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SEASONALITY AND HOST PREFERENCE OF ARBUSCULAR MYCORRHIZAL FUNGI OF FIVE PLANT SPECIES IN THE INNER MONGOLIA STEPPE, CHINA

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ABSTRACT

The seasonal change and host preference of arbuscular mycorrhizal (AM) colonization and community composition of five common plant species *Agropyron cristatum*, *Anemarrhena asphodeloides*, *Cleistogenes squarrosa*, *Leymus chinensis*, and *Stipa grandis* in the Inner Mongolia steppe were investigated. The AM root length colonization rates were different among the five plant species and were generally high in early (May and June) and late (September) growth seasons and low in August. A total of 18 AM fungal species representing five genera were isolated from rhizosphere soils of the five plant species, and most AM fungi had not host specificity, except that *Acaulospora* sp., *Glomus constrictum*, *G. diaphanum* and *Glomus* sp. showed a certain degree of host preference. *Glomus albidum*, *G. etunicatum* and *G. geosporum* were the dominant species and showed various sporulation patterns in the five plants during the growth seasons. The AM fungal spore densities and species richness increased from May to September and decreased in October and were different in the same month in the five plants. Multivariate analyses revealed that season and host significantly co-affected the AM fungal spore density, species richness, and Shannon-Wiener diversity index, and the season had higher influence than the host.

Key words: seasonal dynamics, arbuscular mycorrhizal fungi, diversity, grassland

INTRODUTION

Arbuscular mycorrhizal (AM) fungi are widely distributed and form mutualistic symbioses with most vascular plants in grassland ecosystems (40). AM fungi comprise the largest component (mycelia and spores) of the microbial biomass in soil (14, 30, 32) and can increase plant nutrient and water uptake, particularly in nutrient poor soil of arid and semiarid ecosystems (1, 8, 10, 22, 24). AM fungi therefore play an important ecological role in determining the plant diversity, productivity, and species composition in terrestrial ecosystems (26, 43, 44, 45). Mycorrhizal dynamics and host specificity provides insights into the factors and processes regulating ecosystem development. Therefore, understanding how the dynamics and host specificity of AM fungal communities in colonization, composition, and diversity are key to understanding the ecology and function of fungus-plant association in natural ecosystems.

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Previous studies of AM fungal dynamics have yielded conflicting results. For examples, some studies indicated that maximal AM fungal spore densities were found in the end growth season (Autumn) of five grasses in mountain grassland of Argentina (28), of *Schizachyrium scoparium* (Michx.) Nash in sand prairies in Illinois (12), and in sand dune in Dartmouth of Massachusetts (17). Yet the highest AM fungal spore densities were reported in summer of *Spartina ciliate* Brongn. in the island of Santa Catarina (41), of *Lotus glaber* Mill. in temperate grasslands of Argentina (15), and of two fruit species (*Theobroma grandiflorum* Schum. and *Paullinia cupana* var. *sorbilis* Mart.) in a *terra firme* ecosystem in Central Amazonia (33). Therefore, the seasonal dynamics of AM fungal sporulation need further to be documented.

Most previous studies indicated that AM fungi had not host specificity (9, 36, 40). However, some studies showed that the sporulation and community compositions of AM fungi have been found to be host dependent (6, 28). For examples, Bentivenga and Hetrick (4) found that sporulation of AM fungi was influenced by hosts in tallgrass prairie grasses. Li et al. (27) investigated three plants in a hot and arid ecosystem of southwest China, and the results indicated that the sporulation and community compositions of AM fungi were different. Therefore, host specificity of AM fungi, which may play an important role in the maintenance of plant diversity in natural ecosystems, need further to be studied.

Inner Mongolia steppe, distributed at the eastern end of Eurasian steppe zone, is the largest grassland in China and is an important natural resource in arid and semiarid regions, which significantly contributes to the Chinese economy and ecology. In recent years, severe degradation and desertification were found due to intense human activities such as grazing, mowing, and crop cultivation in grassland. Many ecological studies concerning animals and plants have been carried out in this ecosystem (e.g., 2, 21). However, AM fungi, which have an important ecological function in grassland ecosystems, have not been studied in seasonal dynamics and host specificity in the Inner Mongolia steppe, except that the response of AM fungi to non-grazed, restored, and over-grazed was investigated (42).

