Plants alter their aboveground and belowground biomass allocation and affect community-level resistance in response to snow cover change in Central Asia, Northwest China

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HIGHLIGHTS

- Increasing snow cover significantly increases plant community diversity and above-ground biomass.
- Increased snow cover will lead to an increase and redistribution of subsurface biomass in plant communities.
- The increase of snow cover causes the resistance of the above-ground part to decrease, and the resistance of the underground part to increase.

GRAPHICAL ABSTRACT
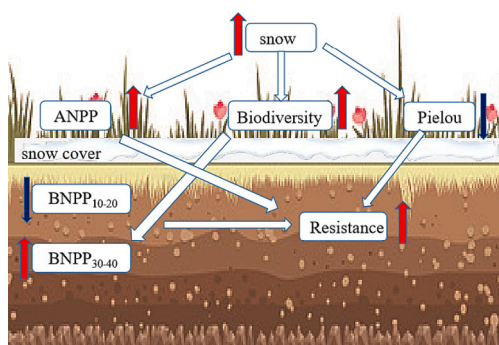
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ABSTRACT

It is important to elucidate the changing distribution pattern of net primary productivity (NPP) to mechanistically understand the changes in aboveground and belowground ecosystem functions. In water-scarce desert environments, snow provides a crucial supply of water for plant development and the spread of herbaceous species. Yet uncertainty persists regarding how herbaceous plants' NPP allocation responds to variation in snow cover. The goal of this study was to investigate how variation in snow cover in a temperate desert influenced the NPP allocation dynamics of herbaceous species and their resistance to environmental change in terms aboveground and belowground productivity. In the Gurbantunggut Desert, wintertime snow cover depth was adjusted in plots by applying four treatments: snow removal (−S), ambient snow, double snow (+S), and triple snow (+2S). We examined their species richness, aboveground NPP (ANPP), belowground NPP (BNPP), and the resistance of ANPP and BNPP. We found that species diversity of the aboveground community increased significantly with increasing snow cover and decreased significantly Pielou evenness in plots. This resulted in greater ANPP with increasing snow cover; meanwhile, BNPP first increased and then decreased with increasing snow cover. However, this productivity in different soil layers responded differently to changed snow cover. In the 0–10 cm soil layer, productivity first rose and then declined, while it declined linearly in both the 10–20 cm

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and 20–30 cm soil layers, whereas in the 30–40 cm soil layer it showed an increasing trend. Belowground resistance would increase given that greater snow cover improved the BNPP in deeper soil and maintained the resource provisioning for plant growth, thus improving overall belowground stability. These results can serve as a promising research foundation for future work on how the functioning of desert ecosystems becomes altered due to changes in plant community expansion and, in particular, changes in snow cover driven by global climate change.

1. Introduction

Among all the components of the Earth's cryosphere, snow cover is one of the most active environmental factors and has a great impact on the climate system (Lopez-Moreno, 2005; Mote et al., 2005; Henry et al., 2018). Under ongoing global warming, snow cover, being the most widely distributed resource in the cryosphere, is among the most sensitive components to climate anomalies (Inouye and Wielgolaski, 2003). Recent data shows that the warming trend is mainly occurring in winter, which will lead to a trend of increasing winter precipitation at high latitudes, and snow cover, as a special form of winter precipitation, will lead to more snow at high latitudes (Bonsal et al., 2001; Shabbar and Bonsal, 2003; Groleau et al., 2007; IPCC, 2007). Snow cover changes are known to affect soil nutrient cycling, plant growth, energy exchange, and climate change; hence, it is imperative that more attention be paid to the impact of snow cover changes (Mitchell et al., 1996; Brooks et al., 1998; Groffman et al., 1999).

Resistance usually refers to the ability of an ecosystem to maintain its functioning and remain stable in the face of a climate perturbation or extreme climatic change, which is a key indicator of ecosystem stability (Grime et al., 2000; Grman et al., 2010; Pfisterer and Schmid, 2002). Previous research has found that the resistance of ecosystems to climate extremes can be characterized by assessing productivity, changes in diversity, functional traits, and species composition (Griffin-Nolan et al., 2019a, 2019b; Knapp et al., 2015; Ruppert et al., 2015; Schumacher and Roscher, 2009). As a hot topic in ecological research, the community-level resistance of ecosystems has drawn mounting attention. Yet previous studies have mainly focused on the exploration of aboveground rather than belowground responses, thus precluding a full understanding of the ecological mechanisms of community resistance (Donohue et al., 2013; Li et al., 2019).

Optimal allocation theory is a general theory followed by the allocation of ecosystem community biomass under environmental changes. The theory is widely used to explain the response of species and ecosystems in natural systems to environmental changes (Bloom et al., 1985; Hui and Jackson, 2006; van Wijk, 2011). According to optimal allocation theory, plants will distribute more carbohydrates to their stems and leaves in areas with favorable conditions, so that these aboveground parts can fully grow as much as possible, thus enabling those plants to obtain better light resources. Under harsh conditions, plants distribute more carbohydrates to their roots, thus occupying a better ecological niche and providing more subsurface water and nutrients to sustain plant growth, resulting in an increased BNPP/NPP ratio (f_{BNPP}; Hui and Jackson, 2006, Mokany et al., 2006, van Wijk, 2011).

