons during longer drought periods, which allows them to complete a growth cycle with sufficient water supply (Nippert & Knapp, 2007a; Sala et al., 1997). Therefore, the performance of distinct functional groups in acquiring water during the growing season can be affected by variation in precipitation patterns, which in turn affects the competitive interactions that determine ecosystem stability (Cleland et al., 2013; Hautier et al., 2015; Liu et al., 2018; Smith et al., 2009).

In sum, future changes in winter snowfall have the potential to substantially alter arid temperate grassland ecosystems. However, due to the harsh environment in winter, very few long-term field experiments have explored plant growth responses to changes in winter snow cover over time-frames that could reveal shifts in ecosystem structure and functioning (Brooks et al., 2011). We aimed to address this with a five-year manipulative experiment using a snow fence to simulate increasing winter snowfall in a temperate grassland in Inner Mongolia. We assessed how deepened winter snow cover regulates community composition and ecosystem stability via changes in plant growth and resource allocation to test the following hypotheses: H1) Deepened winter snow cover will result in a short-lived increase in surface soil moisture after snowmelt, followed by increased water availability from drained snowmelt in deeper soil horizons at later stages of the growing season. H2) Greater water and nitrogen availability in the deep-snow treatment will promote plant carbon uptake and greater belowground biomass allocation to improve resource acquisition later in the growing season. H3) Changes in resource availability and biomass allocation with deepened snow cover will have variable effects on the performance of distinct plant functional groups (grasses and forbs), resulting changes in aboveground biomass, net ecosystem exchange and plant community composition.

MATERIALS AND METHODS

Study site and snow manipulation experiment design

The research was conducted at the Inner Mongolia Grassland Ecosystem Research Station (IMGERS, 43°38'N, 116°42'E) of the Chinese Academy of Sciences. The grassland in the region is characterized by a semiarid temperate continental climate with an elevation of 1200 m and mean annual temperature of 0.9 °C (Chen et al., 2019). The mean annual precipitation is 334 mm, of which *c.* 80% falls during the growing season, which lasts for *c.*150 days from May to September (Chen et al., 2014). Mean winter snow depth has increased in Inner Mongolia in the past few decades (Huang et al., 2016; Peng et al., 2010) and at our study site, snow depth has increased by 133 ± 2.7 mm over the last 37 years, with an avaerage of 3.6 ± 0.7 mm yr^{-1} (Fig. S1). The grassland plant community is dominated by perennials, including *Leymus chinensis* (Trin.) Tzvel., *Stipa krylovii* Roshev., *Artemisia frigida* Willd. Sp. Pl. and *Potentilla chinensis* Ser. The soil at the study site is a loamy-sand.

Our field experiment comprised deepened winter snow (deep-snow) and ambient snow (control) treatments, which were established in October 2013 using a snow fence (1.25 m tall and 100 m long) made of polyethylene mesh to create deepened snow treatment. The fence was arranged perpendicular to the prevailing winter wind direction (northwest) to increase snow depth by acting as a barrier to wind-drift. The fence was secured by 2-m tall fixed stainless-steel posts, each spaced 2 m apart. From 2013 to 2018, we erected the snow fence at the beginning of October each year and removed it at the end of the following March. Three replicate plots measuring 4-m × 8-m each were arranged along the snow fence for the deep-snow treatment. Three corresponding control plots were established parallel to the snow fence along a 100-m transect, leaving a buffer zone of >20 m buffer to ensure the controls were not influenced by the snow fence. All plots of both treatments were also separated by at least 10 m. To assess the efficacy of the deep-snow treatments, winter snow depth was measured in each plot during late January to early February each year; measurements were taken at a distance of 1 m from the snow fence in deep-snow plots and at the corresponding direction and intervals in control plots. Snow depth for both treatments was recorded as the mean depth of four measurements at 1-m intervals.

Soil moisture and nitrogen concentrations

To test our first hypothesis of altered soil moisture distribution under deepened winter snow cover, soil moisture was measured every 30 minutes at 10 cm and 40 cm soil depth in one deep-snow plot and one control plot using a soil temperature and moisture sensors (5TM, METER Group Inc., Pullman, WA, USA) attached to a data logger (EM50/G, METER Group Inc., Pullman, WA, USA) from April 2016 to 2018. In addition, we took daily measurements of soil moisture in all plots during the growing season (April to September) in 2017 and 2018; soil moisture was measured using a capacitance probe sensor (Diviner 2000, Sentek, Australia) at 10-cm increments from 10-40 cm depth via an access tube (polyvinylchloride, 50 cm long) installed in the centre of each plot.

To examine the effects of deepened winter snow on soil nitrogen, we collected soil samples at 0-5 cm depth from each plot during winter snow cover (23 January 2018 and 28 January 2019) and after snowmelt on 2 April 2019. Inorganic nitrogen (ammonium-N and nitrate-N) was extracted with 0.5 mol L^{-1} K_2SO_4 (henceforth "extractable N") and subsequently measured using a continuous flow injection analyser (AA3 HR, SEAL Analytical GmbH, Germany).

Ecosystem CO_2 fluxes

Net ecosystem exchange of CO_2 (NEE) was measured using an infrared gas analyser (LI-6400, LiCor, Lincoln, NE, USA) attached to a transparent chamber (0.5 m × 0.5 m × 0.5 m). CO_2 flux measurements were made over a stainless-steel frame (0.5 m × 0.5 m), which was sunk into the soil to *c*. 3-cm depth in each plot in October 2013. The frames were placed at least 2.5 m from the fence in deep-snow treatment plots and in the corresponding direction and location in control plots. Net ecosystem exchange was estimated from CO_2 flux rates under lighted conditions (see Li et al., 2018 for details). Ecosystem carbon (C) fluxes were measured three times a month throughout the growing season (May to September) from 2014 to 2018. CO_2 flux rates were determined from the increase in CO_2 concentrations within the chamber, which were recorded at

10-s intervals for 80 s.

Plant biomass

To assess changes in plant community composition and plant biomass (hypothesis 3), vegetation surveys were conducted annually in August in one randomly placed 0.5-m × 1-m quadrat in each plot from 2015 to 2018. The number of species and individuals and the height of individuals of each species were recorded to calculate species richness, Shannon's diversity (*H'*) and Simpson's diversity Index (*D'*). The peak aboveground biomass (AGB) in each quadrat was harvested by species and samples were stored for laboratory analyses.

To determine changes in belowground biomass allocation (hypothesis 2), root samples were obtained annually in August using a 7-cm diameter corer at five depth increments (0-5 cm, 5-10 cm, 10-20 cm, 20-40 cm, 40-60 cm) from 2014 to 2018. Three samples were taken diagonally across each plot and mixed carefully to give one replicate sample per plot and depth increment. Root samples were cleaned on the same day by removing soil particles under running water, then soaked in deionized water and cleaned of residual soil using a 0.2 mm mesh sieve. Live and dead roots were separated manually under a magnifying glass, whereby live roots were distinguished visually by their bright colour, flexibility, consistency and soft texture (Gao et al., 2008) and dead roots were removed. Finally, plant AGB and root biomass samples were oven-dried at 65 ℃ for 48 hours to constant weight with the nearest 0.1 g.