Agropyron cristatum (L.) Gaertn., *Anemarrhena asphodeloides* Bunge, *Cleistogenes squarrosa* (Trin.) Keng, *Leymus chinensis* (Trin.) Tzvel., and *Stipa grandis* P. Smirn. are the most common plant species, which are highly important nutritional forage value for sheep and cattle in the Inner Mongolia steppe. This study focused on these five common plant species in this grassland. The basic aims were 1) to investigate the seasonal changes of AM fungal colonization, sporulation, species composition, and diversity and 2) to understand whether there was host preference of AM fungi in the five common plant species in the Inner Mongolia steppe.

MATERIALS AND METHODS

Study site

This study was conducted in the Inner Mongolia Grassland Ecosystem Research Station, the Chinese Academy of Sciences (43°26′–44°08′N, 116°04′–117°05′E), located in typical steppe zone of the Inner Mongolia Plateau. The area has a semiarid continental temperate steppe climate with a dry spring and moist summer. Annual mean temperature is 2°C, and annual precipitation is 350 mm. The soil water content of sampling time was listed in Figure 1.

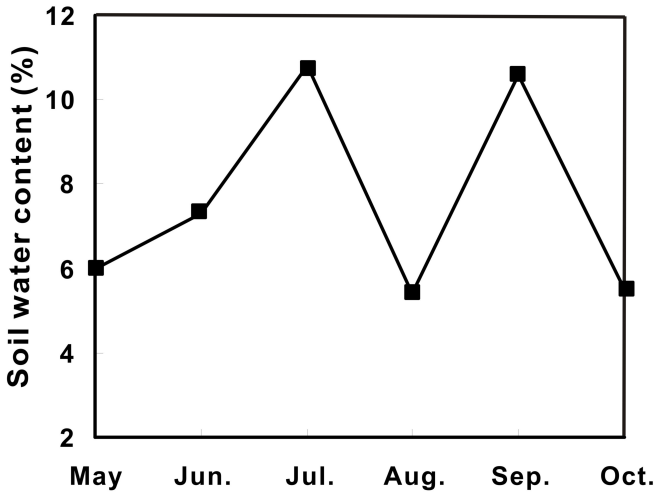

Figure 1. The soil water content of the six sampling months.

A permanent plot (ca. 500 m × 500 m), which has been fenced since 1979, was selected in this study. There are about 30 plant species in the plot, and five dominant plants, such as *S. grandis*, *A. cristatum, A. asphodeloides*, *C. squarrosa*, and *L. chinensis*, were chosen for the present study. These five plants begin growing in early May and end growth in October, and produce seeds in late August. Ten subplots (1 m × 1 m) of each plant species were randomly established and were more than 10 m away from each other.

Sampling procedure

Sampling was carried out at the beginning of each month from May to October 2006. On each sampling date, three sample cores (5 cm diam × 15 cm deep) were randomly taken in each subplot. The three soil samples from rhizospheres of the same plant species along with the roots were placed in the sterilized cotton-cloth bag and labeled as one representative sample. The root systems were separated from the soil samples and processed within one day in the laboratory. The soil samples were air dried in the shade for one week. Then they were sifted with a 2 mm sieve, stored at 4ºC, and processed within 3 months.

AM structure and colonization

Root (0.2 g) of each sample was rinsed with tap water, cleared in 10% (w/v) potassium hydroxide (20–50 min, 92ºC), acidified in lactic acid (3 min), and stained (20 min, 92ºC) with 0.5% acid fuchsin (5). A total of 50 root fragments (ca. 1-cm long) from each plant were mounted on slides in a polyvinyl alcohol-lactic acid-glycerol solution and examined with a compound microscope (Olympus BH-2) at × 100–400 to ascertain the presence of AM fungal structures, i.e. arbuscules, vesicles, hyphal coils, and non-septate hyphae. The percentage of root length colonized by AM fungal structures was determined using the following formula: %Colonization rate = (total length of root segments colonized / total length of root segments examined) × 100.

