

Fine root distribution and belowground interactions in an alley silvopasture system in northern China

Zongrui LAI, Yuqing ZHANG*, Bin WU, Tianshan ZHA, Shugao QIN, Xin JIA, Jiabin LIU, Wei FENG
Yanchi Research Station, College of Soil and Water Conservation, Beijing Forestry University, Beijing, P.R. China

Received: 04.01.2014 • Accepted: 04.05.2014 • Published Online: 15.08.2014 • Printed: 12.09.2014

Abstract: Successful agroforestry management depends on the interactions between the mixed species. Belowground interactions between shrubs and native grasses are complicated and poorly understood in China's agroforestry practice, especially in the silvopasture systems of droughty northern China. The distribution of fine roots (<2 mm) in an alley silvopasture system consisting of *Caragana microphylla* Lam. and local grasses was compared to those in a degraded pasture plot using soil cores. Fine root production was examined in these plots using ingrowth cores. We found that the introduction of *C. microphylla* did not change the vertical distribution pattern of fine roots of grassy plants but had a great impact on belowground production in the ecosystem. Grass fine roots decreased with depth in both the silvopasture system and the degraded pasture. Grass fine roots were mostly distributed in the top 40 cm of the soil, but they extended to deeper soil layers through root elongation. *C. microphylla*, in contrast, occupied the deeper soil layer, in which water was continuously available. We conclude that the belowground interactions between native grasses and *C. microphylla* in sandy soil can be explained by Walter's 2-layer hypothesis, which is used to explain the coexistence of trees and grasses. Our results draw attention to the interspecific configuration of the silvopasture system and belowground interactions of plants in semiarid and arid regions.

Key words: *Caragana microphylla*/grasses coexistence, fine root production, root forage strategy, root behavior

1. Introduction

Dryland desertification constitutes one of the major environmental challenges of the 21st century (Reynolds et al., 2007); more than one-third of the earth's land surface is undergoing this type of change. Dryland desertification is particularly problematic in China, especially in the northern region. Prevention measures, such as grassland fencing, straw checkerboards, vegetation restoration, and converting degraded farmlands to grasslands (Cao et al., 2008), have been implemented to control wind erosion. Shrubs that have strong resistance to drought are often planted in desertified pastures due to certain characteristics of shrubs, including high biomass for forage, wind depression in winter and spring, erosion prevention, and branches that can be used for weaving. A combination of shrubs and native grasses has been gradually developed in the alley silvopasture system, which is considered an environmentally and economically effective means for controlling desertification in northern China (Zhang et al., 2013). However, the success and sustainability of an agroforestry system greatly depends on the interactions of shrub and grass species, especially when resources are limited.

Intensive research on belowground interactions has been conducted in natural and experimental fields (Ludwig et al., 2004a; Rodríguez et al., 2007) in climates ranging from tropical and temperate (Mommer et al., 2012) to arid and semiarid (Bartelheimer et al., 2006; Fernández et al., 2006a; Segarra et al., 2009). Walter (1939) proposed a 2-layer hypothesis to explain the coexistence of savanna trees and grasses. This hypothesis is based on vertical niche partitioning and assumes that grasses are more efficient in using water from surface soil than trees (Hipodonka et al., 2003; Ward et al., 2013). Ward et al. (2013) found that the 2-layer model worked in some moist savannas and tallgrass prairies and that it was an appropriate model to explain soil-water spatial partitioning and tree-grass codominance in dry savannas. However, the soil-water spatial partitioning of some plant communities is not explained by the 2-layer model. Roux et al. (1995) tested the 2-layer hypothesis using shrubs and grasses in a humid savanna. They found that the top soil layer contained sufficient water to satisfy the demands of both plant types during both rainy and dry periods. Rodríguez et al. (2007) also noted that shrubs (*Larrea divaricata*) and grasses (*Stipa tenuis*) were able to occupy

* Correspondence: zhangyqbjfu@gmail.com

the upper soil layer using similar fine root systems in an arid ecosystem. Hydraulic lift, a process of upward water movement from relatively wet to dry soil layers through the roots of plants (Caldwell et al., 1998; Ludwig et al., 2004a), occurs between trees and understory savanna ecosystems (Ludwig et al., 2003). Hydraulic lift provides an alternative explanation for the coexistence of trees or shrubs and grasses. Most of the water absorbed by grasses is reportedly hydraulically lifted by trees to the upper soil layers (Fernández et al., 2006a, 2008). However, Ludwig et al. (2004a) suggested that any facilitative effect of hydraulic lift would be negated by water competition among plants in arid and semiarid regions. Root competition is defined as a reduction in the availability of a soil resource to roots that is caused by other roots (Schenk, 2006). Root competition should be considered in the study of the coexistence of trees and grass or shrubs and grass. Dawson et al. (2001) investigated the effect of competition from grass roots in an agroforestry system, finding that the number of tree roots was greatly affected by the grass roots in the surface horizons.

