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RESEARCH ARTICLE

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Root system plays an important role in responses of plant to drought in the steppe of China

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Abstract

In the temperate grasslands of northern China, there exists a large range of soil texture. However, previous studies have mainly focused on the effect of climate water deficit on plant traits and have paid little attention to the effect of soil water deficit because grasses tend to use rainfall water directly. We measured eight drought-related plant traits of 12 widely distributed perennial species in the temperate grassland in northern China and examined drought-related plant traits under different aridity index ($[ET_0 - P]/ET_0$) and soil sand/clay ratio. The 12 species were categorized into three functional groups: fibrous-rooted C_4 species, fibrous-rooted C_3 species, and tap-rooted C_3 species. Our results showed that increasing climate drought had influence on all selected functional groups, and the influence on aboveground biomass and height was especially large on fibrous-rooted C_3 species. Coarse soil led to increased root length of fibrous-rooted C_3 and tap-rooted C_3 species. Our results imply that root system can be important to plant responses under drought, and soil texture can have influence on plant, though most of the traits show resistance to coarser soil.

KEYWORDS
biomass, drought, functional traits, soil texture, temperate grassland

1 | INTRODUCTION

Plant traits are widely used to show the adaptation of plants to environmental change, especially plant functional traits and biomass (Liu & Ma, 2015; Meng, Ni, & Wang, 2007; Díaz et al., 2004; Breitschwerdt, Jandt, & Bruelheide, 2018; Violle et al., 2007). Many studies have focused on plant traits and grassland ecosystems that are sensitive to climate change especially under human disturbance (Jones, Barber, & Gibson, 2019; Kröel-Dulay et al., 2015; Li et al., 2013; Schnoor, Bruun, & Olsson, 2015). Several studies have shown that climate dryness could decrease aboveground biomass and belowground biomass in grassland ecosystems (Gao, Chen, Lin, Giese, & Brueck, 2011; Liu, Liu, Gong, Wang, & Sun, 2014), as well as cause changes in plant morphological and physiological traits, which usually help plants better adapt to water stress (Wright et al., 2004). Plants under water stress often have small and thick leaves with small special leaf areas and high $\delta^{13}C$ values (Ivanova et al., 2018; Lv, He, & Zhou, 2019), and tend to allocate larger percentage of biomass to belowground (Schenk & Jackson, 2002; Sitch et al., 2003). Previous studies also showed that deep roots are often associated with water stress (Jackson et al., 1996).

Drought has different influences among functional groups (Sitch et al., 2003), and these differences can reflect different drought adaptation abilities and drought-resistance strategies (Fort et al., 2017; Liu & Ma, 2015; Zhou et al., 2018). C_4 species have stronger photosynthetic capacity and higher water-use efficiency than C_3 species (Griffith et al., 2015; Way, Katul, Manzoni, & Vico, 2014), thus C_4 species are better adapted to drought, and tend to distribute under conditions of high temperature, high light intensity and low concentration of CO_2 (Auerswald et al., 2009; Ni, 2003; Osborne & Freckleton, 2009; Pyankov, Gunin, Tsoog, & Black, 2000; Taylor et al., 2014; Wang &

Ma, 2016). Plant species with fibrous root systems have thin and long roots, which help absorb unstable soil water in the surface soil layer; in contrast, plant species with tap-root systems have a thick tap-root, which helps to constantly absorb water from subsurface soil (Fry, Evans, Sturrock, Bullock, & Bardgett, 2018; Ravenek et al., 2016). Considering the different water uptake strategies, the amount and distribution of precipitation may have different influences on fibrous-rooted species and tap-rooted species (Didiano, Johnson, & Duval, 2016; Padilla et al., 2013).

Another important factor influencing plant water uptake is soil texture, the composition of soil particles of different sizes. Several studies have highlighted the influence of soil texture on the vertical distribution and dynamics of soil water (Bharali, 2019; Hou, Wenninger, & Li, 2014). Fine particles in soil make soil more hydrophilic, which decreases the soil infiltration rate (Hou et al., 2014; Muñoz-Carpena, Lauvernet, & Carluer, 2018), while coarse particles in soil would decrease the water content in surface soil (Bharali, 2019).