Statistical analysis

All statistical analyses were performed in R version 3.5.3 (R Development Core Team, 2018). The effects of deepened winter snow cover on soil moisture at different soil depths were assessed with linear mixed effects models using the *lmer* function of the lme4 package (Bates, Mächler, Bolker, & Walker, 2015), with treatment as a fixed effect, and time (day of year) and plot as random effects; to assess differences in soil water content at distinct plant growth stages, we ran separate models for soil moisture in the early (1 April to 31 May), mid (1 June to 15 August) and late (16

August to 30 September) growing season. The significance of snow depth treatments was determined by comparison to the corresponding null model, which only included time and plot as random effects. The effect of deepened winter snow cover on soil moisture during winter was not assessed due to lack of replication.

Repeated-measures analysis of variance (ANOVA) was used to evaluate the effects of deepened snow treatment on snow depth, extractable N during winter snow cover, seasonal dynamics of NEE, annual means of NEE, total AGB, grass AGB, forb AGB, species diversity indices, annual root biomass, and the intra-annual coefficient of variation (CV) for NEE. Total AGB, grass AGB and forb AGB were $\log_{10}$-transformed to meet data normality assumptions before analysis and differences between years were assessed with Tukey's post-hoc tests. One way ANOVA was used to test the effects of deepened snow on extractable N after snow melt, the inter-annual CV of NEE, total AGB, grass AGB, forb AGB and root biomass as well as mean annual root biomass at individual soil depths. A two-way factorial ANOVA was used to assess the effects of deepened winter snow cover and soil layer on root biomass from 2014 to 2018. For all the ANOVAs, plot was included as an error term.

Trends in AGB and species richness with experimental duration were assessed using generalized linear models (GLMs) with Gamma or Poisson distribution, respectively. A t-test was used to compare AGB and species richness between grasses and forbs in each year. Finally, to assess changes in plant community composition in control and deep-snow plots during the experiment, we used nonmetric multidimensional scaling (NMDS) ordinations based on Bray-Curtis dissimilarity (metaMDS function in the ‘vegan’ package; Oksanen et al. 2009). We then tested for differences in plant communities among years using permutational multivariate analysis of variance (PERMANOVA, adonis function).

RESULTS

Climate conditions, soil moisture and nitrogen concentrations

The deep-snow treatments effectively increased snow depth by 491 ± 78 mm yr^{-1} during our experimental period and the difference between deep-snow treatments and controls demonstrated relatively thicker winter snow and a greater increase under the deep-snow treatments during drier years (2015-2016; Fig. S2). The greatest increase in snow depth was 980 mm in 2016, and smallest increase in snow depth was 270 mm in 2018.

Soil moisture was greatest during snow melt in March, and peak soil water content at 40 cm lagged one to two days behind the surface soil (Fig. 1b). During the early growing season, deep-snow increased soil moisture throughout the profile with the greatest increase in deeper soil layers, although the treatment effect was only statistically significant in 2018 (Fig. S3a). During the time of year with most precipitation (June to September), the response of soil moisture to deepened winter snow varied with soil depth (Table S1; Fig. 1b; Fig. S3b,c). By the peak of the growing season in 2018, soil moisture in the upper soil layers of the deep-snow treatment declined rapidly to control levels and was lower than the controls (Fig. 1b); soil moisture at 30-cm depth under the deep-snow treatment showed a similar pattern to upper horizons, but declined more slowly; whereas deep soil moisture (40-cm) remained slightly higher than the controls (Table S1; Fig. 1b; Fig. S3). Although deepened winter snow had no significant effect on the distribution of soil water during the drier year (2017), the temporal pattern in soil moisture with depth was nonetheless similar to 2018 (Fig. 1b; Fig. S3).

Soil extractable N concentrations at 0-5 cm depth were greater under the deep-snow treatment during winter snow cover (Fig. 2a) but there was no significant effect of deep snow on soil extractable N at the end of snowmelt in April 2019 (Fig. 2b).

Ecosystem CO_2 fluxes

Overall, mean annual NEE increased significantly with deepened winter snow, but the response of NEE to deep-snow treatments varied during the growing season and from year to year (Fig. 3a,b). There were no discernible effects of deepened winter snow cover on NEE during the early growing season in most years, but NEE increased significantly during the peak growing season in years with high snowfall (Fig. 3a). The increase in annual NEE in the deep-snow plots relative to the controls was greatest in 2015 (61.21%) and 2016 (238.60%; Fig. 3b), when the difference in winter snow depth was also particularly large (Fig. S2). Importantly, deepened winter snow buffered both annual and seasonal variation in NEE, demonstrated by the lower inter- and intra-annual CVs for NEE from 2014 to 2018 compared to the control plots (Fig. 3c,d).

Ecosystem plant biomass and community composition

Deepened winter snow had a stabilising effect on plant AGB and community composition. Although there was no overall change in plant AGB in the deep-snow plots, the inter-annual variation was lower than in the control plots and AGB was relatively stable from year to year, even during particularly dry years (Fig. 4a,d). The AGB of the two plant functional groups also remained constant over the study period in the deep-snow plots (Fig. 4b,c; Fig. 5b), resulting in lower inter-annual variation for both grass and forb AGB with deepened winter snow (Fig. 4d). However, in the control plots the AGB of grasses and forbs showed contrasting trends over time: forb AGB increased significantly in the control plots from 29.6 g m^{-2} in 2014 to 122.3 g m^{-2} in 2018 ($P < 0.01$), whereas grass AGB decreased linearly from 148.4 g m^{-2} to 19.2 g m^{-2} over the same time period (Fig. 4b,c; Fig. 5a).

Deepened winter snow cover had no discernible effect on plant diversity or community composition. The Shannon-Wiener index, Simpson's diversity index and plant species richness all remained unchanged in deep-snow plots (Fig. S4), and there were no changes in species abundances and plant community structure with experimental duration (Fig. 5d,f). By contrast, in the control plots the AGB of forbs increased significantly with years since the start of the experiment, whereas grass biomass declined (Fig. 5a). At the start of measurements in 2015, the number of grass and forb species was equal, but the diversity of grasses declined, while the diversity of forbs increased, resulting in a significant difference between grass and forb species richness in the control plots by 2018 (Fig. 5c). Consequently, the original plant community structure appears to be shifting from a grass-dominated ecosystem to a forb-dominated ecosystem in the controls (Fig. 5a,c,e), whereas the plant community composition under deepened winter snow has remained relatively stable (Fig. 5b,d,f).

