

# Increasing aridity may reduce productivity and soil organic carbon storage with woody plant encroachment

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## Research Article

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# Abstract

## Aims

We have found a positive effect of woody plants on total plant carbon (C) storage in less arid grassland was shifted to a negative effect in arid grasslands in Xinjiang, a typical arid region in China. In this study, we further assessed the effects of woody plants on aboveground primary productivity (ANPP) and soil organic C (SOC) storage and explored the mediation of climate conditions on these effects. We also aimed to elucidate the reasons for the effects on SOC storage in terms of ANPP and belowground biomass C (BGC).

## Methods

We compared the difference in ANPP and SOC content between pure and wooded grasslands and evaluated the relation between SOC content and ANPP and BGC in six grassland types along the altitude (climatic) gradients.

## Results

In three arid types, woody plants had a negative effect on ANPP due to their more negative impacts on herbaceous plants and lower ANPP. The negative effect on ANPP and BGC led to that on SOC storage in these types. In less arid types, there had a positive effect on ANPP because woody plants had weaker negative impacts on herbaceous plants and higher ANPP. A positive effect on ANPP combined with a neutral impact on BGC contributed to a positive effect on SOC storage in these types.

## Conclusions

Woody plants had a negative effect on ANPP and SOC storage in most arid grasslands in Xinjiang. We predicted that increasing aridity may reduce ANPP and SOC storage with woody plant encroachment in the future.

## Introduction

Woody plant encroachment into grassland, characterized with the increases in the density, cover and biomass of native or exogenous woody plants, has been frequently reported worldwide, especially in arid and semiarid regions during the past century (Asner et al. 2003; Hughes et al. 2006; Van Auken 2000). The possible reasons for this phenomenon are grazing regime changes, nitrogen deposition, CO<sub>2</sub> concentration increasing and their complex interactions (D'odorico et al. 2012; Eldridge et al. 2011; Hibbard et al. 2003; Hughes et al. 2006; Van Auken 2000). Woody plant encroachment has a potential to alter the functions and processes of grasslands (Eldridge et al. 2011). How it alters the amount of carbon

(C) sequestered in soil, an important function of grasslands, has attracted many interests from ecologists because grasslands contain approximately 10% ~ 30% of global soil organic C (SOC) and any tiny change in the amount of SOC in grasslands will have an important implication to the global CO<sub>2</sub> concentration and related climate change (Jackson et al. 2002; Scurlock and Hall 1998; Tang et al. 2018).

Woody plant encroachment is likely to alter SOC storage because woody plants differ from herbaceous plants in terms of productivity, biomass allocation pattern and the quantity and quality of litter (Hibbard et al. 2003; Jackson et al. 2002; Wessman et al. 2012). In addition, the changes in physiognomic types from pure to wooded grasslands may also affect soil temperature, moisture and microbial biomass and activity, thereby affecting SOC decomposition and accumulation (Mcculley et al. 2004). However, the magnitude and direction of change in SOC storage with woody plant encroachment are highly mixed (Eldridge et al. 2011). Moreover, few studies have given a lucid explanation for the change in SOC storage. Several studies reported that SOC content increased, which may result from the increasing in the amount and lignification of litter inputs or the slower turnover of soil organic matter associated with the improvement in microclimate in wooded grasslands (Montané et al. 2010; Smith and Johnson 2004). However, Jackson et al. (2002) found SOC content decreased in wetter sites in south-western United State. Hughes et al. (2006) and Smith and John (2003) reported no net change in SOC storage. These effects are inconsistent may be due to the mediation of abiotic and biotic factors. For example, SOC are more likely to accumulate in fine-textured than in coarse-textured soil after woody plant encroachment (Liao et al. 2006). Grazing can dampen the positive effects on plant diversity and multifunctionality in arid region (Eldridge et al. 2013).

Meta analyses or regional studies found climate conditions could also mediate the change in SOC storage with woody plant encroachment. However, the mediation of climate conditions is complex, which may be at least due to the different spatial scale of analysis. For example, Jackson et al. (2002) found that, in the south-western United States, SOC content increased at drier sites and decreased at wetter sites and there was a negative relationship between the change in SOC storage and mean annual precipitation (MAP). In contrast, Li et al. (2016) reported that at a global scale, the change in SOC was positively correlated with MAP and mean annual temperature (MAT). Previous studies posited that the mechanisms for the mediation of climate conditions was through their influences on the quantity of plant inputs and the rates of decomposition outputs (Wheeler et al. 2007). However, few studies have assessed the change in SOC storage with woody plant encroachment and that in plant inputs to it, such as primary aboveground productivity (ANPP) simultaneously and this mechanism needs a further confirmation.