Previous studies have proven that aboveground net primary productivity (ANPP) is the paramount indicator or function when evaluating the resistance of plant communities to environmental changes (Hoover et al., 2014; Knapp et al., 2015; Ruppert et al., 2015). However, belowground net primary productivity (BNPP) of plants is more than half of the total productivity in arid and semi-arid regions (Fan et al., 2009; Gao et al., 2011; Milchunas and Lauenroth, 2001). Therefore, in the last decade, studies have begun investigate BNPP, and it is increasingly considered an important indicator of plant community resistance to global environmental change (Byrne et al., 2013; Wilcox et al., 2017). It is also known that species in water-limited regions have a larger root-shoot ratio than those in water-sufficient ecosystems (Fan et al., 2014; Jackson et al., 1996; Hui and Jackson, 2006). Studies have also

confirmed that precipitation changes differentially impact f_{BNPP} in ecosystems, and the precipitation–f_{BNPP} relationship can vary, with reports of positive, neutral, and negative effects (Byrne et al., 2013; Xu et al., 2013; Xu et al., 2013; Ren et al., 2017; Zhang et al., 2017a, 2017b; Byrne et al., 2013, Wilcox et al., 2015).

The desert ecosystem is a region limited most by water, and fluctuations in water availability significantly affect the abundance, diversity, and productivity of its plant community (Yin et al., 2021). The Gurbantunggut Desert is a typical temperate desert located in the northwestern China and the middle of Central Asia. It is an extremely arid desert with little annual precipitation but a special desert nonetheless, given its relatively large amount of winter snowfall (Fan et al., 2014; Yin et al., 2021; Zhou et al., 2009). The snow cover there enables many herbs to germinate yearly in early spring, with the vegetation coverage reaching 40 %–60 % (Zhang and Chen, 2002). Due to the snow's thermal insulation effect, it can increase the soil moisture and temperature in winter, and protect the seeds and microorganisms in soil over the winter (Aanderud et al., 2013; Brooks and Williams, 1999; Mariko et al., 1994; Rey et al., 2005). Snowmelt can significantly increase the soil water content, and promote seed germination and plant growth, thereby maintaining species diversity in early spring (Fan et al., 2014).

Gurbantunggut Desert, in Central Asia, has a special precipitation mode in the form of snow cover. Whether its desert ecosystem community resistance and predictions of optimal allocation theory are like in other ecosystems is unknown. Uncertain change of community resistance and optimal allocation theory based on precipitation change. To investigate the responses of community resistance and optimal allocation theory to changes in snow cover, in this study we set up four different snow depth treatments for five years in the center of the Gurbantunggut Desert. We addressed three questions: (1) Whether snow cover changes had a similar effect on the aboveground and belowground net primary productivity? (2) Whether snow cover changes affect the redistribution of underground productive? (3) Snow changes will lead to community resistance to change and lead to changes in the way is what?

2. Materials and methods

2.1. Study area

Our experimental site were set in the middle portion of the Gurbantunggut Desert (45°14′ N, 87°36′ E), the second largest desert in China which covers an area of 4.88×10^4 km^2. This region has a typical continental arid climate, with hot summers and cold winters. The highest and lowest temperature in a year is respectively 42.6 °C and −41.6 °C, with an annual average temperature of 6.6 °C. The average annual precipitation is 70–180 mm, while the annual potential evaporation is >2000 mm (Yin et al., 2021). From late November to late March of the following year, the winter snowpack will persist with a 20-cm thickness for about 100–160 days. The snow maintains ground surface temperature in winter and melts rapidly in early spring to increase the soil water content, which promotes the seed germination and growth of short-lived annuals (Yin et al., 2021).

2.2. Experimental design

The experiment was conducted in a relatively uniform and flat interdune area in the middle of the Gurbantunggut Desert in November

2017. Within this area, places with consistent vegetation and biological crust development were selected to set up the plots (each 3 m × 5 m). These plots were assigned to four snow treatments, each with five replicates, for a total of 20 plots. A 2-m wide buffer area was left between adjacent plots. Snow treatments included snow removal (snow removal, −S); ambient (environment); adding the same thickness of snow to environment snow (double snow, +S), and adding double thickness of snow to environment snow (triple snow, +2S). (1) *Snow removal*: a 20-cm high shelf was set up with steel bars, surrounded by ventilated nylon nets to prevent snow entering from the sides, and transparent panels covered the shelf as snow-shielding material to ensure that snow did not enter the plot sample. (2) *Ambient*: no treatment after snowfall. (3) *Double snow treatment*: according to the amount of natural snowfall on each occasion, snow of the same area and depth in the snow treatment plot was shifted to the double snow treatment plot. (4) *Triple snow treatment*: the snow added to this plot was increased by two times. We added snow after each snowfall event and measured snow depth until the snow began to melt. In order to maintain the accuracy of snow additions, snow with the same area outside the sample plot was selected for each addition made (Yin et al., 2021).

2.3. Plant biomass measurements

We randomly selected a quadrat (1 m × 1 m) in each sample plot in May 2018, 2019, and 2022, and recorded all live herbs in it. There is high species richness at our study site, with many ephemerals (*Erodium oxyrhinchum, Leptaleum, Alyssum linifolium, Nonea caspica*), annuals (*Ceratocarpus arenarius, Sageretia thea*), and ephemeroid species (*Carex physodes, Scorzonera pusilla, Astragalus propinquus*). We collected the aboveground parts of herbaceous plants on a species basis, packed them in envelopes, and brought them to the laboratory. These samples were oven-dried at 65 °C for 48 h. The mass measured after drying was the aboveground biomass of herbaceous plants in the quadrat (Yin et al., 2021).

BNPP was measured on roots, using the growth core method (Persson 1980), in 2018, 2019, and 2022. In each year, in early March, well before the germination of plants, a 6-cm diameter root drill was used to drill a 40-cm deep hole in each plot, into which a nylon mesh root bag (2 mm) was placed. The bag is filled with a 2 mm sieve and the in-situ soil of plant roots is removed. A complete soil core was extracted and treated in mid-May; each sample was divided into four soil layers of 0–10 cm, 10–20 cm, 20–30 cm, and 30–40 cm. The soil column was soaked and rinsed with clean water to obtain complete root samples. These samples were then dried in an oven to a constant weight and their dry weight measured. The dry root weight per square meter in the 0–10 cm, 10–20 cm, 20–30 cm, and 30–40 cm depth segments were calculated as the BNPP (hereon referred to as $BNPP_{0-10}$, $BNPP_{10-20}$, $BNPP_{20-30}$, $BNPP_{30-40}$, respectively). In this study, total BNPP was the sum of $BNPP_{0-10}$, $BNPP_{10-20}$, $BNPP_{20-30}$, and $BNPP_{30-40}$ as defined above. The f_{BNPP} was calculated by dividing BNPP by total NPP (BNPP/[ANPP + BNPP]) (Ma et al., 2020).