We found significant plant responses to deepened winter snow belowground. Total root biomass was significantly greater under the deep-snow treatment throughout the study, despite similar inter-annual variation compared to the controls (Fig. 6a). Deepened winter snow cover also altered the vertical distribution of root biomass, whereby the mean root biomass from 2014 to 2018 increased significantly at the soil surface (0-5 cm) and in the deep soil horizons (20-40 cm) under the deep-snow treatment (Fig. 6b, Fig. S5).

DISCUSSION

Our five-year winter snow fence experiment demonstrated that deepened winter snow enhanced mean annual NEE and had a stabilising effect on grassland aboveground biomass production and plant community composition. The effects of deepened winter snow can largely be attributed to the immediate and legacy effects of enhanced water supply after snowmelt, and concomitant changes in vertical root distribution, which highlight the buffering effect of winter snowfall on the impact of long-term drought conditions across Eastern Inner Mongolia.

Deepened winter snow enhances net ecosystem exchange

Although we observed an overall increase in mean annual NEE in deep-snow plots during our study, seasonal and annual differences in the impact of the deep-snow treatment were largely determined by the amount of snowfall during winter. In arid ecosystems, there is a critical threshold for winter precipitation, which constrains annual net primary productivity (Knapp, Ciais, & Smith, 2017); we would therefore expect little impact of deepened winter snow cover on NEE if this threshold is not substantially exceeded. Accordingly, in years with low snowfall (2014, 2017 and 2018) we observed no overall increase in annual NEE in deep-snow plots (Fig. 3b). The strong seasonal differences in NEE with deepened winter snow can also be attributed to variable snow volume. Increased winter snow accumulation could constrain spring "green up" by delaying the date of snowmelt and suppressing plant growth and development in early spring (Wang et al., 2017). Indeed, the lack of response in NEE to deepened winter snow in the early growing season can be explained by a 20-day delay in snowmelt in the deep-snow plots compared to controls (Fig. S6), which also delayed plant growth until mid-April, indicated by lower green chromatic coordinates (GCC) in deep-snow plots (Peichl, Sonnentag, & Nilsson, 2015; Fig. S7). However, plant growth proceeds rapidly during spring with enhanced water and nutrient supply from snowmelt (Archibald & Scholes, 2007; Wang, Li, Wang, & Wu, 2008) and differences in soil water availability between treatments are likely to have a greater effect on plant productivity later in the growing season.

We recorded the greatest increase in NEE with deepened winter snow during the peak growing season (Fig. 3a). Enhanced NEE later during the growing season is likely a legacy effect of greater accumulation of nitrogen during snow cover (Fig. 2a) and the improved soil moisture status we measured after snowmelt in early spring (Fig. 1b; Peng et al., 2010; Schimel et al., 2004; Semenchuk et al., 2015; Wipf & Rixen, 2010), which are critical to alleviate water stress and nutrient limitation for plant germination and development in the early growing season. Furthermore, with deepened winter snow, more meltwater was transferred and stored in deep soil horizons (Fig. 1b), which can promote plant productivity by enhancing water availability during the following growing season (Grippa et al., 2005; Peng et al., 2010).

Deepened winter snow stabilises plant communities

One of the most striking results of our study was the stabilising effect of deepened winter snow on aboveground biomass production and plant community composition. Although we observed no changes in plant species richness at community level during our study, we found that the aboveground biomass of grasses in the control plots decreased during our experimental period. Additionally, by the end of the experiment the number of forb species in the control plots had increased, whereas the number of grass species had declined (Fig. 5c), which suggests a shift from the original grass-dominated ecosystem to a forb-dominated ecosystem (Fig. 5a,c,e). A similar reduction in grass biomass production was also observed from 2013 to 2018 in three other locations in the region, which were up to 300 km away from our research site (Fig. S8), demonstrating widespread changes in the contribution of grasses to ecosystem productivity. Plant species diversity and community composition are being strongly perturbed by the changing climate (Cleland et al., 2013; Liu et al., 2018; Luo et al., 2011; Smith et al., 2009). The decline in grass biomass production and species richness across eastern Inner Mongolia can be attributed to the drought that the region has experienced over the past five years. Indeed, mean annual precipitation during our study (313 mm from 2014 to 2018) was lower than the long-term average from 1982 to 2009 (334 mm; Chen et al., 2014) due to reduced precipitation during the growing season, especially in summer (Fig. 1a). The stabilising effect of our deep-snow treatments is therefore likely to result from the alleviation of drought conditions during the growing season.

Belowground niche partitioning between plant functional groups, and the observed changes in vertical root distribution in our deep-snow plots could explain the stabilising effect of deepened winter snow cover on aboveground biomass and plant community composition. In arid ecosystems, competition for soil water reserves is a particularly strong driver of competition and niche partitioning among plant species and functional groups (Nippert & Knapp, 2007a; Nippert & Knapp, 2007b). Grasses mainly rely on fibrous branched roots to acquire surface soil water (Li et al., 2017; Nippert & Knapp, 2007b; Roumet et al., 2006), whereas many forbs are characterized by a taproot system to access deep water reserves (Nippert & Knapp, 2007a; Sala et al., 1997). As the soil surface dries out rapidly due to active exchange with the atmosphere, water stress occurs more frequently in surface soil layers (Jochen, 2002; Sala et al., 1997). In our study, the continuous drought during several growing seasons therefore had a particularly strong negative impact on grass productivity in the control plots, allowing deep-rooted forbs to become dominant. By contrast, the changes in water availability with deepened winter snow cover appear to help alleviate the negative effect of lower precipitation during the growing season, allowing the two functional groups to coexist and thus stabilizing plant community composition and aboveground biomass (Hautier et al., 2015). Indeed, we found that deepened snow reduced inter-annual variation of net ecosystem carbon flux and aboveground biomass, suggesting that higher winter snowfall helps stabilize ecosystem productivity (Fig. 3d; Fig. 4d). The stabilization effect of winter snowfall may be associated with greater carbon allocation to root biomass at the community level, as higher NEE in the deep-snow plots was accompanied by higher root biomass, but no changes in aboveground biomass (Fig. 4a; Fig. 6). Although it is conceivable that the lower root biomass at the soil surface in control plots is due to the decline in the abundance of grasses (Fig. 5; Fig. 6), the greater root biomass at depth in the deep-snow plots may indicate greater investment of individual plants in roots in the deep-snow plots in response to enhanced soil water availability in deeper soil horizons (Fig. 1b; Fig. 6).