Most of previous works studied the effect of woody plant encroachment through comparing paired wooded grasslands and adjacent or former pure grasslands at a plot scale in a given site with similar environmental conditions (e.g. Knapp et al. 2008). Xinjiang, located in Northwest China, is a typical arid and semi-arid region. Woody plants are a common vegetative component in Xinjiang grasslands. In Xinjiang, the special landforms that three mountains and two basins are arranged alternatively makes precipitation and temperature change regularly with altitudes increasing. In the classification system of China's grasslands, grassland types can well reflect this variation in climate conditions along the altitudes

(Xu, 1993). It is not clear to us that whether Xinjiang grasslands experienced woody proliferation. However, we can predict the future changes in C storage following woody plant encroachment through assessing the effects of existing woody plants on C storage along the altitude (climatic) gradients. Our previous work has selected six grassland types along the altitudinal (climatic) gradients across Xinjiang, and used a large number of replicate but unpaired pure and wooded grassland sites (a total of 284 sites) and a consistent sampling and measuring methods to examine the effects of woody plants on plant C storage and the mediation of climate conditions on these effects. We found a positive effect of woody plant encroachment on plant C storage in less arid grassland types at higher altitudes was shifted to a negative effect in arid types at lower altitudes. In this study, we still used the same sites as our previous work and aimed to further assess the effects of woody plant encroachment on SOC storage and ANPP, another indicator of functions and processes of grasslands. We predicted that climatic conditions also mediated the effects on ANPP and SOC storage and the effects varied with grassland types. Our previous work found that woody plants increased the living aboveground C (AGC) across the six grassland types but the magnitude of increase was weaker in three arid types. We predicted the effects on ANPP was analogous to that on the living AGC. Despite the increases in ANPP, we predicted a negative effect on SOC storage in three arid types because our previous work found a negative impact of woody plants on vegetation-level belowground biomass C (BGC), a more important plant inputs to SOC (Pregitzer 2002). We predicted a positive effect on SOC storage in less arid types due to a more positive effect on ANPP and a neutral impact of woody plants on BGC in these types that we have found in previous study. In this study, we also aimed to elucidate the reasons for the effects of woody plants on SOC storage and to confirm the mediation of climate conditions on these effects in terms of ANPP and BGC.

## Materials And Methods

### Study area

Xinjiang is the biggest province in China, far away from the sea and situated the inland. There are high mountains around it and the ocean air flow is not easy to reach, forming a typical temperate continental climate characterizing with low rainfall, high evapotranspiration, long sunshine time, cold winter and hot summer. There are three mountain ranges in the north, south and middle of Xinjiang, respectively and two basins lie between them. Natural grasslands are widely distributed in these mountains and basins. The area of natural grasslands is  $5.72 \times 10^7$  ha, accounting for 34.4 percent of the total land area of Xinjiang (Xu 1993).

### Sampling sites

We first selected six grassland types with precipitation as water source and woody plant presences. Along the altitudes, these selected types are temperate desert, temperate steppe desert, temperate desert steppe, temperate steppe, temperate meadow steppe (hereafter the word “temperate” were omitted in these type names) and mountain meadow.

Then we used the distribution map of Xinjiang grasslands (1:1 000 000) and selected grassland forms (grassland forms is the most basic classification unit in the classification system of China's grasslands and named by dominant species) dominated only by herbaceous plants and only by woody plants. The distribution map of Xinjiang grasslands was drawn in the 1980s, so woody plants were present at least 30 years ago. Here, herbaceous plants indicate any grasses or herbaceous species while woody plants include shrubs and trees (House et al. 2003). Among these forms, we further selected ones which are common and have a large distribution area. In each grassland form, there had at least three sampling sites. There is little international agreement on the name and classification of mixed woody- herbaceous systems (House et al. 2003). In our study, wooded grasslands were defined as grasslands where the relative aboveground biomass of woody plants are greater than or equal to 50%. Pure grasslands defined as grasslands where woody plants are not present. After surveying and measuring, we excluded the sampling sites with heavy grazing and where woody plants were present but their relative biomass were lower than 50%. Finally, there were 284 sampling sites covering 87 grassland forms. See Table 1 and Fig. 1 in our previous work and Table 1 in this study for more description of the location and sampling sites (Liu et al. 2020).