2.4. Structural equation modeling

We used mixed model structural equation modeling (SEM) (Keane and Crawley, 2002) to assess the interactions among nine parameters: snow change, ANPP, BNPP, diversity, BNPP (0–10 cm), BNPP (10–20 cm), BNPP (20–30 cm), BNPP (30–40 cm), and f_{BNPP}. We tested whether snow change affected ANPP, BNPP, and diversity. Snow change, ANPP, BNPP, diversity could influence both f_{BNPP} and BNPP distribution, and all variables influenced BNPP, which could also co-vary.

SEM was used to analyze the direct and indirect responses of biomass, species diversity, and community resistance to different horizontal gradients. The SEM allows for the testing of multivariate hypotheses, in which some variables could act as predictors and response variables at the same time (Doncaster, 2006). Therefore, we first

established an initial model and then combined variables (diversity and functional traits) according to prior theoretical knowledge. We adjusted the model and removed each path that was not statistically significant or had a weak correlation in the model, to eventually arrive at the final model. Data were fitted to these models using the maximum likelihood estimation method (Liu et al., 2021). Statistical analyses were implemented in SPSS 22.0 and Origin 9.3 software programs; Amos (22.0) software using for structural equation modeling.

2.5. Statistical analysis

We first checked the normality of the experimental data. ANOVA was used to determine the effects of the four snow treatments on the richness, Shannon–Wiener index, Simpson index, Pielou index, ANPP, BNPP, and BNPP distribution and resistance (using SPSS for Windows, Version 22, Chicago, IL, USA). The differences in the diversity indexes, ANPP, BNPP, and resistance among four snow treatments were analyzed. For each index, Tukey's HSD test was used for the multiple pairwise comparisons of means. The relationships between ANPP, BNPP, diversity, BNPP distribution, and snow depth were determined by fitting simple linear regressions. For all statistical tests, the 0.05 alpha level was set for significance (Yin et al., 2021).

To convey these changes, well-established diversity indexes were used here to represent species richness, evenness, dominance, community structure, and spatial heterogeneity (Whittaker and Niering, 1965). We calculated them based on the species data obtained from the vegetation survey; the specific indexes derived were as follows:

Pielou evenness index (Jsw)

$$Jsw = H/\ln S$$

The community resistance was calculated for ANPP and BNPP by following Isbell et al. (2015):

$$Resistance = \frac{\overline{Control_Y}}{|Drought_Y - Control_Y|}|$$

where $Control_Y$ is the mean productivity value of the control for the Y year, and $Drought_Y$ is mean productivity value of drought treatment for Y year. A low resistance value is characteristic of large proportional changes of community productivity, indicating higher drought sensitivity; and vice versa. The resistance value has no upper boundary. These statistical analyses were performed in R v3.4.2.

3. Results

3.1. Diversity response to snow treatment

With the increasing of snow cover, there was a significant trend of increasing community richness in the sample, but there was no significant difference between years (Fig. 1a; $P < 0.05$). On the contrary, Pielou index showed a decreasing trend with the increase of snow cover depth. There was also no significant difference between different years (Fig. 1b; $P < 0.05$).