The changes in the vertical distribution of roots largely followed the pattern of increased soil moisture in the deep-snow plots. During early spring, the higher root biomass under deepened winter snow cover increased water holding capacity in surface soils (McKinney & Cleland, 2014) and thus more water from snowmelt or summer rainfall can be retained in the rooting zone. Increased winter snowfall also resulted in more snowmelt infiltrating into deep soil horizons, where the increased root biomass in deep soil layers provides access to water reserves later in the year (Dorji et al., 2013; Wang et al., 2017). Indeed, access to deep soil water supply, known as the "maintenance water pool", could explain the greater stability of NEE and biomass productivity in the deep-snow plots, as water transportation by tap roots not only helps to maintain the physiological activity of forbs (Ryel, Ivans, Peek, & Leffler, 2008; Ryel, Leffler, Ivans, Peek, & Caldwell, 2010), but is also beneficial to relieving water-stress in grasses with shallow roots by "hydraulic lift": the passive transport of water by deep-rooted plants to drier surface soil layers (Caldwell, Dawson, & Richards, 1998; Horton & Hart, 1998; Ryel et al., 2008; Ryel et al., 2010). Consequently, we propose that deepened winter snow cover mitigated competition between plant functional groups by alleviating water stress, and thus stabilized plant community composition and ecosystem productivity in grasslands under prolonged annual drought conditions.

In conclusion, knock-on effects of modified winter snow depth associated with climate change may have important consequences for plant communities and broad ecological processes (Cleland et al., 2013; Leffler et al., 2016; Luo et al., 2011; Smith et al., 2009). To date, the impacts of changes in snow cover on community-level processes and ecosystem dynamics remain poorly characterized because they require long-term research, particularly in systems with slow-growing vegetation and many perennial species (Sayer et al., 2017). In our five-year study, we demonstrated positive effects of deepened winter snow cover on net ecosystem carbon exchange and productivity of plants during the following growing season via enhanced nitrogen and water supply and associated shifts in vertical root distribution. Our findings highlight the critical role of deepened winter snow cover in regulating plant productivity and community composition, which ultimately increased ecosystem stability under a changing environment (Fig. 7). Given the important contribution of winter snow to ecosystem dynamics during the growing season, we emphasize the importance of considering the ecological consequences of winter climatic change to predict ecosystem structure and function in the future.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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Tables

None

Figure captions

Figure 1 | Environmental variables measured in a snow-depth manipulation experiment in a grassland in Inner Mongolia, showing **(a) Precipitation** from 2013 -2018 observed from a weather station 0.5 km away, where grey bars indicate daily precipitation, the red line with dots indicates precipitation during the growing season and the blue line with diamonds indicates precipitation during non-growing season; the red and blue dashed lines indicate mean precipitation from 1982 to 2018 during the growing season (274 mm) and non-growing season (56 mm), respectively. **(b) Soil water content** at 10 cm increments to 40 cm depth under deep-snow (blue lines) and control (red lines) treatments and the difference in mean soil moisture in deep-snow plots relative to controls (black solid line) measured daily from 2016 to 2018; the grey dashed lined lines denote zero difference of soil water content between treatments and shading indicates the growing season (April-September); measurements in 2016 and from January - March 2017 and 2018 (10 cm and 40 cm depth only) are from one deep-snow plot and one control plot via EM50 data logger; all other values via Diviner 2000 are means with standard error bars for *n* = 3 plots per treatment.

Figure 2 | Soil inorganic nitrogen concentrations (K_2SO_4 extractable N) in the soil at 0-5 cm depth under deep-snow (blue bars) and control (red bars) treatments, during **(a)** winter snow cover in January; *P*-values from repeated-measures analysis of variance are given for significant differences between treatments and years, and **(b)** the end of snow-melt in April 2019 (no samples were collected in 2018); *P*-values from one-way analysis of variance (ANOVA) are given for significant differences between treatments; means and standard errors are given for *n* = 3.

Figure 3 | Net ecosystem exchange (NEE) and coefficients of variation (CV) in NEE from 2014 to 2018 under deep-snow (blue triangles or bars) and control (red dots or bars) treatments, showing **(a)** the dynamics of CO_2 measured weekly during the growing season, **(b)** mean annual NEE per treatment, **(c)** intra-annual variation and **(d)** inter-annual variation in NEE; *P*-values from repeated-measures analysis of variance and one way ANOVA are given for significant differences between treatments and date or year, where '*ns*' is non-significant; different letters above bars indicate significant differences between years in each treatment; means and standard errors are given for *n* = 3.

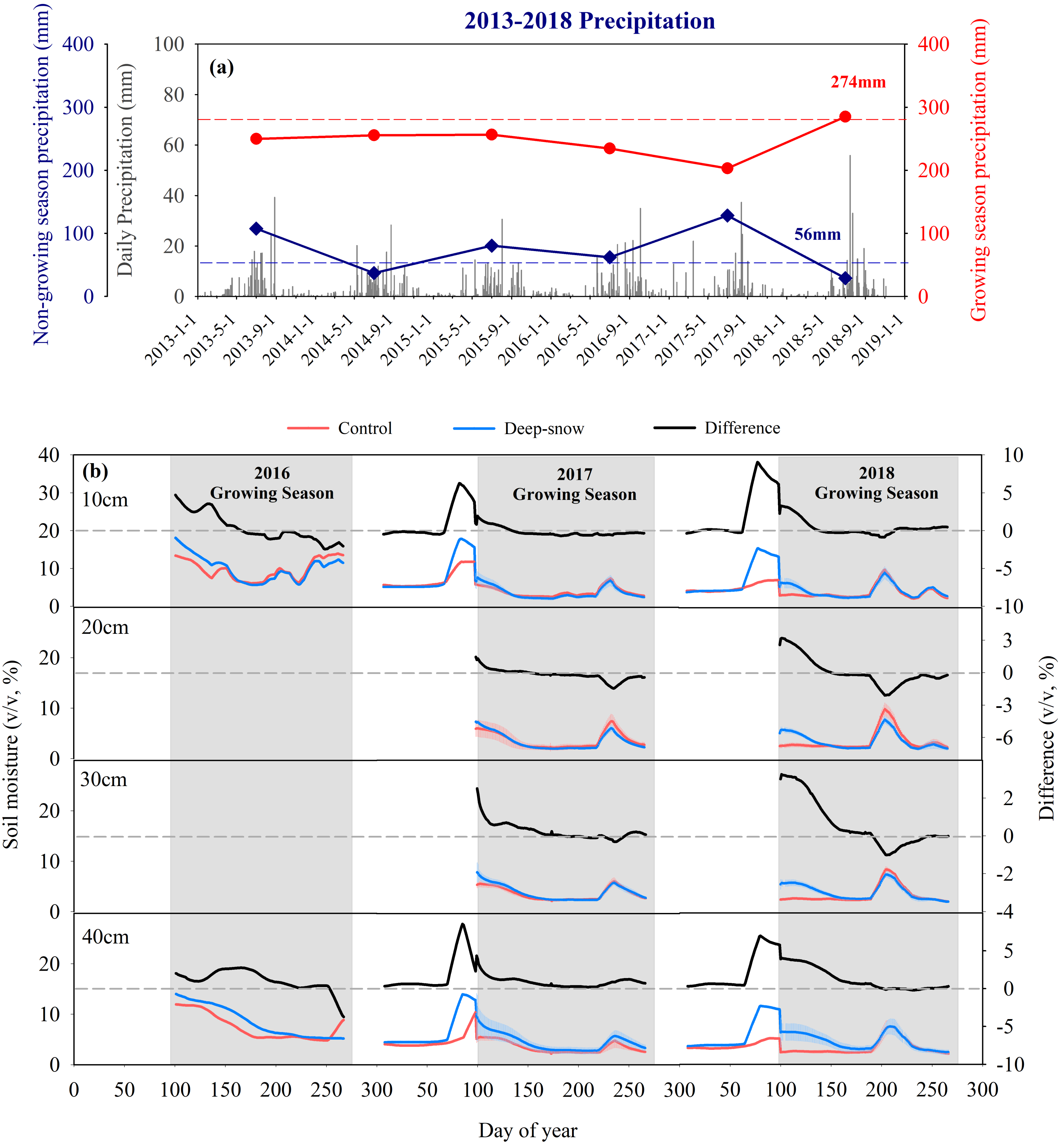
Figure 4 | Aboveground biomass (AGB) under deep-snow (blue) and control (red) treatments from 2015 to 2018, showing **(a)** annual total AGB, **(b)** annual forb AGB, **(c)** annual grass AGB and **(d)** the inter-annual coefficients of variation (CV) for total AGB, forb AGB and grass AGB, showing means and standard errors for *n* = 3. In (a), (b), and (c), significant differences between treatments and years are shown as *P*-values from repeated-measures analysis of variance based on $\log_{10}$-transformed data, where '*ns*' is non-significant and letters above bars indicate differences between years for each treatment; in d) differences between treatments are given as * for $0.01<P<0.05$, ** for $0.001<P<0.01$, *** for $P<0.001$).