Based on the different water-holding abilities, the 'inverse texture hypothesis' had suggested that coarse-textured soils in arid and semi-arid regions could increase aboveground net primary production by decreasing evaporation (Noy-Meir, 1973; Sala, Parton, Joyce, & Lauenroth, 1988). However, some studies suggested communities with coarse soil have decreased aboveground biomass (Li, Okin, & Epstein, 2009; Wen et al., 2013), decreased root length (Schenk & Jackson, 2002; Wen et al., 2013; Zuo et al., 2009), and decreased plant height, vegetation coverage and species richness (Zuo et al., 2009). Specific studies on the relationship between plant traits of different functional groups and coarser soil 'remain limited'.

In this study, we selected the agro-pastural transitional zone with mixed land uses of agriculture and animal husbandry in the temperate steppe in northern China as our study area, a large range of different soil texture exits in this region. We intended to answer the following scientific questions: Does climate dryness has different influence on functional groups with different root system? Does soil coarsening has an influence on drought-related plant traits? If so, how has soil coarsening changed the plant traits? Based on the previous studies, we developed the following hypotheses: (1) climate dryness can lead to increasing water stress on grassland plants and the influence is larger on fibrous-rooted species than on taprooted species, larger on C_3 species than on C_4 species; (2) coarser soil can also have a similar influence on plants from different functional groups as climate dryness.

2 | METHODS

2.1 | Study area

Our study area is located in the temperate grassland in northern China (36°N–46°N, 105°E–125°E), including the south-eastern part of the Inner Mongolian Plateau and surrounding areas (Figure 1). The average annual temperature is approximately 0.7–9.1°C, and the

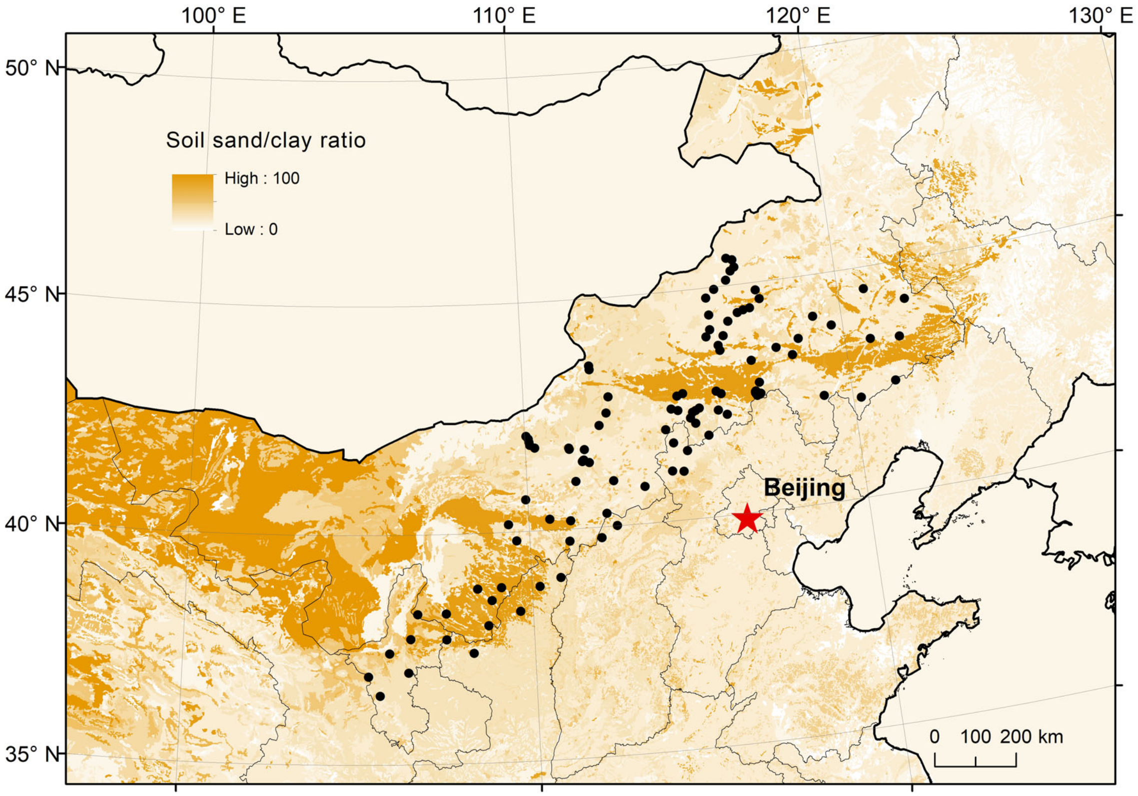

FIGURE 1 Location of the study zone with sample plots shown by black dots [Colour figure can be viewed at wileyonlinelibrary.com]

annual precipitation is approximately 150–450 mm. Affected by the East Asian monsoon, the mean annual precipitation decreases from the southeast to northwest. Correspondingly, the soil type changes from Chernozem soil to chestnut soil to brown calcic soil, and the vegetation type changes from meadow steppe to typical steppe and desert steppe.