3.2. Productivity response to snow treatment

Greater snow depth led to higher ANPP, it showing a significant increase with increasing snow in both 2018 and 2019, but in 2022 it significantly increased at first and then decreased, reaching its maximum under the ambient treatment (Fig. 2a–c; $P < 0.05$). BNPP showed a significant trend of first increasing and then decreasing with greater snow depth, attaining maximum values in the ambient and double snow treatments (Fig. 2c–e; $P < 0.05$). With more snow added, the ANPP and BNPP under the same snow treatment both showed a significant decreasing trend in 2022.
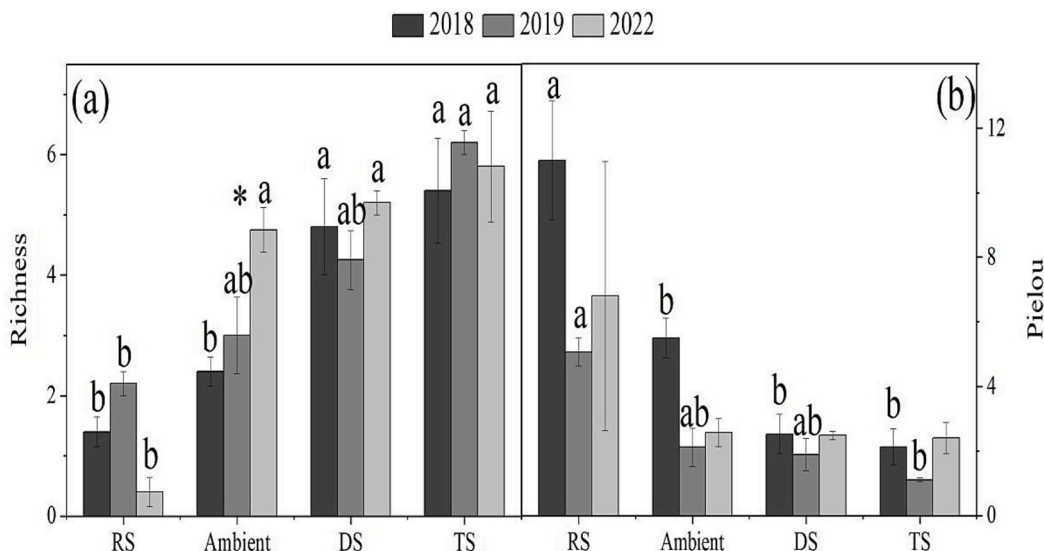
Fig. 1. Responses of Richness (a) and Pielou index (b) (means ± SE) to four snow cover treatments: Snow removal, Ambient, Double snow and Triple snow in 2018 (Dark gray), 2019 (Gray) 2022 (Light gray). Significant differences between treatments are indicated by different letters (P < 0.05).
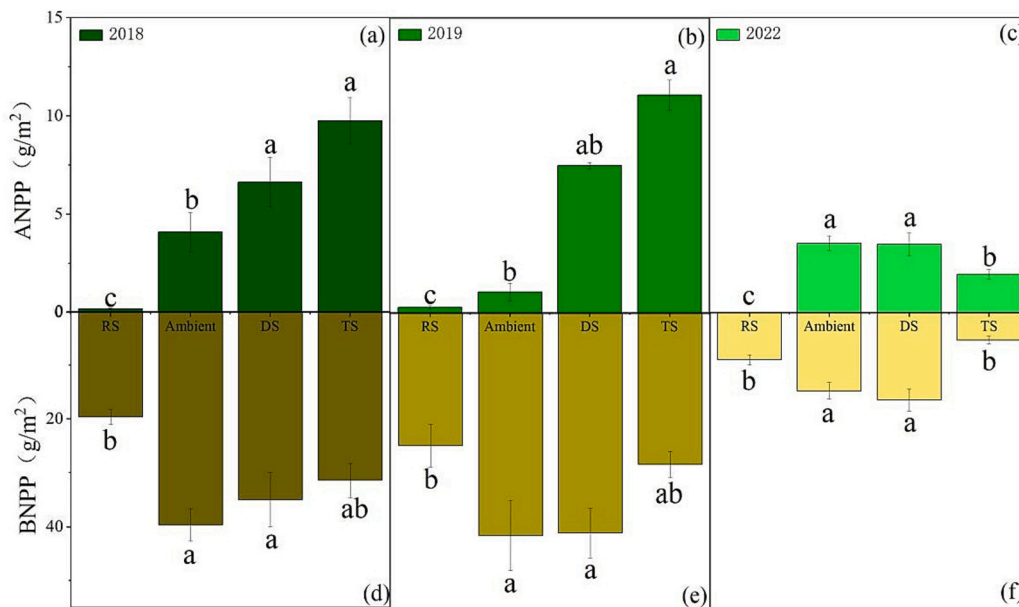

Fig. 2. Responses of above-net primary productivity (ANPP) and belowground net primary productivity (BNPP) to experimentally imposed growing season snow cover treatment in the 2018 (a, d) 2019 (b, e) and 2022 (c, f). Significant differences between treatments are indicated by different letters (P < 0.05).

3.3. Changes in the vertical distribution of BNPP

About 50 % of the root biomass was distributed in the 0–10 cm soil layer, and with the change of snow cover and years, we expected the distribution of root biomass in different soil layers would also follow different trends. The root distribution in the topsoil (0–10 cm) significant increased with greater snow cover depth, while the root mass in the 10–20 cm, 20–30 cm, and 30–40 cm soil layers significantly decreased (Fig. 3a–d; P < 0.05). The BNPP in the topsoil changed significantly across different years only under snow removal treatment and the ambient treatment, while the BNPP in deeper soil layers of 10–20 cm, 20–30 cm, and 30–40 cm changed significantly in the presence of snow. Greater snow cover reduced the f_{BNPP}, whose minimum was reached under the triple snow treatment (Fig. 3e; P < 0.05).

In all snow treatments, ANPP increased as snow cover increased, whereas for BNPP it increased and then decreased, leading to a declining

f_{BNPP} (Fig. 4). Across all treatments, BNPP in 0–10 cm soil layers showed a nonlinear decrease as snow cover increased (Fig. 5a; P < 0.01). In the 10–20 cm and 20–30 cm soil layers, BNPP decreased linearly as snow cover increased, but vice versa in the 30–40 cm soil layer had a contrast trend (Fig. 5b–d; P < 0.01). To sum up, BNPP changed differentially in all the soil layers among the snow treatments (Fig. 5).

Resistance is a crucial indicator of the community's ability to maintain stability despite changes in the external environment. After 5 years of running the snow manipulation experiment, it was found that ANPP and BNPP resistance changed significantly in response to snow addition. ANPP resistance reached a maximum (1.12 ± 0.1) under the snow removal treatment, while BNPP resistance peaked (8.53 ± 0.02) under the double snow treatment (Fig. 6a, b; P < 0.05).