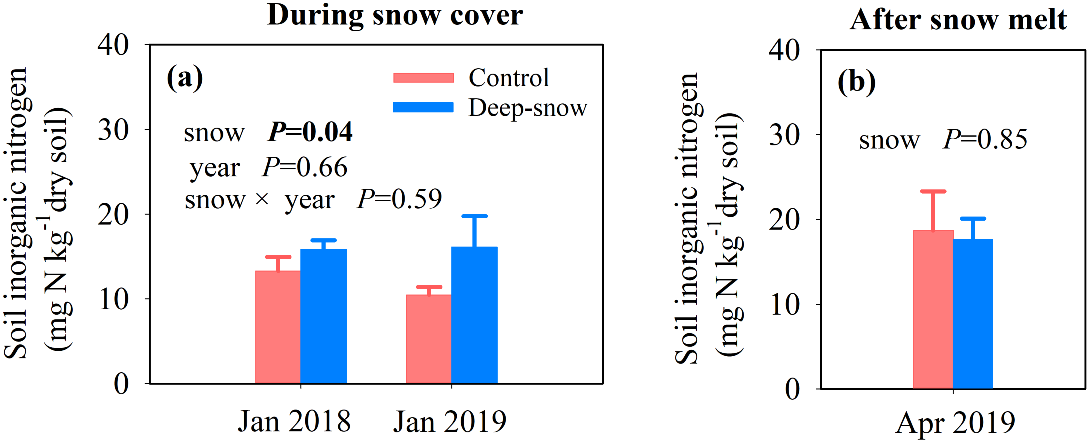
Figure 5 | Changes in aboveground biomass (AGB), species richness and plant community

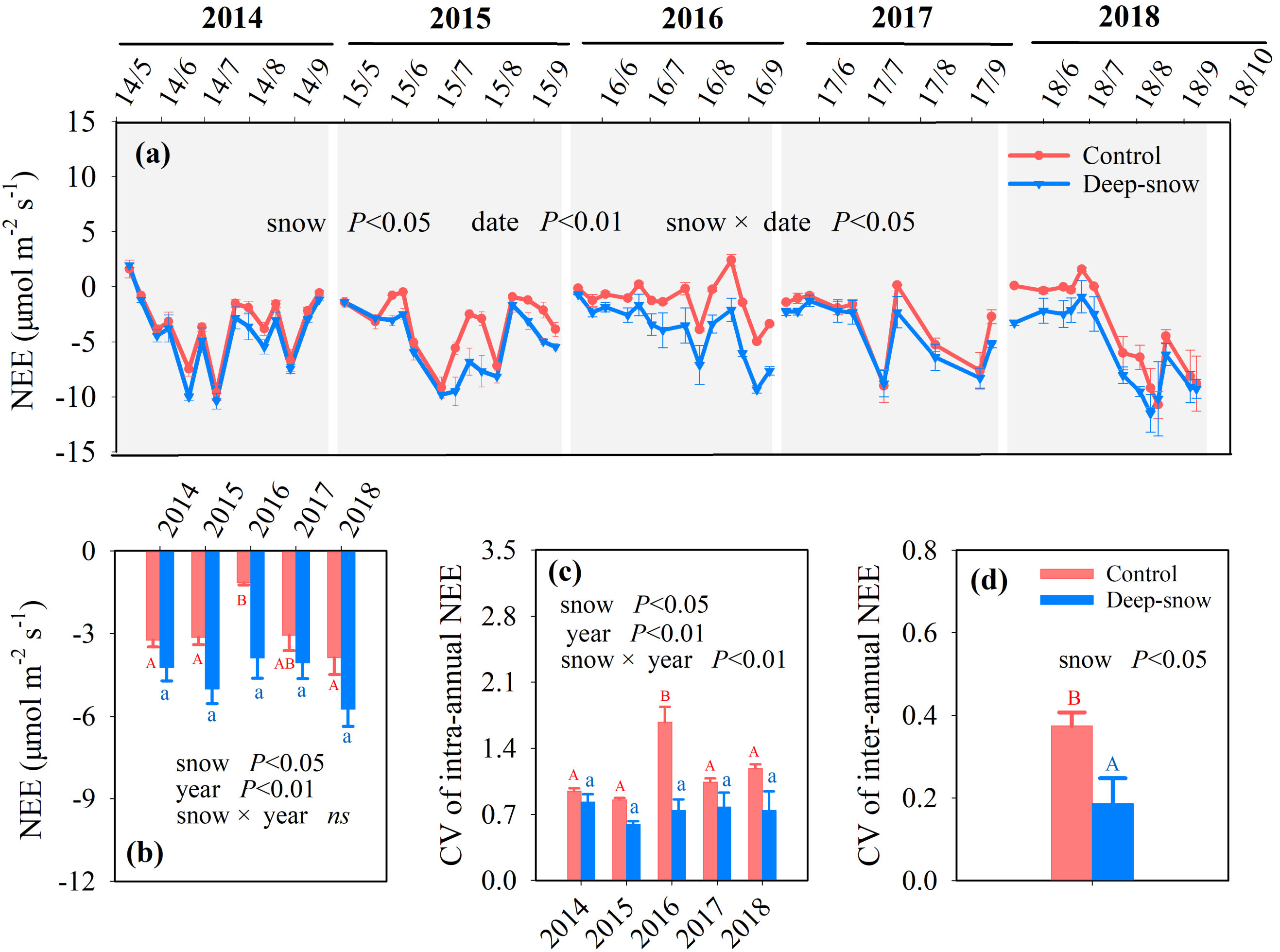
structure in **(a), (c), (e)** control plots and **(b), (d), (f)** deep-snow plots during a snow-depth manipulation experiment from 2015 to 2018; green dots and orange triangles with error bars denote grasses and forbs, respectively; *P*-values are given for significant trends over time in AGB and species richness (derived from generalised linear models), and plant community structure (derived from PERMANOVA); differences between grasses and forbs in each year (t-tests) are given as * for $0.01<P<0.05$, ** for $0.001<P<0.01$, *** for $P<0.001$), where '*ns*' is non-significant; means and standard errors are given for $n = 3$.