Spore isolation and identification of AM fungi

Fifty grams of each air-dried soil sample was used for spore isolation. AM fungal spores were isolated using the wet-sieving and decanting method of Gerdemann and Nicolson (19), modified by Daniels and Skipper (11). AM fungi were identified following the descriptions of Schenck and Pérez (37), the information on the International Culture Collection of Arbuscular and Vesicular–Arbuscular Mycorrhizal Fungi on the internet (www.invam.caf.wdu.edu) and the original species descriptions with their corrections. Spores were first mounted in water and morphological characteristics were measured. Melzer's reagent and cotton blue were also used in the identification. The permanent slides were mounted in polyvinyl-lacto-glycerol, sealed with nail varnish, and stored in the Herbarium Mycologicum Academiae Sinicae in Institute of Microbiology, Chinese Academy of Sciences, Beijing, China.

Data analysis

Spore density (spores per 50 g air-dried soil) was calculated from direct counts of spores. Species richness was defined as the number of AM fungal species per soil sample (25). Shannon-Weiner diversity index (*H'*) was calculated according to the formula: $H' = -\sum_{i=1}^{s} p_i \times \ln p_i$, where S is the number of species in the sample, and P_i is the relative abundance of AM fungus species of one site (38).

Data on AM colonization rate, spore density, and species richness were analyzed using one-way analysis of variance (ANOVA) to determine any significant difference (SPSS for windows, version 11.5, SPSS Inc, Chicago, USA). Data on season and host co-affect on the AM fungal spore density, species richness, and Shannon-Wiener diversity index were analyzed using multivariate analysis of variance. The statistically significant difference was determined at $p < 0.05$ level.

RESULTS

AM colonization rate

AM colonization rates were generally high in May, June, and September and low in August in the five plant species, except for a lower AM colonization rate in *S. grandis* in

September (Table 1). There were significantly higher overall root colonization rates of AM fungi in *A. cristatum*, *L. chinensis* and *S. grandis* than in *A. asphodeloides* and *C. squarrosa*, but no significant difference between *L. chinensis* and *S. grandis* and between *A. asphodeloides* and *C. squarrosa* (Table 1).

AM fungal composition

A total of 18 AM fungi belonging to five genera were identified (Table 2). Of these one belonged to *Acaulospora*, one to *Archaeospora*, one to *Entrophospora*, 14 to *Glomus*, and one to *Scutellospora*. *Glomus albidum*, *G. etunicatum* and *G. geosporum* were the dominant species in the five plant species.

There were 15, 16, 16, 15, and 14 AM fungal species isolated from *A. cristatum*, *A. asphodeloides*, *C. squarrosa*, *L. chinensis*, and *S. grandis*, respectively, and most AM fungi had not host specificity (Table 2). However, *Glomus constrictum* was only associated with *A. cristatum*. *Acaulospora* sp. occurred in *C. squarrosa* and *S. grandis. Glomus* sp. 1 was isolated from *A. cristatum* and *A. asphodeloides*. *Glomus diaphanum* was found in *A. asphodeloides*, *C. squarrosa*, and *L. chinensis*.

Table 1. The root length colonization rate (CR), spore density (SD) and species richness (SR) of AM fungi in the five plant species in different months.