In the SEM analysis, changing snow cover directly and positively influenced both ANPP and diversity, but negatively influenced $BNPP_{10–20}$ (Fig. 7). Greater diversity promoted BNPP's distribution in
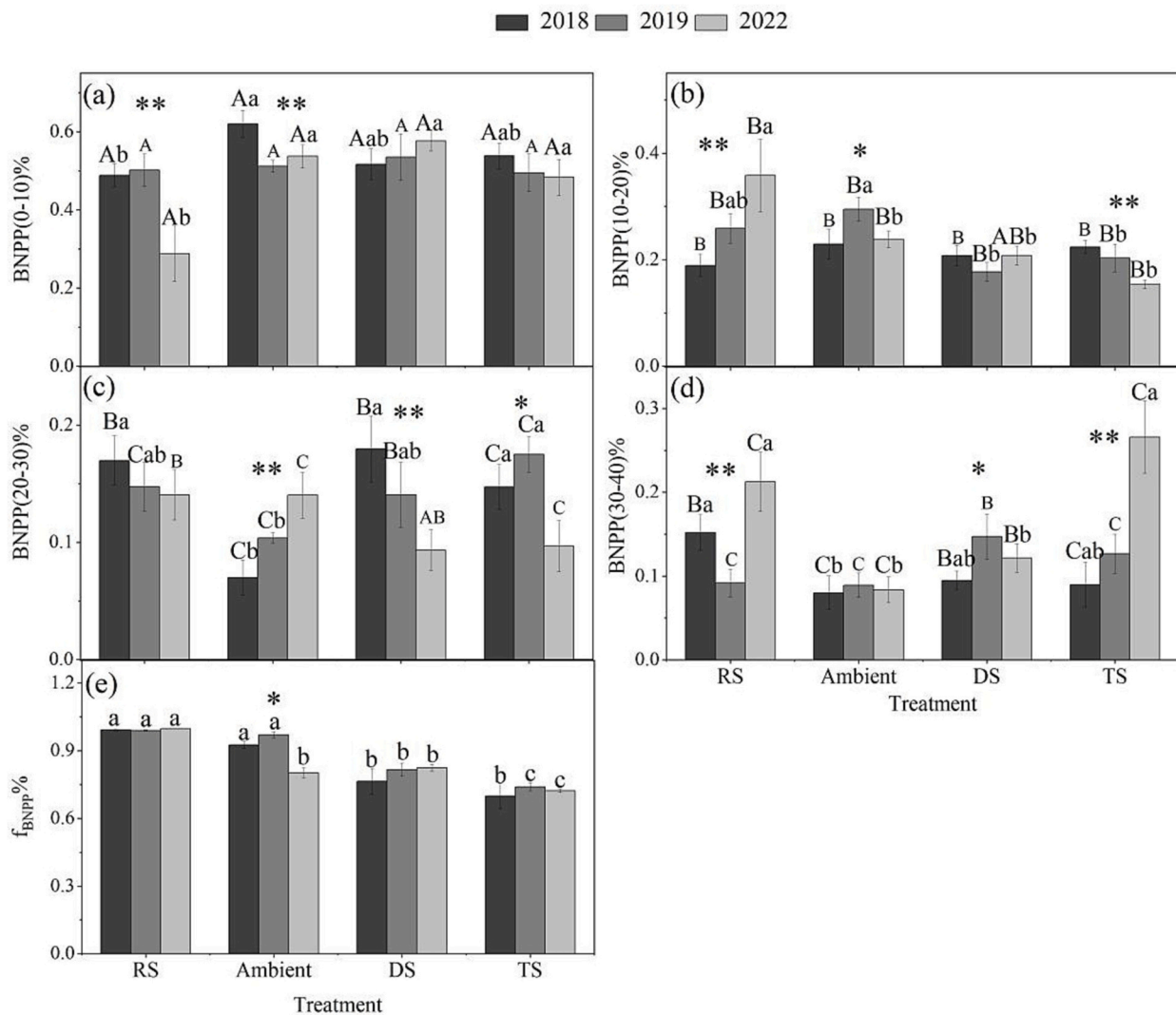
Fig. 3. Inter-annual changes in belowground net primary productivity (BNPP) vertical distribution in (a) 0–10 cm, (b) 10–20 cm, (c) 20–30 cm, (d) 30–40 cm soil layers and f_{BNPP} for the four snow cover treatments in 2018, 2019, 2022. Significant differences between treatments are indicated by different letters ($P < 0.05$).

the 30–40 cm soil layer, which significantly reduced the Pielou index (Fig. 7). Snow cover also had a positive effect on the ANPP and increased the belowground resistance. Additionally, greater biodiversity increased the root distribution in the 30–40 cm soil layer (Fig. 7). However, a higher Pielou index led to lower root biomass in the 10–20 cm soil layer but higher root biomass in the 30–40 cm soil layer, as well reducing the distribution of plant roots at 10–20 cm (Fig. 7). The decrease in $BNPP_{10-20}$ had a negative effect on belowground resistance whereas the increase in $BNPP_{30-40}$ had a positive effect on it.

4. Discussion

How snow cover changes affect NPP allocation patterns is critical for understanding changes in aboveground and belowground ecosystem functions (McCarthy and Enquist, 2007; Bardgett and Wardle, 2010; van Wijk, 2011). In the typical temperate deserts in the arid area of northwestern China, water is the most limited resource for ecosystem productivity (Bai et al., 2008). In this arid area, NPP allocation of herbaceous plants was studied via a 5-year-long snow cover manipulation experiment, from which related mechanisms and plant strategies for maintaining water acquisition are discussed.

During the last 30 years, the winter snow depth has been increasing across northern China, especially in the arid and semi-arid areas of

northwest China, which are dominated by grasslands and deserts (Peng et al., 2010). More snow cover can significantly increase the soil water content in early spring, thereby providing sufficient water for the germination of herbaceous seeds in soil, which should improve the survival rate of herb plant species in deserts (Went, 1949; Gutterman, 2000; Levine et al., 2008). Previous studies have shown that most plant species have an optimal snow depth range, leading to a positive effect on biodiversity with greater snow depth (Walker et al., 1993; Chen et al., 2008). Accordingly, we would expect species richness to also increase with increasing snow cover depth in desert ecosystems. Our results show that species richness does significantly increase with snow addition. Likewise, the Shannon–Winner index, Simpson index, and Pielou index also shows a trend of increasing diversity as snow cover increases, similar to the results of previous studies. Yet we found no significant pattern of change between sampling years, indicating that inter-annual variation in snow cover negligibly impacted plant community diversity in the studied desert.