Table 1  
Aridity index of the six grassland types

TD	TSD	TDS	TS	TMS	MM
1.32 ± 1.33	7.92 ± 1.48	4.89 ± 1.40	3.18 ± 0.62	2.42 ± 0.53	2.02 ± 0.44
TD: temperate desert; TSD: temperate steppe desert; TDS: temperate desert steppe; TS: temperate steppe; TMS: temperate meadow steppe; MM: mountainous meadow. The same below					

### Plant sampling and analysis

In this study, ANPP was expressed as the C quantity per square metre and obtained by multiplying the peak biomass produced in the current year by their C content. The peak biomass sampling was conducted in mid-July to early August from 2011 to 2013. In each sampling site, a 100m ×100 m sampling plot was set. On each side of one diagonal of plot, five 1 m×1 m quadrats at 20-m intervals were established and they were staggered. In each sampling site of wooded grasslands, there had two and three additional 5 m×5 m quadrats at 20-m intervals on two sides of this diagonal. The five 1m×1 m quadrats of ten 1 m×1 m ones were uniformly arranged at the same position in five 5 m×5 m quadrats, such as the lower right corner.

In 1 m×1 m quadrats, all the green parts of herbaceous plants was collected by clipping to ground level. The current year biomass of woody plants were harvested by species. For woody species with a high number of plants, all the plants were classified into three size levels based on the crown diameter, i.e., large (> 1 m), intermediate (0.5 ~ 1 m) and small (< 0.5 m). The quantity of individuals in each size class were recorded and then randomly selected 3, 5 and 10 plants in the large, intermediate and small size classes, respectively. For woody plant individuals with intermediate and large sizes, we sampled one-quarter or one-eighth of the whole plant. For woody species that were low in number, we sampled all the

plants of this species. The sampled parts were separated into leaves, current-year twigs, stem, flower and fruit.

In the lab, all the plant material was dried at 60°C for 48 h and weighed, then ground in a ball mill (Retsch MM20, Germany). Then the C concentration was measured using an elemental analyser (Euro Vector EA3000, Italy). The ANPP of herbaceous plants was determined by multiplying the living biomass of herbaceous plants by their C concentration. For each sampled woody plant, the ANPP was the sum of the product of leaves, current-year twigs, flower and fruit and their respective C concentration. ANPP of a given species in a 5 m×5 m quadrat was calculated by multiplying the average ANPP for each size class with the corresponding number of woody plant individuals. The ANPP in a 5 m×5 m quadrat was the sum of ANPP all the woody species.

BGC were expressed as the amount of C per square meter. See our previous work (Liu et al. 2020) for its sampling and analysis.

### Soil sampling and analysis

After plant sampling, soil profiles were dug in two and three 1 m×1 m quadrats at 20-m intervals on both sides of the diagonal of sampling plot, respectively. This soil sampling method can address the spatial heterogeneity of SOC storage caused by woody plants. Soil samples for C content analysis were taken at depths of 0–5, 5–10, 10–20, 20–30, 30–50, 50–70 and 70–100 cm. Some profiles could only be dug to the bedrock and cannot reach a soil depth of 1 m. In the laboratory, soil samples were air-dried and then sieved through a 2 mm mesh to remove gravels and roots. The obtained fine earth (< 2 mm) was used for the further analysis.

The fine earth were ground in a ball mill (Retsch MM20, Germany) and its total C (TC) content were determined using an elemental analyser (Euro Vector EA3000, Italy). The soil inorganic C was analysed using a carbonate analyser (Eijkelkamp, Netherlands). The SOC content was calculated as the difference between the TC and SIC (Lange et al. 2015).

### Climate data

Table 1 in our previous work has listed average MAP and MAT of each grassland type sites. In this study, we used the aridity index to indicate the degree of aridity. Aridity index was defined as the ratio of the MAP to potential evapotranspiration. It involves both MAP and potential evapotranspiration and therefore a more accurate metric of aridity. The potential evapotranspiration of each sampling site was derived using the Consortium for Spatial Information (<http://www.cgiar-csi.org/>).