Plant		May	Jun.	Jul.	Aug.	Sep.	Oct.	Overall
Agropyron cristatum	CR	55.6±5.5abAB	58.7±3.4bA	47.1±4.2acAC	39.5±2.0cAC	61.6±3.4bA	40.7±3.7cA	50.6±1.9A
	SD	22.8±1.2aA	38.1±5.5bAB	39.5±3.2bA	74.6±6.1cAB	93.8±3.5dA	47.5±5.8bAC	54.4±3.7AB
	SR	1.9±0.2aA	2.4±0.4abA	3.1±0.4bA	5.1±0.3cA	5.1±0.3cA	4.4±0.5cA	3.6±0.2A
Anemarrhena asphodeloides	CR	41.4±5.3abAC	44.2±6.1bB	30.3±3.2acB	20.9±3.3cB	41.7±2.3abBC	31.4±3.5acA	34.8±1.9B
	SD	35.3±7.3aB	40.2±5.9aA	44.8±6.6acA	77.8±9.2bdB	94.9±8.3dA	64.7±6.1bcBC	62.1±4.9A
	SR	2.4±0.2aA	2.7±0.3aA	2.7±0.4aB	5.1±0.2bA	5.2±0.2bA	4.3±0.2cA	3.7±0.2A
Cleistogenes squarrosa	CR	37.9±0.6abA	45.4±1.7aB	36.7±2.7abB	32.5±3.3bA	37.7±2.6abB	41.5±4.7abA	38.6±1.5B
	SD	30.6±4.0aA	28.7±4.5aAB	37.7±3.8abA	47.3±4.7bC	97.1±10.5cA	36.7±3.7abA	46.6±3.8B
	SR	3.5±0.4abB	2.6±0.5aA	3.4±0.5abAB	4.2±0.4bcA	5.2±0.2cA	4.2±0.3bcA	3.9±0.2A
Leymus chinensis	CR	59.0±8.5aBC	71.7±3.2aC	62.3±3.8aC	37.6±3.2bA	63.2±3.8aA	38.0±3.7bA	54.9±2.8AC
	SD	11.0±1.7aC	26.1±3.3aB	54.3±9.5bAB	51.6±4.7bC	71.7±5.8cB	52.0±5.0bBC	45.9±3.6B
	SR	2.0±0.3aA	2.6±0.3aA	3.9±0.3bA	4.3±0.3bcA	5.0±0.1cA	4.5±0.3bcA	3.7±0.2A
Stipa grandis	CR	63.9±5.5abB	72.7±4.0bC	55.1±2.5acC	46.2±2.9cC	46.6±1.8cC	56.0±3.4acB	56.8±1.8C
	SD	22.8±3.1aA	28.1±1.8aAB	71.3±8.5bB	59.7±5.0bdAC	91.9±7.4cAB	50.8±3.9dABC	54.3±3.8AB
	SR	2.2±0.2aA	2.2±0.2aA	4.9±0.1bC	4.8±0.3bA	5.0±0.2bA	4.6±0.2bA	4±0.2A

Values within the same row followed by the same lower case letter were not significantly different between months in each host, and values within the same column followed by the same capital letter were not significantly different between hosts in each month (mean±SE, n=10 in each month, n=60 in overall, $p < 0.05$).

Table 2. Overall mean spore densities of AM fungi in the five plant species (mean±SE, n=60).