Because of snow cover's presence, it will first modulate soil moisture and temperature, thereby altering the biochemical cycle of soil in winter, as well as microorganismal activity and plant dynamics in the growing season. (Jones et al., 1998; Weih and Karlsson, 2002; Campbell et al., 2005; Sturm et al., 2005). As such, snowmelt can affect the growth of plants (Walker et al., 1993; Galen and Stanton, 1995; Wipf et al.,
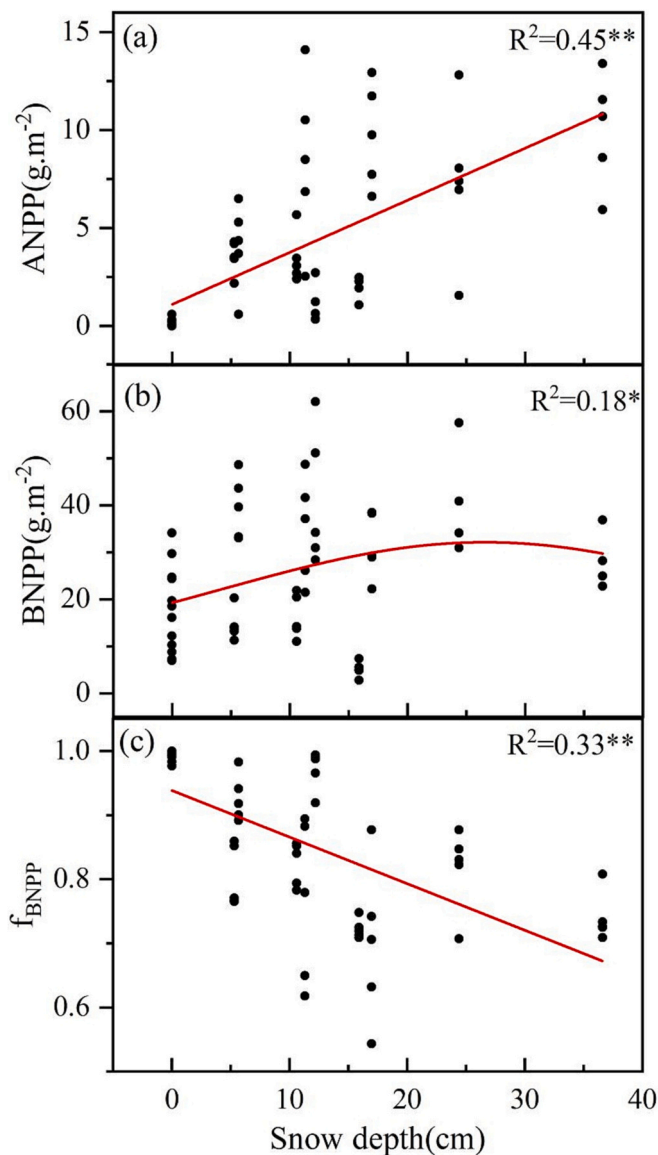
Fig. 4. Linear responses of (a) above-ground (ANPP), (c) the fraction of BNPP to total net primary productivity (fBNPP) and nonlinear responses (quadratic curve) of (b) belowground (BNPP), to changing snow cover depth. *, and *** indicated significant relationships at the levels of $P < 0.05$, and $P < 0.0001$, respectively.

2006) and their community composition and structure (Galen and Stanton, 1995; Seastedt and Vaccaro, 2001; Welch et al., 2005; Wipf et al., 2005). Studies have found that with changes in snow cover, plant phenology and functional traits can also change, which would affect plant biomass and community productivity (Baptist et al., 2010; Ernakovich et al., 2014; Inouye, 2000). Our results demonstrated that aboveground and belowground productivity increased with the increase of snow cover, but the latter decreased under the triple snow treatment. This may be because having too much prior snow cover increases the number of species and intensifies competition among plants during the growing period, leaving too little soil water and nutrients to maintain the energy levels needed to create more root structures, thus leading to a trend of reduced plant root biomass.

Snow cover is a vital water source in arid and semi-arid areas. Snow cover on the surface in winter is conducive to the maintenance of surface temperature and soil moisture, and melting in early spring can rapidly increase soil moisture content, providing sufficient water for the germination and growth of plant seeds in early spring (Bilbrough et al.,

2000; Grippa et al., 2005; Fan et al., 2014). Changes in precipitation will affect the growth and distribution of plant biomass, both aboveground and belowground, and snow cover, as a special mode of precipitation, will certainly affect the growth and distribution of plants (Wilcox et al., 2015; Ren et al., 2017; Zhang et al., 2017a, 2017b; Felton et al., 2019). We found that with more snow cover, the snowfall thickness had a significant positive effect on aboveground biomass, yet a significant negative effect on belowground biomass. However, in response to increasing snow cover, the biomass of the belowground part of plants, namely the root system, first increased and then decreased. The reason for this may be that plants tend to reduce their aboveground growth in order to conserve and redistribute aboveground and belowground biomass in a water- or nutrient deficient environment (Granier and Tardieu, 1999; Skirycz et al., 2010; Yin et al., 2021). Some plants are capable of augmenting the water absorption capacity of their root system and the photosynthetic rate of the aboveground parts to adapt to water-deficient conditions (Zlatev and Lidon, 2012). In addition, a plant does not need to allocate more biomass to its root system, but must rather ensure that aboveground parts grow first when there is sufficient water available in the local environment (Murphy et al., 2009). In this way, the root biomass of herbs first increased and then decreased with greater snow cover.