## Statistical analysis

To assess the effects of woody plants across the six grassland types, we used a two-way ANOVA and general linear-mixed models to assess the main and interactive effects of grassland types and physiognomic types (there also had explanatory variable “soil depth” on SOC content) on ANPP and SOC

content. Then Tukey's multiple-range test was used to compare the differences in ANPP and SOC content between specific combinations of grassland and physiognomic types. We also used general linear-mixed models to further explore the effects of aridity index and physiognomic types (there also had explanatory variable "soil depth" on SOC content) on ANPP and SOC content. To elucidate the reasons for the effects on SOC storage, we used general linear-mixed models to explore the main and interactive effects of grassland types, ANPP, BGC and soil depth on SOC content and then used a simple linear regression to evaluate the relationship between the SOC content at different depths and ANPP and BGC in each grassland type. All the analysis was conducted using GenStat (19th, VSN International, UK).

## Results

Grassland types, physiognomic types and their interaction had a significant effect on ANPP (Table 2). ANPP both in pure and wooded grasslands increased significantly from desert to mountainous meadow (Fig. 1a). They were negatively correlated with aridity index (Tables S1; Fig. S1a). In three arid grassland types, pure grasslands had a higher ANPP than wooded grasslands while in other three less arid types, wooded grasslands had a higher ANPP (Fig. 1a).

Table 2  
The effects of grassland types (GT) and physiognomic types (PT) on aboveground primary productivity (ANPP)

Dependent Variables	Explanatory terms	DF	SS (%)	MS	Pvalue
ANPP	GT	5	66.81	28093.7	< 0.001
	PT	1	2.72	5712.2	< 0.001
	GT*PT	5	9.18	3861.8	< 0.001
	Residual	272	21.29	164.6	
ANPP of herbaceous plants	GT	5	63.15	28062.1	< 0.001
	PT	1	14.69	24270.0	< 0.001
	GT*PT	5	3.16	1043.9	< 0.001
	Residual	272	18.99	115.3	
ANPP of woody plants	GT	5	30.22	2309.2	< 0.001
	Residual	100	69.78	266.6	

DF: degree of freedom; SS (%): percentage sum of square; MS: mean square. The same below

The ANPP of herbaceous plants was significantly affected by grassland types, physiognomic types and their interaction (Table 2). See Fig. 6a in our previous work for the difference in ANPP of herbaceous plants (in our previous work, the ANPP of herbaceous plants was expressed as the living aboveground C of herbaceous plants) across grassland and physiognomic types.

The ANPP of woody plants was affected by grassland types and increased from desert to mountainous meadow (Table 2; Fig. 1b). It was negatively correlated with aridity index (Table S1; Fig. S1 b).

Grassland types, physiognomic types, soil depth and their interaction had a significant effect on SOC content (Table 3). SOC content at different depth both in pure and wooded grasslands increased significantly from desert to mountainous meadow (Fig. 2) and were negatively related to aridity index (Table S2; Fig.S2). The significant differences in SOC content between the two physiognomic types were mostly confined to the upper soil layer (Fig. 2). In arid types, pure grasslands had a higher SOC content at the depth of 0-5cm, 5-10cm and 10-20cm (Fig. 2a, b, c) while in less arid types, wooded grasslands had a higher SOC content at the 0-5cm, 5-10cm, 10-20cm and 20-30cm (Fig. 2a, b, c, d).

Table 3  
The effects of grassland types (GT), physiognomic types (PT) and soil depth (SD) on soil organic carbon (SOC) content

<b>Explanatory terms</b>	<b>DF</b>	<b>SS (%)</b>	<b>MS</b>	<b>P value</b>
GT	5	75.82	92019.57	< 0.001
PT	1	0.03	183.96	< 0.001
SD	1	11.59	70339.85	< 0.001
GT*SD	5	6.90	8379.72	< 0.001
PT*SD	1	0.03	211.00	< 0.001
GT*PT	5	1.29	1561.41	< 0.001
GT*PT*SD	5	0.29	352.57	< 0.001
Residual	1727	4.03	14.19	

Grassland types, soil depth and their respective interaction with ANPP and BGC has a significant effect on SOC content (Table 4). Further analysis showed that in desert and desert steppe, SOC content at the upper soil layer was positively related to ANPP and in all three arid types, it was positively related to BGC (Table 5, 6). In less arid types, SOC content at the upper soil layer was only positively related to ANPP (Table 5).