This region has become warmer and drier during the last 70 years, and the Palmer drought severity index (PDSI) has been increasing, with a trend that is larger than the world average (Dai, 2011; Dai, Trenberth, & Qian, 2004). How local ecosystems change under warming and drying climates has attracted attention (Han et al., 2018; Lv et al., 2019).

2.2 | Field sampling and laboratory measurements

We sampled 107 plots in the growing seasons (June–August) of 2012, 2017, and 2018 and collected species that are widely and frequently found, including fibrous-rooted C_4 species, fibrous-rooted C_3 species, and tap-rooted C_3 species. A total of 12 species were selected (Table 1).

We selected mature and healthy leaves from the middle of plants, scanned 5–10 leaves from different individuals with a scanner to calculate leaf area, measured three overlapped leaves with a vernier caliper to calculate leaf thickness, and took leaves from different individuals back to laboratory to measure $\delta^{13}C$. We also gathered at least three plant samples with undamaged roots to measure root length (length of the longest root for fibrous-rooted species, length of the taproot for -species) and measured aboveground biomass, belowground biomass as well as total biomass after cleaning with water and drying at 65°C for 48 hr. In addition, we collected three soil samples from a depth of 0–10 cm to conduct laser particle size analysis. Soil particles were divided into three size groups, namely, clay (< 2 μm), silt (2–63 μm), and sand (63–2,000 μm), and the ratio of sand/clay were calculated. Most measurements were repeated three times. The measurements were conducted at the Plant and Soil Laboratory of Peking University.

TABLE 1 Selected 12 species and their functional groups

	Family	Functional group
Cleistogenes squarrosa	Poaceae	Fibrous-rooted C_4
Leymus chinensis	Poaceae	Fibrous-rooted C_3
Agropyron cristatum	Poaceae	Fibrous-rooted C_3
Lespedeza davurica	Fabaceae	Tap-rooted C_3
Medicago ruthenica	Fabaceae	Tap-rooted C_3
Gueldenstaedtia verna	Fabaceae	Tap-rooted C_3
Heteropappus altaicus	Asteraceae	Tap-rooted C_3
Artemisia frigida	Asteraceae	Tap-rooted C_3
Potentilla longifolia	Rosaceae	Tap-rooted C_3
Potentilla bifurca var. *major*	Rosaceae	Tap-rooted C_3
Thalictrum petaloideum	Ranunculaceae	Tap-rooted C_3
Stellera chamaejasme	Thymelaeaceae	Tap-rooted C_3

We collected and calculated data of the aridity index from CGIAR (https://cgiarcsi.community), which has a resolution of 1×1 km^2 and is averaged over 50 years. The aridity index was defined as $(ET_0 - P)/ET_0$; where P is the mean annual precipitation and ET_0 is the mean annual reference evapotranspiration. The aridity index can represent the long-term climate condition across the study area, and a larger value of aridity index represents a drier climate.

We also calculated the human disturbance index (HDI) from plant composition using the methods of Liu, Yin, Tian, Ren, and Wang (2008), and divided sample plots equally into 5° of human disturbance based on HDI.

All the response and driving variables are listed in Tables 2 and 3.

2.3 | Statistical analyses

We used the Kruskal-Wallis method to test the differences in root lengths among functional groups, this method can be used even when the sample size differs among functional groups. We used a linear mixed model (LMM, with the R package lme4) with species as random effect to examine how plant traits change with aridity index and soil sand/clay ratio. For the thickness of fibrous-rooted C_3 species and Fabaceae species, the random effect is removed from models because the models failed to converge, the random effect is also removed if the variance of random effect is close to zero.

Soil sand/clay ratio is generally positively related to aridity index (correlation coefficient = 0.287, $p = 0.002$), adding the interaction of aridity index causes the problem of multicollinearity (variance inflation factors > 10), so the interaction effect was removed from the models. Aridity index, soil sand/clay ratios, and plant traits are all standardized before putting into models to make results more comparable.