Several studies have shown weak responses to climate and environmental changes, including precipitation, snowfall, and nutrient deposition, by arid and semi-arid plant communities (Gilgen and Buchmann, 2009; Tielbörger et al., 2014; Vicente-Serrano et al., 2013), which suggests these harbor relatively high resistance. Other research has demonstrated that community richness, biodiversity, and certain indicators of community functional composition, such as weighted average traits (CWM) and functional dispersion (FDis), are able to influence the aboveground and underground biomass of plant communities (Griffin-Nolan et al., 2019a, 2019b; Ma et al., 2020). In parallel, most studies have shown that species richness has an important effect on ecosystem resistance to disturbance, whereas the impact of biomass change is rarely studied (Maestre et al., 2012; Kunert and Cárdenas, 2015; Pennekamp et al., 2018). Our results show that with greater snow cover depth, the aboveground resistance of plants gradually decreased; that is, community resistance peaked when the snow cover was removed. This is most likely because snow cover has a very specific short-term effect that primarily benefits the growth of short-lived plants in the desert. Therefore, in the presence of snow cover, plants prioritize growth of their aboveground parts, resulting in higher plant diversity and ANPP, which in turn will intensify competition among species, and thus reduce the aboveground resistance of vegetation.

A change in snow cover will affect not only the growth of plants' aboveground parts but also that of their roots by modulating the soil water content. According to many previous studies, when plants are growing in well-watered soil it is more cost effective to spread their roots across the top layer of soil, but when faced with drought conditions they are spread deeper into the soil (Jackson et al., 1996; Huxman et al., 2004; Knapp et al., 2008; van Wijk, 2011; Chen et al., 2016). Recent work has shown that, to optimize the water absorption of plants under water shortage conditions, the distribution pattern of plant biomass can be modified via the vertical distribution of roots, thus promoting the growth of plant communities (Zhang et al., 2019). We found that belowground resistance rose and then fell, that is, it was greatest under the double snow treatment. To resist environmental change, the root system would distribute itself into different soil layers, accordingly. From our study we find that increasing snow cover depth improves plant diversity, this leading to high root biomass in the 30–40 cm soil layer. Moreover, increasing snow cover depth reduces the root biomass in the 10–20 cm soil layer. Altogether, these responses will help improve the belowground resistance of plant communities. In this extremely water-limited desert, snowmelt would provide sufficient water for the growth of plants, so the biomass of plant roots will increase with more snow. When conditions are adequate, plants will increase the growth of
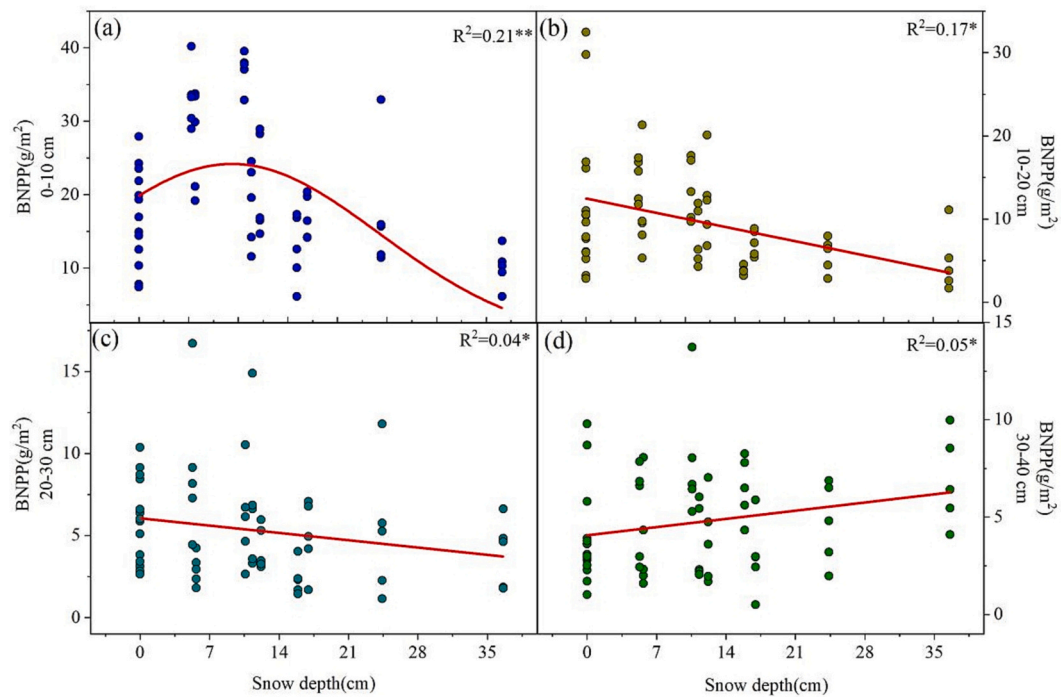
Fig. 5. Nonlinear response (quadratic curve) of belowground net primary productivity (BNPP) at (a)–(b) different soil depths and liner responses of belowground net primary productivity (BNPP) at (c)–(d) their vertical distributions to changing snow cover depth. *, **, and *** indicated significant relationships at the levels of $P < 0.05$, $P < 0.01$, and $P < 0.0001$, respectively.
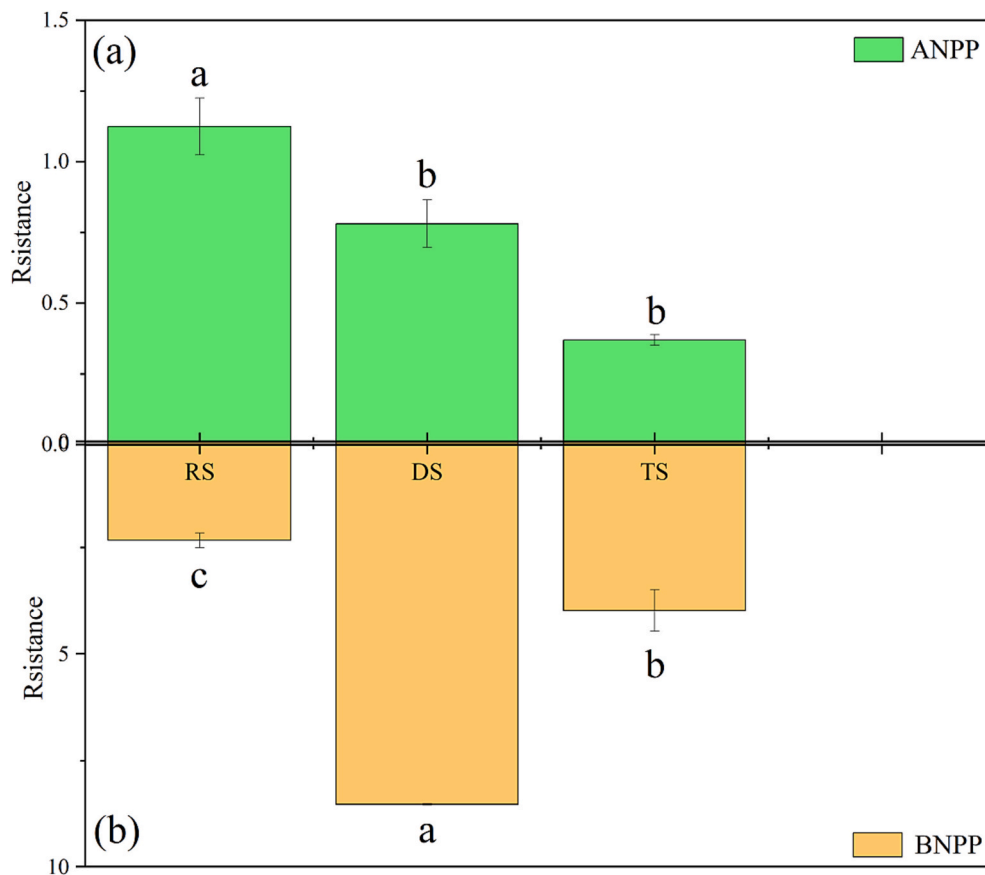