Table 4

The effects of grassland types (GT), soil depth, aboveground primary productivity (ANPP) and belowground biomass carbon (BGC) on soil organic carbon (SOC) content

Explanatory terms	DF	SS (%)	MS	P value
GT	5	75.82	92019.57	< 0.001
SD	1	11.72	71142.26	< 0.001
ANPP	1	0.44	2657.15	< 0.001
BGC	1	0.09	523.29	< 0.001
GT*SD	5	6.87	8342.51	< 0.001
ANPP*SD	1	0.008	475.61	< 0.001
BGC*SD	1	0.00	55.41	0.067
GT*ANPP	5	0.12	150.50	< 0.001
GT*BGC	5	0.12	149.80	< 0.001
GT* ANPP*SD	5	0.04	40.62	< 0.05
GT*BGC*SD	5	0.04	44.61	< 0.05
Residual	1715	4.64	16.45	

Table 5

Coefficients of determination ( $R^2$ ) between aboveground primary productivity (ANPP) and soil organic carbon (SOC) content at different depth. Abbreviations are the same as those in Table 1. Asterisks indicate the significance level: \* $P < 0.05$ ; \*\* $P < 0.01$ ; \*\*\* $P < 0.001$

Grassland types	0-5cm	5-10cm	10-20cm	20-30cm	30-50cm	50-70cm	70-100cm
TD	0.08*	0.10**	0.08*	0.059*	0.05	0.037	0.04
TSD	0.12	0.10	0.06	0.029	0.001	0.058	0.002
TDS	0.05	0.061*	0.07*	0.10**	0.113**	0.103	0.129
TS	0.15***	0.172***	0.13**	0.06*	0.012	0.027	0.028
TMS	0.43**	0.28*	0.27*	0.12	0.138	0.292*	0.266*
MM	0.24**	0.20*	0.15*	0.07	0.004	0.002	0.231*

Table 6

Coefficients of determination ( $R^2$ ) between belowground biomass carbon (BGC) and soil organic carbon (SOC) content at different depth. Abbreviations are the same as those in Table 1. Asterisks indicate the significance level: \* $P < 0.05$ ; \*\* $P < 0.01$ ; \*\*\* $P < 0.001$

Grassland types	0-5cm	5-10cm	10-20cm	20-30cm	30-50cm	50-70cm	70-100cm
TD	0.37***	0.32***	0.25***	0.11**	0.10*	0.12*	0.13*
TSD	0.28**	0.40***	0.36***	0.24**	0.13	0.07	0.01
TDS	0.16***	0.14**	0.14**	0.17***	0.12**	0.07	0.08
TS	0.0001	0.0001	0.001	0.0001	0.003	0.001	0.002
TMS	0.16	0.12	0.035	0.014	0.16	0.20*	0.22
MM	0.001	0.0001	0.024	0.073	0.05	0.11	0.09

## Discussion

The difference between our this study and previous one was that we used a large number replicate but unpaired pure and wooded grassland sites to assess the effects of woody plants across Xinjiang at a regional scale. Moreover, we assessed the effects along the aridity gradient represented by the six grassland types to explore the mediation of climate conditions on the effects.

In our study, the effect of woody plants on ANPP was negative in arid grassland types but positive in less arid types, which matched with our previous finding that the wetter conditions promoted a more positive effect on AGC (Liu et al. 2020). Knapp et al. (2008) also found higher MAP promoted the increases in ANPP with woody plant encroachment in North American. A biotic mechanism for this finding they inferred was that woody plants had a canopy architecture that enabled them to display greater leaf area than the herbaceous plants in mesic regions. In this study, we separated the ANPP in wooded grasslands into that of herbaceous and woody plants to explore the mediation of climate. Our previous work found woody plants had a more negative impact on the ANPP of herbaceous plants (expressed as the living AGC of herbaceous plants in previous study) in three arid grassland types, however, it increased vegetation- level AGC because they had higher living AGC than herbaceous plants (Liu et al. 2020). However, in this study, the ANPP of woody plants cannot offset the reduced amount in those of herbaceous plants in these types, which did not support our prediction. This may be due to the fact that woody plants grow slowly and have a long life span and their biomass of current year (NPP) only account for a small proportion of their total biomass. The mediation of climate conditions on the effect on ANPP was similar to that on AGC in our previous study. Water availability limits the maximum woody cover and there had the relatively lower ANPP of woody plants in three arid types, which also can partly explain the negative effect on ANPP in these types (Chen et al. 2015; Sankaran et al. 2005). Our previous study found that woody plants had a weaker impact on the ANPP of herbaceous plants in other three less arid types probably because the improved water availability permitted more herbaceous plants coexist with woody plants (Liu et al. 2020; Tielbörger and Kadmon 2000). The improved water availability also

led to an increase in the cover and density and thereby of ANPP of woody plants. These findings can explain the positive effect on ANPP in less arid types.