AM fungus	*Agropyron cristatum*	*Anemarrhena asphodeloides*	*Cleistogenes squarrosa*	*Leymus chinensis*	*Stipa grandis*
Acaulospora sp.	0	0	0.05±0.05	0a	0.2±0.1
Archaeospora trappei (R.N. Ames & Linderman) J.B. Morton & D. Redecker	0.2±0.2	0.1±0.1	0.1±0.1	0.03±0.03	0
Entrophospora infrequens (I.R. Hall) R.N. Ames & R.W. Schneid.	0.03±0.03	0.03±0.03	0.05±0.05	0.08±0.06	0.05±0.05
Glomus aggregatum N.C. Schenck & G.S. Sm.	4.4±0.8	1.8±0.5	2.6±0.8	2.0±0.5	2.1±0.6
G. albidum C. Walker & L.H. Rhodes	7.5±0.9	9.8±1.3	5.5±1.3	4.7±0.7	9.6±1.0
G. ambisporum G.S. Sm. & N.C. Schenck	1.2±0.4	0.7±0.2	1.8±0.5	1.6±0.6	1.3±0.4
G. constrictum Trappe	0.1±0.04	0	0	0	0
G. diaphanum J.B. Morton & C. Walker	0	1.8±0.8	0.4±0.3	1.0±0.4	0
G. etunicatum W.N. Becker & Gerd.	20.3±1.3	16.3±2.0	19.9±2.0	18.0±2.0	17.0±1.1
G. fasciculatum (Thaxt.) Gerd. & Trappe	0	0.2±0.2	0.3±0.2	0.4±0.2	0.3±0.2
H*G. fistulosum*H Skou & I. Jakobsen	0.5±0.3	0.5±0.3	0.2±0.2	0.7±0.4	0.1±0.1
G. geosporum (T.H. Nicolson & Gerd.) C. Walker	16.1±1.8	19.3±1.7	12.9±1.3	13.3±1.3	21.1±2.1
G. intraradices N.C. Schenck & G.S. Sm.	0.3±0.1	1.0±0.5	0.1±0.1	0.3±0.2	0.3±0.1
G. microcarpum Tul. & C. Tul.	0.7±0.4	1.8±1.2	0.03±0.03	0.4±0.2	0.08±0.08
G. mosseae (T.H. Nicolson & Gerd.) Gerd. & Trappe	0.5±0.2	0.08±0.08	0.7±0.2	0.3±0.2	0.6±0.2
Glomus sp.1	0.2±0.2	4.9±1.5	0	0	0
Glomus sp.2	0.1±0.1	0.08±0.08	0.8±0.3	0.3±0.2	0.08±0.08
Scutellospora calospora (T.H. Nicolson & Gerd.) C. Walker & F.E. Sanders	0.9±0.2	1.0±0.2	1.0±0.1	1.3±0.2	1.3±0.2

AM fungal spore density, species richness and diversity

The AM fungal spore densities and species richness increased from May to September and decreased in October in the five plant species (Table 1). The spore densities of the three dominant species *G. albidum*, *G. etunicatum* and *G. geosporum* had a similar trend, except that *G. albidum* peaked in August in *S. grandis* and *G. etunicatum* peaked in July in *L. chinensis* (Figure 2). *G. albidum* had lower spore density than *G. geosporum* and *G. etunicatum* in the five plant species. Furthermore, there were the highest spore densities of *G. etunicatum* in *C. squarrosa* and *L. chinensis* and *G. geosporum* in *S. grandis*.

The spore densities of AM fungi were often significantly different in the same month among the five plant species (Table 1). Whereas, AM fungal species richness were not significantly different in the same month, except that the species richness were significantly higher in *C. squarrosa* than in the other four plant species in May and in *S. grandis* than in the other four plant species and in *A. cristatum* and *L. chinensis* than in *A. asphodeloides* in July.

There was no significant difference of the overall spore densities of AM fungi among the five plant species, except for a significantly higher spore density in *A. asphodeloides* than in *L. chinensis* and *C. squarrosa* (Table 1). The overall species richness of AM fungi was not significantly different among the five plants (Table 1).

Multivariate analysis revealed that seasons and hosts significantly co-affected the AM fungal spore density, species richness, and Shannon-Wiener diversity index, and the seasons had higher influence than hosts based on the analyses of F values (Table 3).