We used analysis of variance to show the relationship between the degree of HDI and aridity index, and used linear mix model to examine the influences of aridity index, human disturbance as well as their interaction on soil sand/clay ratio.

TABLE 2 Description of the driving variables

	Unit	Range	Average	*S D*
Annual temperature	°C	0.33–9.03	3.90	2.40
Annual precipitation	mm	183–469	318	69.88
Aridity index	—	0.62–0.88	0.76	0.06
Soil sand/clay ratio	—	0.70–34.20	9.00	6.83
Human disturbance index	—	1.07–2.79	1.40	0.28

Abbreviation: SD = standard deviation.

3 | RESULTS

3.1 | The differences in root lengths among functional groups

Among the selected species, the root lengths of fibrous-rooted C_4 species were the shortest, and those of tap-rooted species varied greatly (Table 4). Among the three functional groups, the root lengths of fibrous-rooted C_4 species were significantly shorter than those of fibrous-rooted C_3 species and taprooted C_3 species ($p < 0.01$) (Figure 2).

3.2 | Changes in plant traits under different climate conditions

With the increase in aridity index, fibrous-rooted C_4 species has opposite response compared with tap-rooted C_3 species and fibrous-rooted C_3 species (Figure 3). The absolute values of the regression coefficients between aridity index and total biomass, aboveground biomass and height are larger for fibrous-rooted C_3 species than tap-rooted C_3 species and fibrous-rooted C_4 species, and larger for family mainly composed of fibrous-rooted C_3 species (Poaceae) than families mainly composed of tap-rooted C_3 species (Asteraceae, Fabaceae, and Rosaceae) (Figure 4).

TABLE 3 Description of the response variables

	Unit	Responses under dryer condition
Leaf area	mm^2	Smaller leaf area (Liu & Ma, 2015)
Leaf thickness	mm	Larger leaf thickness (Ivanova et al., 2018)
$\delta^{13}C$	‰	Larger $\delta^{13}C$ (Niu et al., 2011; Rumman, Atkin, Bloomfield, & Eamus, 2017)
Height	Cm	Smaller height (Ma et al., 2020)
Root length	Cm	Larger or smaller root length (Schenk & Jackson, 2002; Zhou et al., 2018)
Belowground biomass	g	Smaller belowground biomass (Meng et al., 2019)
Aboveground biomass	g	Smaller aboveground biomass (Liu et al., 2014; Meng et al., 2019)
Total biomass	g	Smaller total biomass (Gao et al., 2011)

3.3 | Change in plant traits under different soil coarseness

The relationships between plant leaf traits of the three functional groups and the soil sand/clay ratio showed a few significant relationships (Table 5). With the increase in the soil sand/clay ratio, fibrous-rooted C_3 species increased leaf thickness ($p = 0.004$), and fibrous-rooted C_3 species, and tap-rooted C_3 species had increased root length ($p < 0.05$).

4 | DISCUSSION

Our results are basically consistent with the first hypothesis: climate drying causes plants to be subjected to drought stress, and the influences on several essential traits are larger for fibrous C_3 species. For the second hypothesis, C_3 species shows increased root length with soil coarsening.

Compared with tap-rooted C_3 species and fibrous-rooted C_4 species, fibrous-rooted C_3 species had greater changes in several plant traits with climate drying, though their roots are not the shortest. It is widely recognized that C_3 species have lower water use efficiency than C_4 species (Ivanova et al., 2018; Way et al., 2014). Compared with tap-rooted species that can efficiently absorb stable water supply from deeper soil (Didiano et al., 2016; Nippert & Knapp, 2007a; Nippert & Knapp, 2007b), fibrous-rooted species tend to absorb unstable water in shallower soil and can utilize brief and shallow pulses (Fry et al., 2018; Ravenek et al., 2016; Schwinning &

TABLE 4 Root lengths of selected species, mean ± *SD*

Species	Functional group	Root length (cm)	Sample size
Cleistogenes squarrosa	Fibrous-rooted C_4	10.39 ± 4.35	70
Leymus chinensis	Fibrous-rooted C_3	13.25 ± 0.75	2
Agropyron cristatum	Fibrous-rooted C_3	14.36 ± 6.21	21
Lespedeza davurica	Tap-rooted C_3	25.53 ± 13.68	27
Medicago ruthenica	Tap-rooted C_3	19.69 ± 8.94	15
Gueldenstaedtia verna	Tap-rooted C_3	13.72 ± 4.05	9
Heteropappus altaicus	Tap-rooted C_3	13.28 ± 2.97	22
Artemisia frigida	Tap-rooted C_3	15.09 ± 6.23	15
Potentilla longifolia	Tap-rooted C_3	7.77 ± 4.12	16
Potentilla bifurca var. *major*	Tap-rooted C_3	10.64 ± 5.80	45
Thalictrum petaloideum	Tap-rooted C_3	14.25 ± 7.96	19
Stellera chamaejasme	Tap-rooted C_3	26.60 ± 8.0	