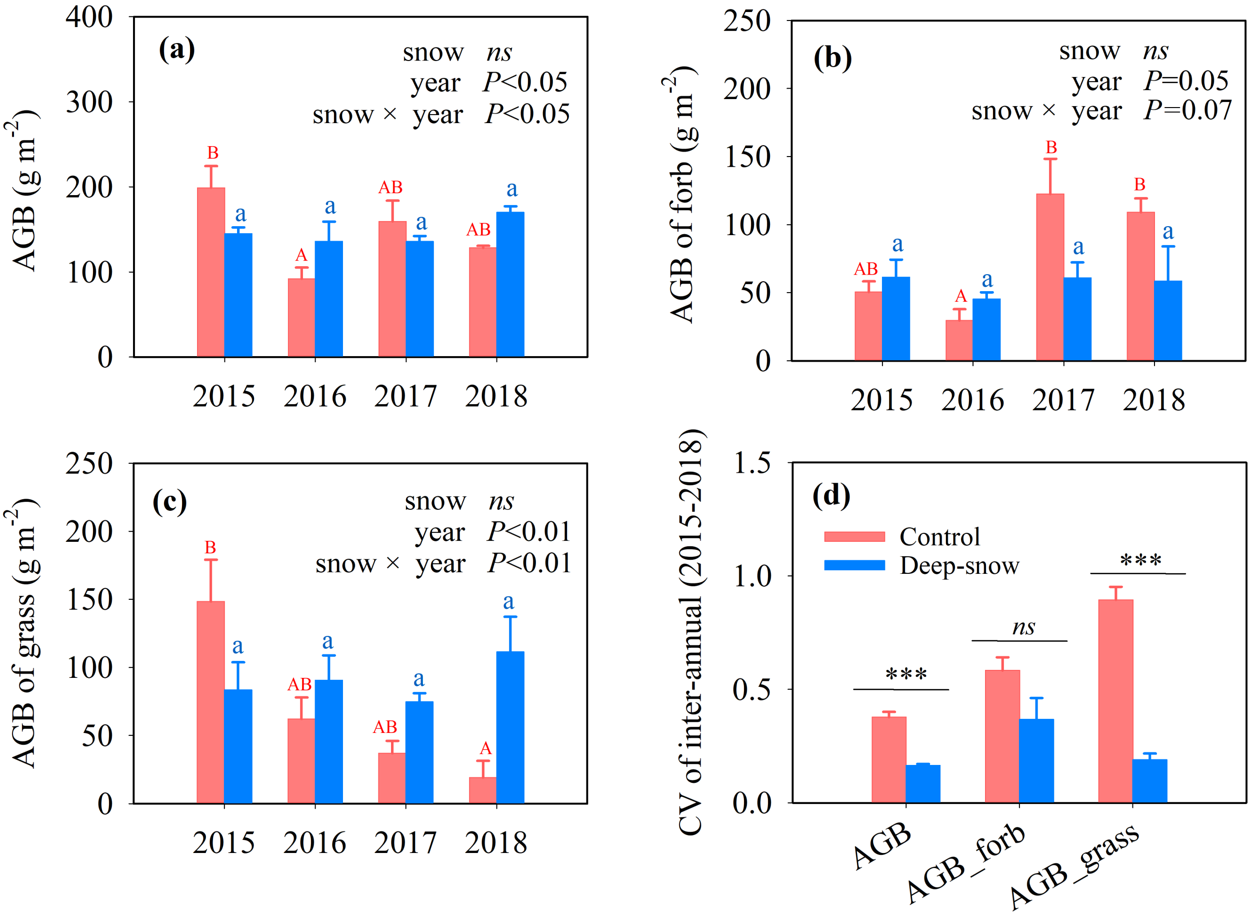
Figure 6 | (a) Total root biomass and (b) mean annual root biomass distribution at different soil depths in deep-snow (blue) and control (red) plots from 2014 to 2018, showing means and standard errors for $n = 3$**.** The inset in (a) shows the inter-annual coefficient of variation (CV) for total root biomass; *P*-values for significant differences between treatments, years or depths are given, where '*ns*' is non-significant and differences between treatments at individual depths in b) are indicated by * for $0.01<P<0.05$.