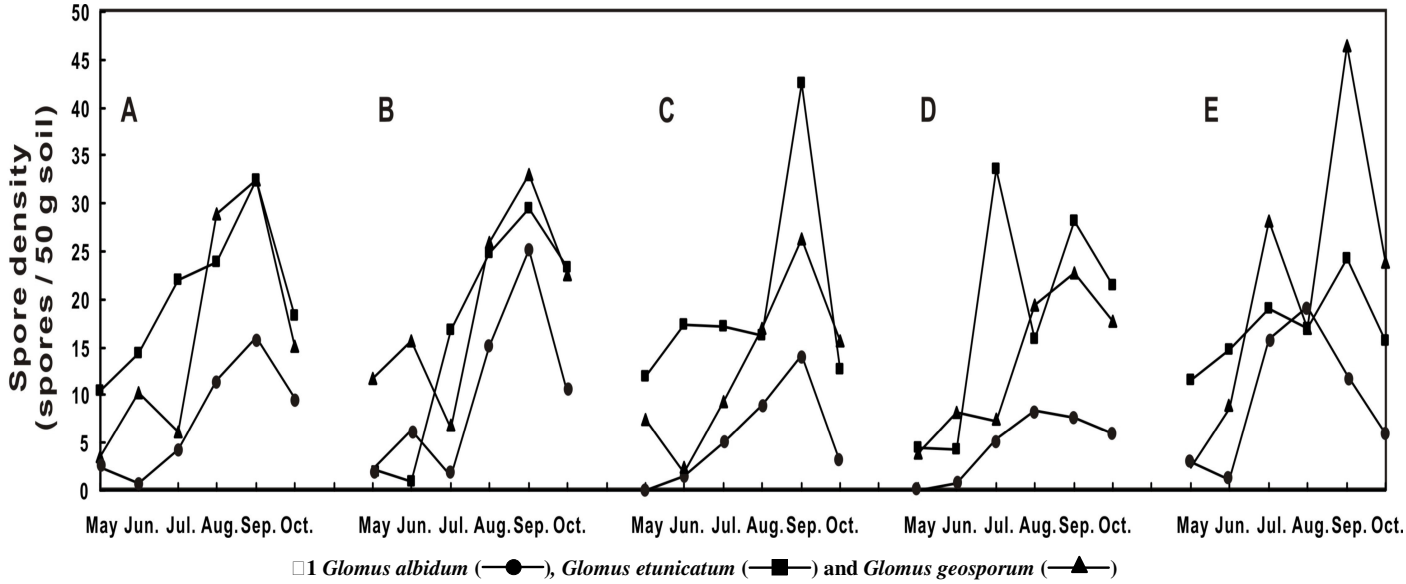

Figure 2. The seasonal dynamics of the spore densities of the dominant species *Glomus albidum* (—●—), *Glomus etunicatum* (—■—) and *Glomus geosporum* (—▲—) in plants *Agropyron asphodeloides* (A), *Anemarrhena cristatum* (B), *Cleistogenes squarrosa* (C), *Leymus chinensis* (D), and *Stipa grandis* (E).

Table 3. The effect of season and host on the AM fungal spore density (SD), species richness (SR), Shannon-Wiener diversity index (H).

	SD		SR		H	
	F	***p***	***F***	***p***	***F***	***p***
Season	80.174	<0.001	67.256	<0.001	46.444	<0.001
Host	6.714	<0.001	1.019	0.398	0.599	0.664
Season × Host	2.878	<0.001	2.709	<0.001	2.334	<0.001

DISCUSSION

Effect of season and host on AM colonization rate

The root length colonization rates of AM fungi were generally high in early (May and June) and late (September) growth seasons in the five plant species in the present study. Similar results of the highest AM colonization rates in early and late growth seasons were found in *Agropyron smithii* Rydb., *Poa pratensis* L., and *Bromus inermis* Leyss. in tallgrass prairie grasses (4) and in *Ammophila arenaria* (L.) Link. in six locations of the European coast (35). This is because the plants grow fast in early growth season and produce seeds in the late growth season, and there were high metabolic activities and nutrient demands of the plants during these seasons (31, 32). The AM structures, i.e., arbuscules, hyphal coils and vesicles, are the sites of storage and exchanging nutrients between fungi and hosts (4, 39), therefore, there were high AM colonization rates in these growth seasons.

Our results indicated that all the five plants had the lowest

AM root length colonization rates in August. The possible reason is that the soil water content was much lower in August than in the other months in the Inner Mongolia steppe (Figure 1), as results were reported by Oliveira and Oliveira (33), which soil water content affected AM fungal sporulation.

There were different overall AM root colonization rates in the five plant species. Similarly, Lugo et al. (29) found that the AM root colonization rates of six hosts were different, and the root length colonization rate of AM fungi was significantly higher in *Sorghastrum pellitum* (Hack.) Parodi than in the other five plant species in a mountain grassland. In the study of Li et al. (27), the total colonization rates of three plants *Bothriochloa pertusa* (L.) A. Camus, *Cajanus cajan* (L.) Millsp., and *Heteropogon contortus* (L.) P. Beauv. ex Roem. et Schult. were different in a hot and arid ecosystem of southwest China. It is highly possible that the plant characters and the host preference of AM fungi co-affected the AM colonization (16, 29).