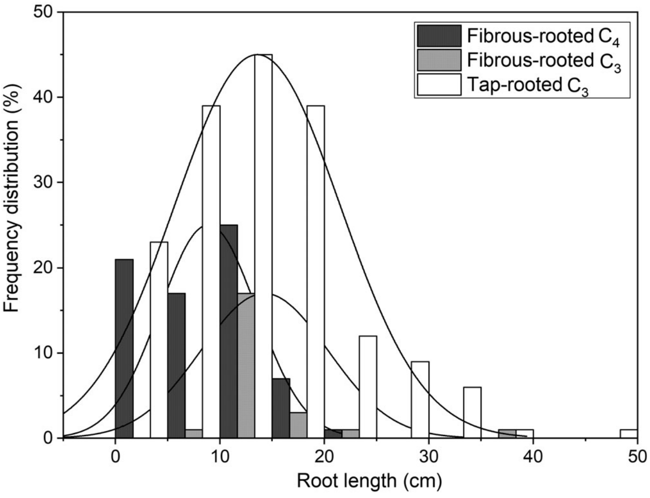

FIGURE 2 The distribution of root lengths of three functional groups

Sala, 2004; Yang, Bastow, Spence, & Wright, 2008), which may account for the more sensitive response of fibrous-rooted C_3 species to drought. However, this does not necessarily lead to the transition of fibrous-rooted C_3 species to tap-rooted C_3 and fibrous-rooted C_4 species under water deficit (Li et al., 2015), for the turnover of community is more guided by competition rather than plant mortality, and fibrous species are more competitive (Stampfli, Bloor, Fischer, & Zeiter, 2017).

Our study is carried on in the arid and semiarid grassland, in this region, studies have suggested different ideas about relationships between plant biomass and soil texture. According to the inverse texture hypotheses, coarser soil should lead to larger aboveground biomass for the decreased evaporation (Noy-Meir, 1973). However, a few field studies show that communities with coarser soil have reduced aboveground and belowground biomass (Li, Zhao, Zhao, Zhang, & Chen, 2006; Zuo et al., 2009). In our research, biomass

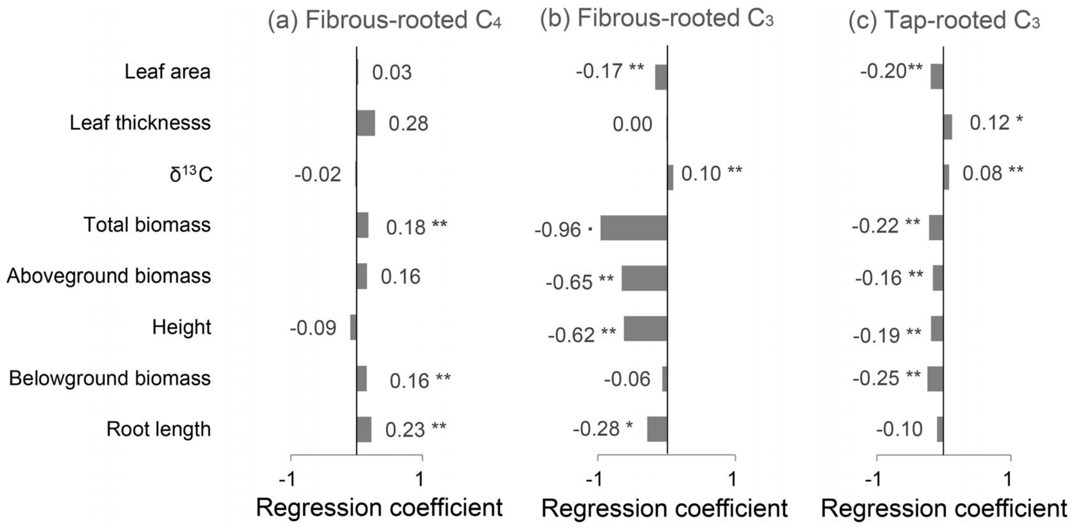

FIGURE 3 The slope of plant traits with aridity index of the three functional groups. (a) fibrous-rooted C_4; (b) fibrous-rooted C_3; and (c) tap-rooted C_3. **$p < 0.01$; *$p < 0.05$; $\cdot p < 0.1$