As we predicted, the effect on SOC storage was negative in arid grassland types while it was positive in less arid types. In arid grassland types, the positive relation between SOC content at the upper layer and ANPP and BGC indicated that the negative effect on ANPP and BGC led to that on SOC storage. In less arid types, the positive effect on SOC at the upper layer mainly attributed to that on ANPP. The neutral of woody plants on BGC that we have found in previous study also contributed to the positive effect on SOC content in these types (Liu et al. 2020). Our two studies showed that the effects of woody plants on ANPP, BGC and SOC storage along aridity gradients were almost coupled. This confirmed that climate conditions mediated the effects of woody plants on SOC storage through their influence on the amount of plant inputs.

In this study, a more negative impact of woody plants on the production of herbaceous plants led to a negative on ANPP in arid grassland types. Our previous work also found that woody plants had a more negative impact on the production of herbaceous plants and allocated less biomass to roots than herbaceous plants, and thereby they cannot make up for the greater loss in the BGC of herbaceous plants and had a negative effect on vegetation-level BGB in these types. Similarly, the decrease in SOC storage in the study of Jackson et al. (2002) was due to more loss of herbaceous plant production (Goodale and Davidson 2002). In arid types, the loss of grass cover and the increase in bare soil may also enhance wind erosion and thus the loss of nutrient-rich soil particles (Li et al. 2008). This finding agreed with that of Soliveres et al. (2014) who found that in global drylands, plant diversity and multifunctionality were associated with the relative woody cover and they decreased once a threshold in the relative woody cover has been reached. Our findings also further supported the points of Soliveres et al. (2014) that the mixed effects of woody plant encroachment was at least due to the difference in woody dominance and there was a need to consider differing levels of woody dominance to properly assess the effects of woody plant encroachment.

In our study, the wetter conditions promoted the positive effect of woody plant encroachment on SOC storage, which was consistent with the findings from the study of Li et al. (2016) who found that at a global scale, higher precipitation enhanced the increase in SOC content through increasing ANPP of woody plants after woody plant encroachment. In our study, the wetter conditions promoted the positive effect on SOC storage not only by increasing the ANPP of woody plants but also by weakening the negative impact of woody plant encroachment on the production of herbaceous plants and thus increasing ANPP and BGC. This finding expanded our understanding about the mediation of climate conditions on the effects of woody plant encroachment on SOC storage. However, previous studies observed an inverse relationship between the change in SOC storage and MAP. In addition to the scale of the analysis and climate zone, these inconsistent results were probably because grazing, soil texture and the species, cover and age of woody plants exert a local influence on the effects of woody plant encroachment on SOC storage (Barger et al. 2011).

Our two studies have completely assessed the effect of woody plant encroachment on aboveground and underground C pools of arid grasslands using a consistent sampling and measuring methods. Grasslands stored most of C in soil and the effect of woody plant encroachment on SOC storage may dominate that on total ecosystem C storage. Our findings enabled us to highlight that there is a need to measure SOC storage in both pure and wooded grasslands to estimate accurately total ecosystem C storage of grasslands. Our previous study found a negative effect of woody plants on total plant C storage in arid grasslands and forecasted woody plant encroachment would decrease plant C storage in grasslands due to the predicted increases in aridity in the future in Xinjiang. In this study, we further found the evidences that increasing aridity in the future would decrease ANPP and SOC with woody plant encroachment in grasslands.

## Conclusions

Woody plants had effects on the ANPP and SOC storage compared with pure grassland in Xinjiang, and the direction and strength of the effects varied with grassland types which represent the variation of climate conditions. The climate conditions mediated the effects by affecting the production of woody and herbaceous plants as well as the impact of woody plants on the production of herbaceous plants.