Effect of season and host on AM fungi

The AM fungal spore densities and species richness increased with plant growth and reached the highest numbers in late growth season (September) in the five plant species. Similar results have been reported in previous studies (12, 18). For examples, Bentivenga and Hetrick (4) found that AM fungal spore densities increased with plant growth and reached the highest numbers in late growth seasons (October and November) in *A. smithii*, *P. pratensis*, and *B. inermis* in tallgrass prairie grasses. The spore numbers were significantly higher in the late growth season (October) than in the early growth seasons (April and July) of *A. arenaria* in Netherlands, United Kingdom England, and United Kingdom Wales (35).

However, our results indicated that the three dominant species had different sporulation patterns during the growth seasons. Similarly, Lugo and Cabello (28) found that *Acaulospora mellea* Spain & N.C. Schenck had the highest spore density in spring, but *Glomus* spp. reached the highest spore numbers in autumn in *Eragrostis lugens* Nees, *Poa stuckertii* (Hack.) Parodi, and *S. pellitum* in mountain grassland of Argentina. This is because the maximal sporulation and diversity occurred near the end of the host growing cycle or reproductive cycle for survival in following cold stage, while individual species of AM fungi show varying patterns of spore abundance in relation to plant growth seasons (12, 13, 18, 35).

The overall spore densities of AM fungi differed among the five plant species. Eom et al. (13) found that the spore densities were different from 15.94 to 61.45 per 1 g soil in hosts *P. pratensis*, *Sporobolus heterolepis* (A. Gray) A. Gray, *Panicum virgatum* L., *Baptisia bracteata* Muhl. ex Ell., and *Solidago missouriensis* Nutt. in a tallgrass prairie. Furthermore, *Acaulospora longula* Spain & N.C. Schenck was the most abundant under stands of *S. missouriensis*, but *Glomus rubiformis* (Gerd. & Trappe) Almeida & Schenck and *G. aggregatum* were most abundant under *S. heterolepis*. The number of spores of *Glomus* white reduced when *Archaeospora trappei* and *Scutellospora calospora* appeared in *Plantago lanceolata* L. (3). Similarly, our study indicated that the three dominant species had different sporulation in the five plants. *G. albidum* had lower spore density than *G. geosporum* and *G. etunicatum* in the five plant species, and *G. etunicatum* produced the maximal spores in *C. squarrosa* and *L. chinensis* and *G. geosporum* in *S. grandis*. AM fungal sporulation can be influenced by host plants, and has competition in the community for host resources and for defence themselves from stress (3, 7, 13, 34).

Our results indicated that AM fungal composition was similar in the five plants and the most AM fungi had not host specificity. However, species *Acaulospora* sp., *G. constrictum*, *G. diaphanum* and *Glomus* sp. 1 showed a certain degree of host preference. Similarly, Lugo and Cabello (28) found that *Glomus fuegianum* (Speg.) Trappe & Gerd. occurred in *Briza subaristata* Lam. and *P. stuckertii*, but *Glomus* sp. 3 was only associated with *P. stuckertii*. Li et al. (27) analyzed the AM fungal composition of plants *B. pertusa, C. cajan*, and *H. contortus* using molecular method, and the results demonstrated that AM fungi had strong host preference. Similar results were also reported in other studies, in which different plant species were associated with divergent AM

fungal communities (13, 20).

Season and host significantly co-affected the spore density, species richness, and Shannon-Wiener diversity index of AM fungi in our study. The season and host are the most important factors influenced AM fungal sporulation and species diversity in natural ecosystems, because host plants can regulate carbon allocation to roots, produce secondary metabolites, and change soil environmental conditions during growth seasons. However, the ecological function of AM fungi in regulating plant ecosystem development and restoring degraded ecosystem needs further to study in the Inner Mongolia steppe.

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