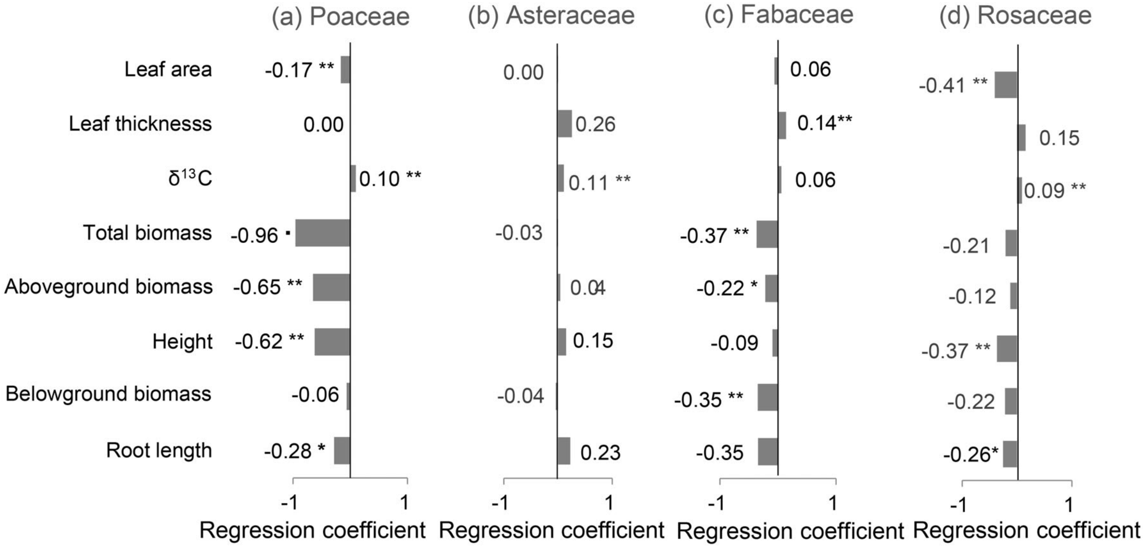

FIGURE 4 The slope of plant traits with aridity index of C_3 families. (a) Poaceae; (b) Asteraceae; (c) Fabaceae; and (d) Rosaceae. **$p < 0.01$; *$p < 0.05$; $\cdot p < 0.1$

TABLE 5 Results of the linear mixed models testing the effects of soil clay/sand ratios on plant traits

	Fibrous-rooted C_4			Fibrous-rooted C_3			Tap-rooted C_3		
	Estimate	Std. error	*p*	Estimate	Std. error	*p*	Estimate	Std. error	*p*
Leaf traits									
Leaf area									
Intercept	−0.582	0.015	**0 .000**	0.204	0.320	0.638	0.060	0.299	0.848
Sand/clay	0.001	0.004	0.863	0.009	0.023	0.687	0.079	0.043	0.064
Aridity index	0.025	0.015	0.099	−0.165	0.042	**0.000**	−0.195	0.054	**0.000**
Leaf thickness									
Intercept	−1.455	0.199	**0 .000**	0.517	0.114	**0 .000**	0.012	0.200	0.952
Sand/clay	−0.028	0.047	0.560	0.114	0.037	**0.004**	0.004	0.039	0.914
Aridity index	0.279	0.194	0.161	−0.001	0.110	0.993	0.121	0.057	**0.034**
Leaf δ^{13}C									
Intercept	3.180	0.035	**0 .000**	−0.108	0.075	0.386	−0.239	0.092	**0.031**
Sand/clay	−0.009	0.009	0.298	0.012	0.010	0.230	0.005	0.011	0.655
Aridity index	−0.022	0.035	0.538	0.096	0.029	**0.002**	0.078	0.016	**0.000**
Plant size									
Height									
Intercept	−0.490	0.263	0.073	0.782	0.126	**0 .000**	−0.105	0.150	0.502
Sand/clay	0.043	0.065	0.513	−0.030	0.062	0.636	−0.080	0.044	0.072
Aridity index	−0.095	0.261	0.719	−0.620	0.118	**0.000**	−0.194	0.064	**0.003**
Root length									
Intercept	−0.436	0.057	**0 .000**	−0.144	0.257	0.715	0.205	0.247	0.431
Sand/clay	0.017	0.045	0.704	0.186	0.036	**0.000**	0.136	0.049	**0.006**
Aridity index	0.225	0.069	**0.002**	−0.281	0.112	**0.021**	−0.103	0.074	0.166
Biomass									
Belowground biomass									
Intercept	−0.431	0.040	**0 .000**	0.681	0.553	0.235	0.035	0.129	0.795
Sand/clay	−0.003	0.010	0.765	0.037	0.163	0.821	**0.013**	0.036	0.725
Aridity index	0.155	0.039	**0.001**	−0.045	0.599	0.941	−0.249	0.066	**0.000**
Aboveground biomass									
Intercept	−0.486	0.094	**.000**	0.318	0.482	0.630	0.016	0.094	0.872
Sand/clay	0.016	0.023	.492	−0.036	0.112	0.748	0.045	0.036	0.211
Aridity index	0.158	0.093	.101	−0.653	0.208	**0.003**	−0.163	0.055	**0.005**
Total biomass									
Intercept	−0.518	0.064	**0 .000**	1.195	0.524	**0 .036**	0.062	0.158	0.709
Sand/clay	0.005	0.016	0.771	−0.002	0.155	0.989	0.024	0.033	0.474
Aridity index	0.179	0.063	**0.009**	−0.977	0.568	0.103	−0.222	0.063	**0.001**