## Declarations

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## Supplementary Table

**Table S1:** The effect of physiognomic types (PT) and aridity index (AI) on aboveground primary productivity (ANPP)

Dependent Variables	Explanatory terms	DF	SS (%)	MS	<i>P</i> value
ANPP	PT	1	1.59	3346.5	<0.05
	AI	1	48.01	100935.5	<0.001
	PT*AI	1	4.89	10292.0	<0.001
	Residual	280	45.46	341.7	
ANPP of herbaceous plants	PT	1	18.12	29922.1	<0.001
	AI	1	39.37	65030.8	<0.001
	PT*AI	1	0.35	582.8	0.127
	Residual	280	42.16	248.7	
ANPP of woody plants	AI	1	25.93	9907.0	<0.001
	Residual	104	74.07	272.1	

**Table S2:** The effect of physiognomic types (PT), aridity index (AI) and soil depth (SD) on soil organic carbon (SOC) content

Explanatory terms	DF	SS (%)	MS	<i>P</i> value
PT	1	0.01	62.6	0.545
AI	1	37.43	227109.2	<0.001
SD	1	9.76	59225.1	<0.001
PT*AI	1	1.17	7074.1	<0.001
PT*SD	1	0.01	67.5	0.529
AI*SD	1	2.37	14407.2	<0.001
PT*AI*SD	1	0.34	2111.8	<0.001
Residual	1743	48.90	170.2	