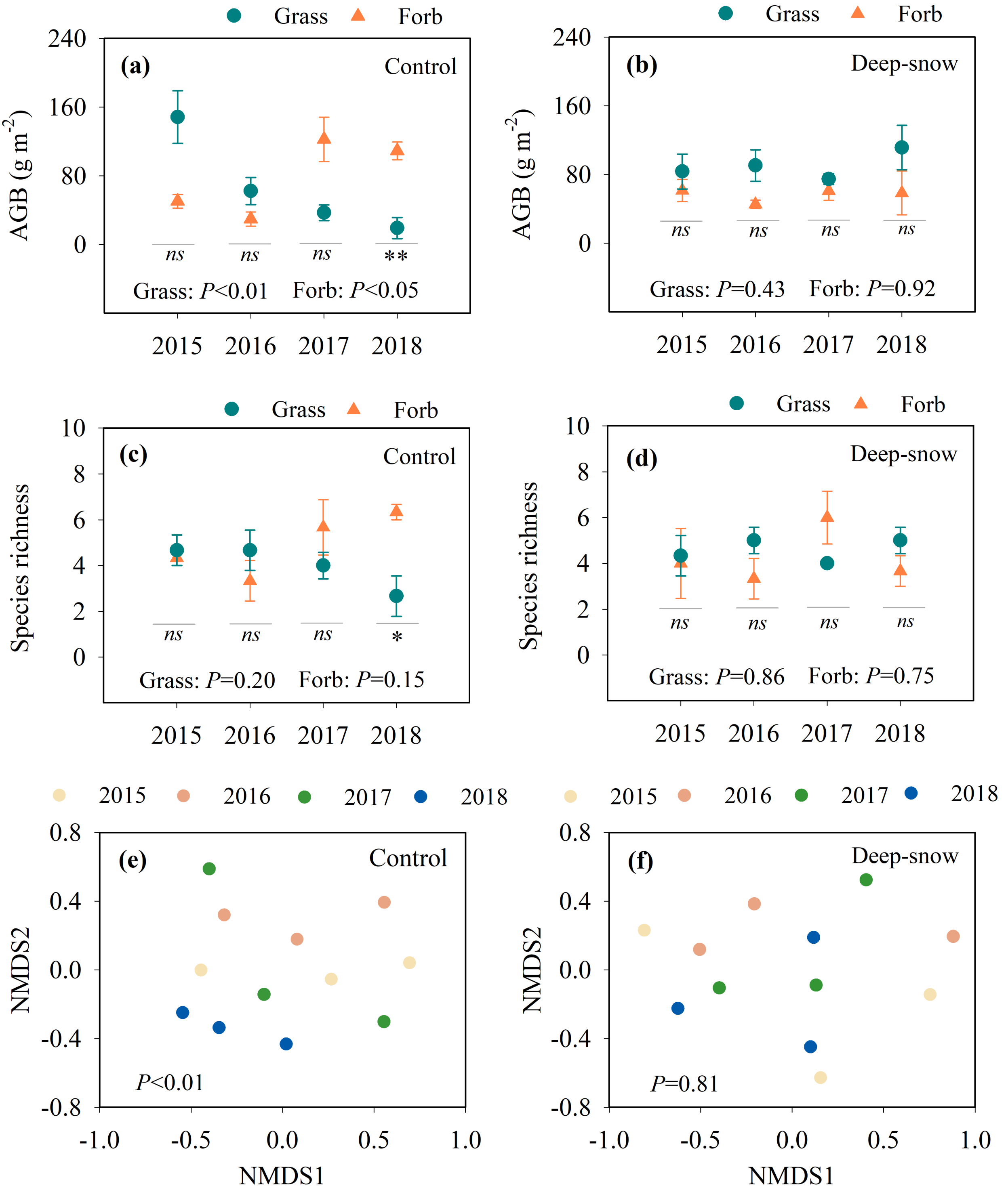
Figure 7 | Schematic showing the response of net ecosystem exchange and plant community composition in a snow-depth manipulation experiment in Inner Mongolia, showing **(a)** control treatment with ambient snow depth and **(b)** deep-snow treatment with experimentally increased winter snow cover. ① Illustrates the increased infiltration of meltwater from deep snow cover to different soil depths during spring. ② Shows high and relative stable net ecosystem exchange (NEE) of CO_2 under deepened winter snow compared with lower and variable NEE due to water stress in control plots. ③ Greater carbon allocation to root biomass in the deep-snow treatment enhances water acquisition from deeper soil layers, which increases plant performance in dry periods during the growing season. ④ Consequently, plant community composition remains relatively stable in deep-snow plots, whereas there is a shift from grasses to forbs as the dominant functional group in control plots, which is likely a result of greater water stress.

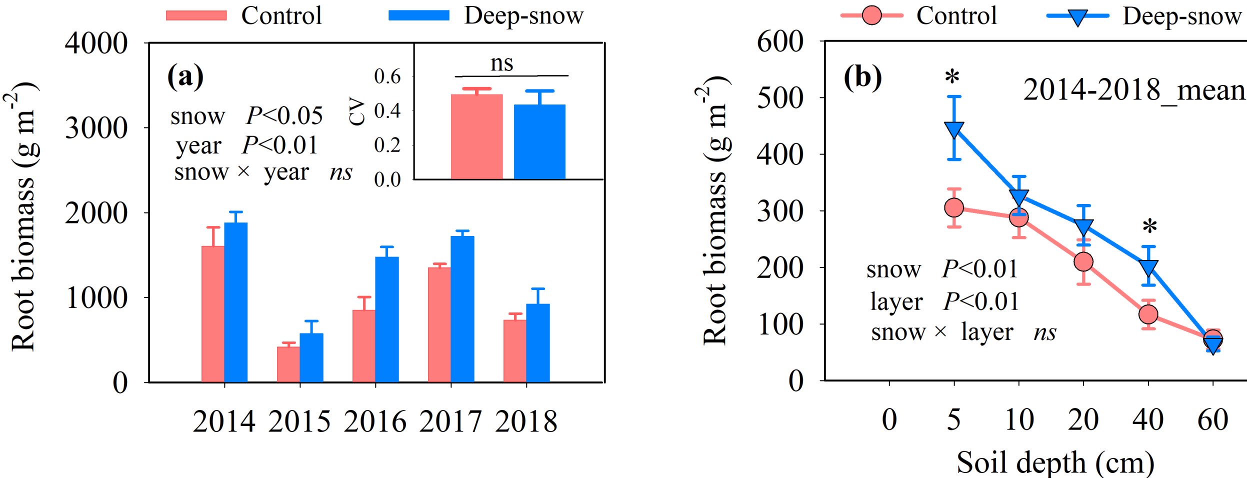

2013-2018 Precipitation
(a)
Non-growing season precipitation (mm)
400
300
200
100
0
Daily Precipitation (mm)
100
80
60
40
20
0
Growing season precipitation (mm)
274mm
56mm
2013-1-1
2013-5-1
2013-9-1
2014-1-1
2014-5-1
2014-9-1
2015-1-1
2015-5-1
2015-9-1
2016-1-1
2016-5-1
2016-9-1
2017-1-1
2017-5-1
2017-9-1
2018-1-1
2018-5-1
2018-9-1
2019-1-1
Control
Deep-snow
Difference
(b)
10cm
20cm
30cm
40cm
2016
Growing Season
2017
Growing Season
2018
Growing Season
Soil moisture (v/v, %)
Difference (v/v, %)
40
30
20
10
0
10
5
0
-5
-10
3
-3
-6
2
-2
-4
0
50
100
150
200
250
300
Day of year