Note: Significance for bold values is $p < 0.05$.

response to aridity index rather than soil texture, suggesting climate condition is still the main restricting factor in this region (Kang et al., 2013; Ma, Yang, He, Zeng, & Fang, 2008).

However, soil texture does have influence on plants. With coarser soil, C_3 plants showed longer root length. A previous study showed that coarser soil still held lower water and nutrient condition in water-limited grassland (Li, Okin, & Epstein, 2009; Singh, Milchunas, & Lauenroth, 1998; Wen et al., 2013), and plants stretch root system to absorb water and nutrient in deeper soil when soil is coarse (Schenk & Jackson, 2002), the longer roots may benefit absorbing water and nutrient from lower layer, and explain the high resistance of other plant traits. Except for the traits mentioned, former studies have also revealed the influence of coarser soil on community composition (Lane, Coffin, & Lauenroth, 1998; Renne, Bradford, Burke, & Lauenroth, 2019). With soil getting coarser, shrubs as well as sand pioneer plants took the place of herbaceous plants (Augustine et al., 2017; Harrison & Shackleton, 1999; Li et al., 2015).

Still, our research could not separate soil coarsened by different factors. Previous studies had revealed that both dryer climate and human disturbance like grazing can lead to weakened vegetation cover (Li et al., 2013; Schönbach et al., 2011), thus a larger wind erosion and soil coarsening (Li, Zhao, Liu, & Huang, 2009; Zhou, Zhang, Zou, Zhang, & Zhang, 2020). In our results, aridity index and the degree of human disturbance are not significantly related (p = 0.163), and climate, human disturbance as well as their interaction have influence on soil texture (Appendix), thus have potential influence on plants. Finally, the temperate grassland in northern China is under strong human disturbance as well as climate change, leading to soil coarsening (Christensen, Coughenour, Ellis, & Zuo, 2004; Dai, 2011; Tong, Wu, Yong, Yang, & Yong, 2004), and learning about the influence of soil texture can help predict grassland response and should be further studied.

5 | CONCLUSIONS

We studied the influence of climate and soil texture on the plant traits of grassland plants. Dryer climate leads to increased drought stress on grassland plants, which had larger influence on several essential plant traits of fibrous-rooted C_3 species rather than tap-rooted C_3 and fibrous-rooted C_4 species, also, the studied functional groups showed longer root length with coarser soil. The results show that root system can be important for grassland plants to cope with dry climate, which is also influenced by soil texture.

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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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APPENDIX

TABLE A1 The results of the general linear models testing the effects of aridity index, HDI degree and their interaction on soil clay/sand ratios

	df	Mean square	*p*
Intercept	1.0	186.278	0.025
HDI degree	4.0	171.188	0.001
Aridity index	1.0	442.970	0.001
The interaction of aridity index and HDI	4.0	181.546	0.001