Fig. 6. Responses of above-ground resistance (a) and belowground resistance (b) (means ± SE) under four snow cover treatments: Snow removal, Double snow and Triple snow. Significant differences between treatments are indicated by different letters (P < 0.05).
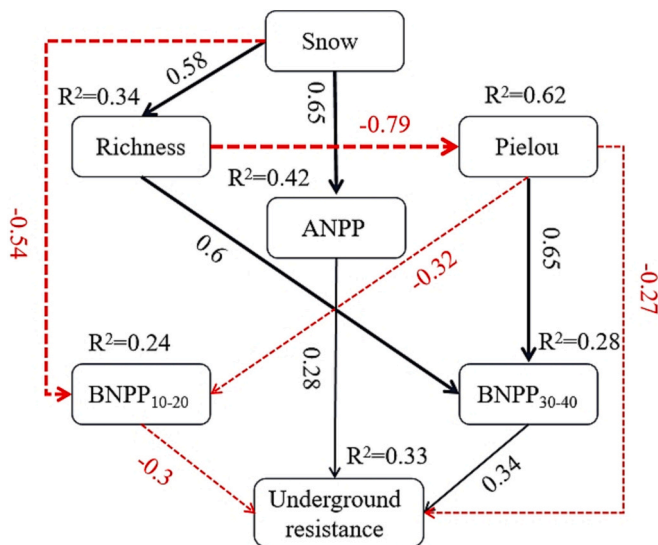
Fig. 7. Structural-equation model (SEM) analysis was performed to evaluate the influence pathways of altered snow on biodiversity, allocation of net primary productivity to the above net primary productivity (ANPP) and belowground net primary productivity (BNPP,) vertical distribution (BNPP$_{0-10}$, BNPP$_{10-20}$, BNPP$_{20-30}$, BNPP$_{30-40}$) and resistance of belowground. The linear mixed-effect model with the effect of year and block as random factors was performed using in the SEM. The results of model fitting are $n = 60$, $P = 0.584$, df = 54, Chi-square = 7.515, AIC = 45.515, RMSEA = 0.000, (a high P value associated with a χ^2 test indicates a good fit of the model to data, i.e., no significant discrepancies). Black and red dashed arrows indicate significantly ($P < 0.05$) positive and negative effects, respectively. Values associated with the arrows and the arrow width represent standardized path coefficients. R^2 values associated with response variables indicate the proportion of variation explained by relationships with other variables.

their belowground roots into deeper soil to resist the arid environment after the disappearance of snow cover effect, thus improving the overall belowground resistance.

5. Conclusion

Our study's results prove that snow is an important water resource for plant growth in the Gurbantunggut Desert. Changing the snow cover depth alters the biodiversity, with more snow leading to higher plant diversity. Our results indicate that snow addition significantly increases the ANPP and BNPP in different ways; however, ANPP increases with snow addition, whereas BNPP increases at first but then decreases, leading to a trend of f$_{BNPP}$ decreasing with increasing snow depth. The resistance of the plant community also responds differently to more snow. The resistance of ANPP is continually reduced that of BNPP increases and then decreases. Through an SEM analysis, we find that the shift in aboveground resistance is mainly due to biodiversity being augmented by the increase in snow cover. This would intensify interspecific competition among plants in the arid desert area and thus reduce the aboveground resistance. Nevertheless, the belowground root system would reduce the root biomass allocation in the surface soil and increase it in deeper soil, to enable desert plants to obtain sufficient water and nutrients in a water-limited environment, thus increasing the belowground resistance.

Author statement

The authors declare that no conflict of interest exists in the submission of this manuscript. We would like to declare that the work described was original that has not been published previously, and not under consideration for publication elsewhere, in whole or in part. All the authors listed have approved the manuscript that is enclosed. if accepted, it will not be published elsewhere in the same form, in English or in any other language, including electronically without the written consent of the copyright-holder.

Declaration of competing interest

We declare that we have no financial and personal relationships with other people or organizations that can inappropriately influence our work, there is no professional or other personal interest of any nature or kind in any product, service and/or company that could be construed as influencing the position presented in, or the review of, the manuscript entitled.

Data availability

The data that has been used is confidential.

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