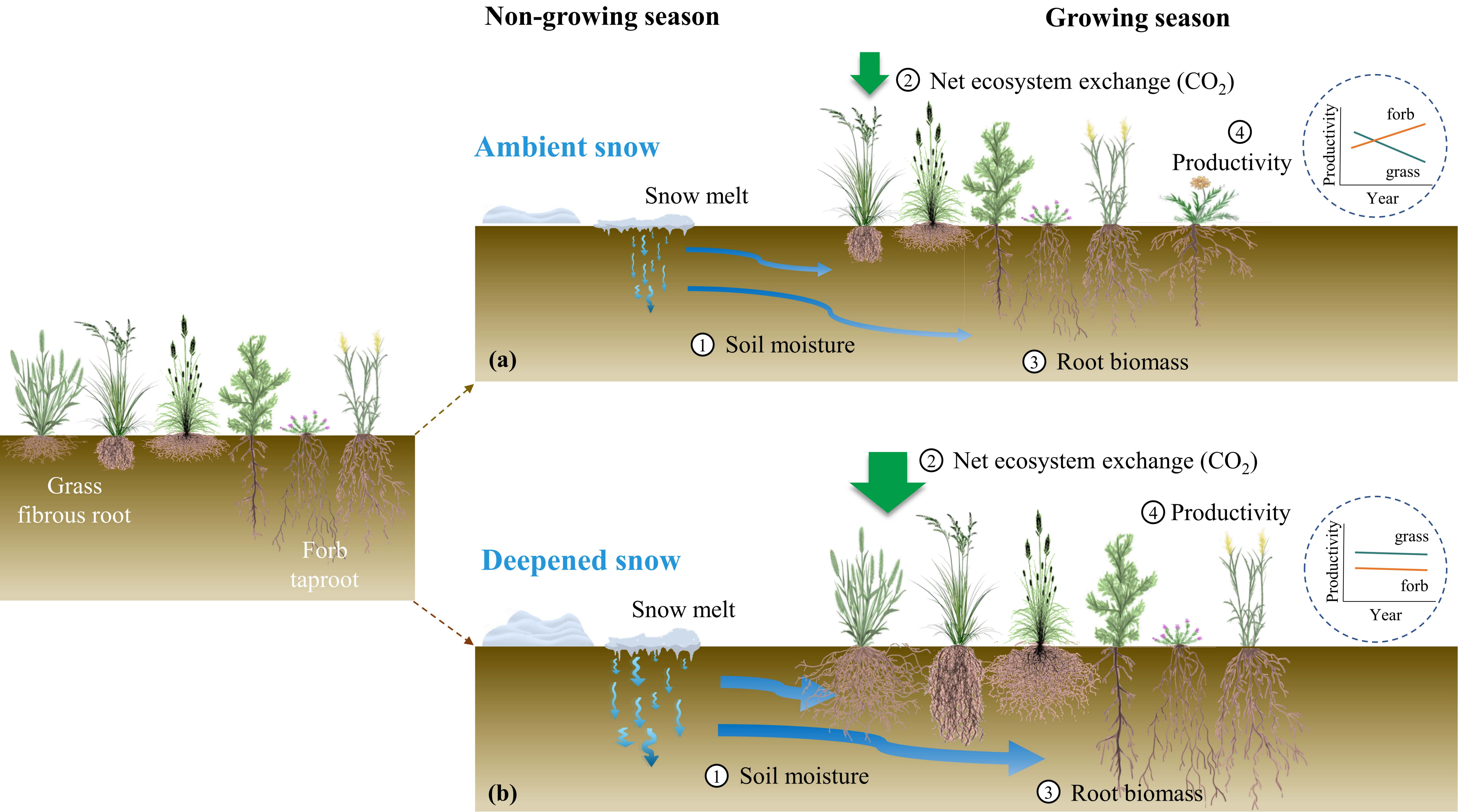

During snow cover
After snow melt
(a)
Control
Deep-snow
snow P=0.04
year P=0.66
snow × year P=0.59
Soil inorganic nitrogen
(mg N kg-1 dry soil)
0
10
20
30
40
Jan 2018
Jan 2019
(b)
snow P=0.85
Apr 2019


2014
2015
2016
2017
2018
14/5
14/6
14/7
14/8
14/9
15/5
15/6
15/7
15/8
15/9
16/6
16/7
16/8
16/9
17/6
17/7
17/8
17/9
18/6
18/7
18/8
18/9
18/10
(a)
NEE (μmol m^{-2} s^{-1})
15
10
5
0
-5
-10
-15
Control
Deep-snow
snow P<0.05 date P<0.01 snow × date P<0.05
(b)
NEE (μmol m^{-2} s^{-1})
0
-3
-6
-9
-12
A
A
B
AB
A
a
a
a
a
a
snow P<0.05
year P<0.01
snow × year ns
(c)
CV of intra-annual NEE
3.5
2.8
2.1
1.4
0.7
0.0
snow P<0.05
year P<0.01
snow × year P<0.01
B
A
A
A
A
a
a
a
a
a
(d)
CV of inter-annual NEE
0.8
0.6
0.4
0.2
0.0
Control
Deep-snow
snow P<0.05
B
A


(a)
snow ns
year P<0.05
snow × year P<0.05
AGB (g m-2)
400
300
200
100
0
B
a
A
a
AB
a
AB
a
2015
2016
2017
2018
(b)
snow ns
year P=0.05
snow × year P=0.07
AGB of forb (g m-2)
250
200
150
100
50
0
AB
a
A
a
B
a
B
a
2015
2016
2017
2018
(c)
snow ns
year P<0.01
snow × year P<0.01
AGB of grass (g m-2)
250
200
150
100
50
0
B
a
AB
a
AB
a
A
a
2015
2016
2017
2018
(d)
Control
Deep-snow
CV of inter-annual (2015-2018)
1.5
1.0
0.5
0.0
***
ns
***
AGB
AGB_forb
AGB_grass


Grass
Forb
(a)
Control
AGB (g m^{-2})
240
160
80
0
ns
ns
ns
**
Grass: P<0.01
Forb: P<0.05
2015
2016
2017
2018
(b)
Deep-snow
ns
ns
ns
ns
Grass: P=0.43
Forb: P=0.92
(c)
Control
Species richness
10
8
6
4
2
0
ns
ns
ns
*
Grass: P=0.20
Forb: P=0.15
(d)
Deep-snow
ns
ns
ns
ns
Grass: P=0.86
Forb: P=0.75
2015
2016
2017
2018
(e)
Control
NMDS2
0.8
0.4
0.0
-0.4
-0.8
P<0.01
-1.0
-0.5
0.0
0.5
1.0
NMDS1
(f)
Deep-snow
P=0.81


Control
Deep-snow
Root biomass (g m-2)
4000
3000
2000
1000
0
(a)
snow P<0.05
year P<0.01
snow × year ns
CV
0.6
0.4
0.2
0.0
ns
2014
2015
2016
2017
2018
Control
Deep-snow
(b)
2014-2018_mean
Root biomass (g m-2)
600
500
400
300
200
100
0
*
*
snow P<0.01
layer P<0.01
snow × layer ns
0
5
10
20
40
60
Soil depth (cm)


Non-growing season
Growing season
Ambient snow
Snow melt
② Net ecosystem exchange (CO_2)
④ Productivity
Productivity
forb
grass
Year
① Soil moisture
③ Root biomass
(a)
Grass
fibrous root
Forb
taproot
Deepened snow
Snow melt
② Net ecosystem exchange (CO_2)
④ Productivity
Productivity
grass
forb
Year
① Soil moisture
③ Root biomass
(b)