## Figures

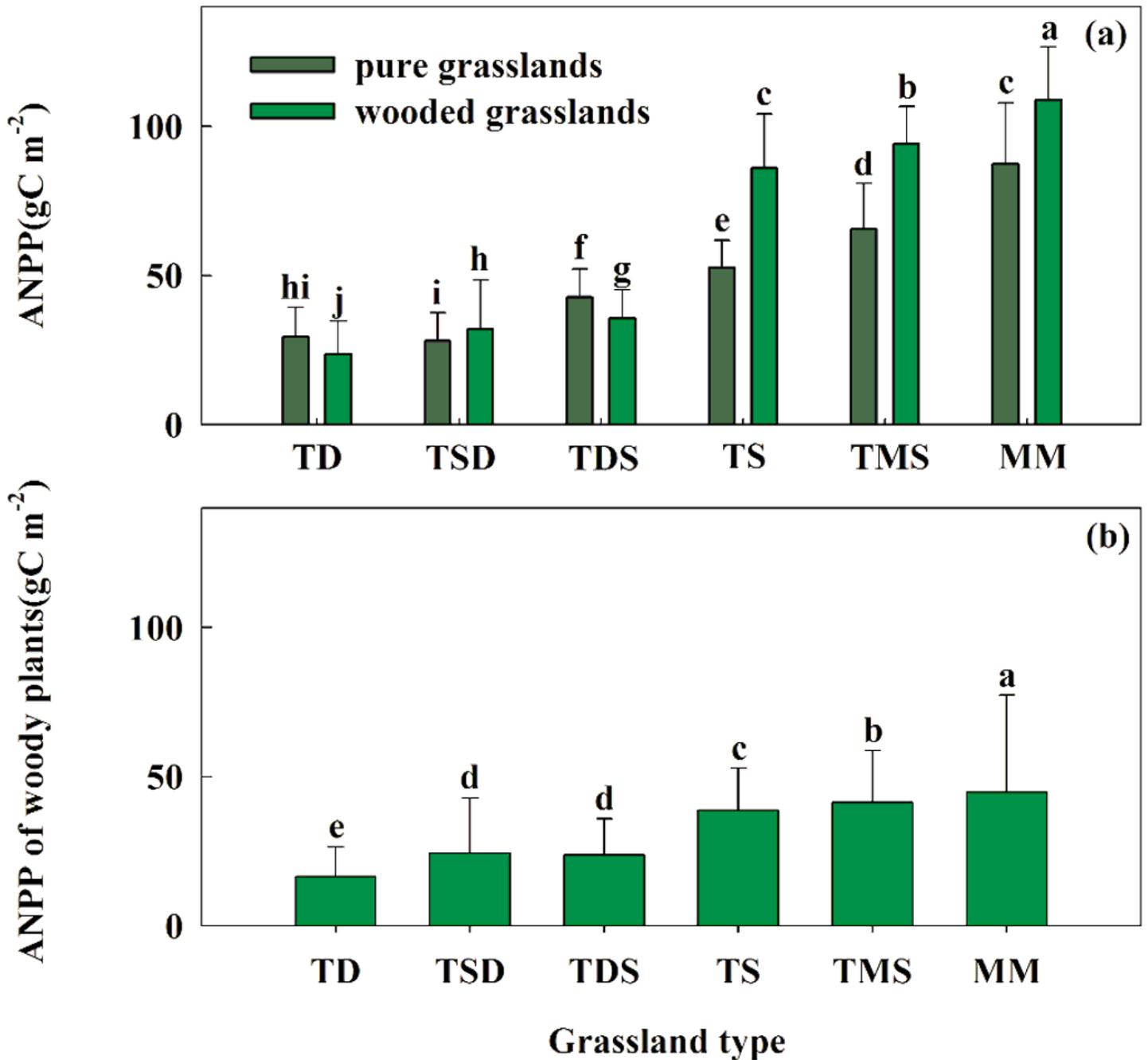
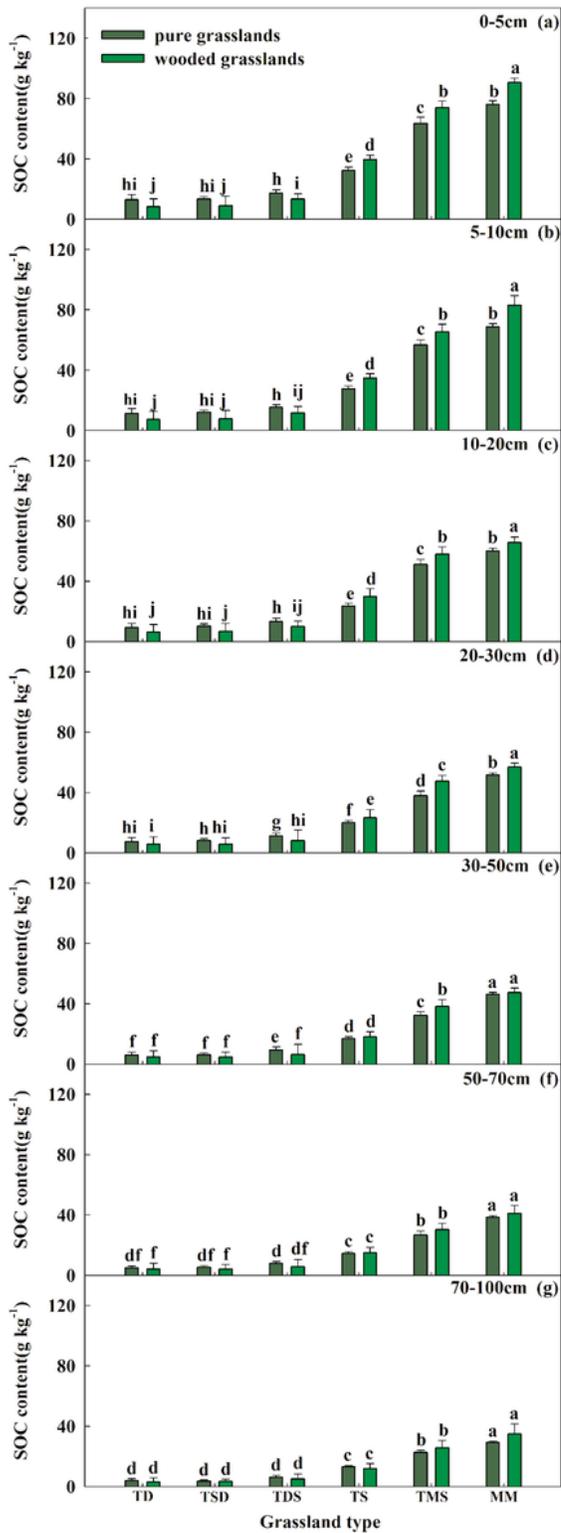


Figure 1

Aboveground primary productivity (ANPP) in pure and wooded grasslands and the ANPP of woody plants in wooded grasslands in the six grassland types. Abbreviations are the same as those in Table 1. Error bars represent one standard deviation. Different letters above the bars indicate significant differences between grassland and physiognomic types according to Tukey's multiple-range test ( $P < 0.05$ )



**Figure 2**

The vertical distribution of SOC content in pure and wooded grasslands in the six grassland types. Abbreviations are the same as those in Table 1. Error bars represent one standard deviation. Different letters above the bars indicate significant differences between grassland and physiognomic types according to Tukey's multiple-range test ( $P < 0.05$ )

## Supplementary Files

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