The mechanisms of belowground interactions between plant species are controversial (e.g., Reynolds et al., 2000, 2004; Hipodonka et al., 2003; Ludwig et al., 2004b). Although a combined system has been developed throughout northern China, there are many technical issues, such as species selection, configuration, and management, that have not yet been solved. The belowground effects of planted shrubs on local pastures are unknown. Moreover, recent studies of interactions in agroforestry are scattered around the world and, therefore, they cannot provide specific direction for agroforestry practice in northern China. Our aims were to: 1) assess the belowground interactions of indigenous grasses and *Caragana microphylla* in northern China, 2) test whether the 2-layer hypothesis is applicable to this alley silvopasture system, and 3) provide some suggestions for the establishment and management of the agroforestry system in northern China.

2. Materials and methods

2.1. Study site

The experiments were conducted in Yanchi County, Ningxia Province, China, which is located at the southwestern edge of the Mu Us desert. The site (37°68'N to 37°73'N, 107°20'E to 107°26'E) has a typical temperate continental monsoon climate. At the study site, the mean annual temperature was 8.1 °C, the mean annual rainfall was about 287 mm, and rainfall events occurred mainly in the summer and autumn (data from Yanchi Research Station). The sandy sierozem soil ranged between 1.05 and 1.20 m in depth, with >70% fine sand (0.02–0.2 mm), and 45.6% mean porosity.

Human activities (i.e. overgrazing) and environmental changes (i.e. sandstorms) resulted in the gradual degradation of pastures in the study area. *C. microphylla* is a leguminous shrub species with developed root systems and strong suitability for xeric site conditions. This species was planted in degraded pastures in rows with variable spacing in order to provide fodder and prevent wind erosion of the soils. In the silvopasture plot, there were 400 *C. microphylla* clusters, or 14,784 individuals/ha, which were planted in the degraded pasture in 1985. Their average height was 1.1 m and average ground diameter was 0.72 ± 0.12 cm. The degraded pasture plot used in this study was not planted with *C. microphylla* in 1985 and is adjacent to the silvopasture plot. The herbaceous plant species in the study plot included *Pennisetum flaccidum*, *Leymus secalinus*, *Setaria viridis*, *Lespedeza davurica*, *Astragalus melilotoides*, *Cynanchum komarovii*, *Salsola collina*, *Glycyrrhiza uralensis*, *Mulgedium tataricum*, and *Neopallasia petinata*.

2.2. Field sampling

In September 2010, fine roots (<2 mm in diameter) of *C. microphylla* and grasses in a silvopasture plot and an adjacent degraded pasture plot were sampled using an auger of 8.5 cm in diameter. In the silvopasture plot, sampling lines were established 1 m apart. Soil cores were collected at 0.75-m intervals along each line. A total of 4 soil cores were collected from each sampling line, and the cores were pooled in order to ensure a good representation of fine roots in each sample (Figure 1). A total of 88 soil cores were systematically taken to create 22 soil samples from the silvopasture in order to determine fine root biomass and fine root length. To evaluate the effects of *C. microphylla* on the belowground root distribution of grasses in the degraded pasture, the number of fine roots was quantified from a total of 66 soil cores that were randomly collected from the degraded pasture. The soil

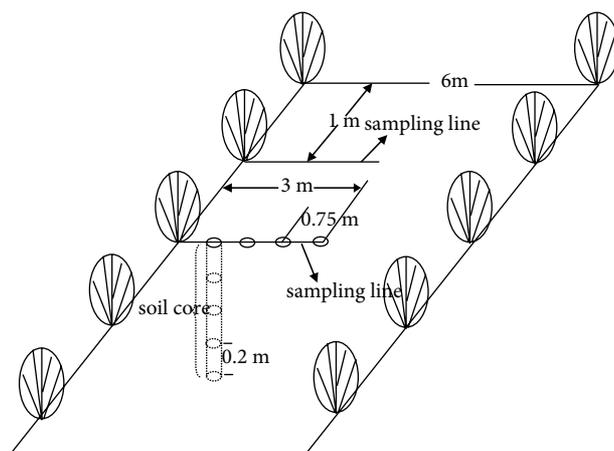


Figure 1. Sketch of sampling design.

cores were taken from 0–20, 20–40, 40–60, and 60–80 cm layers and were then sieved to <0.5 mm. All roots and root nodules were carefully picked out by hand and all sieved soils were stored in plastic basins according to soil layer. Root samples were kept in zip polythene bags to avoid dehydration and were stored in a cold room at –10 °C until processing.

2.3. Ingrowth core

In September 2010, after sampling soil cores, we prepared nylon mesh bags (80 cm in length and 8.5 cm in diameter; 2 mm mesh size). Each bag contained four 20-cm layers of root-free soil. Each layer was from the corresponding soil-core layer and was sieved and homogenized prior to being placed in the bag. Eighty-eight bags in the silvopasture and 66 bags in the degraded pasture were inserted into the holes created by soil-core sampling. These ingrowth core samples were harvested in September 2011. The ingrowth cores, removed using a special spade and divided using scissors, were sieved to <0.5 mm. All roots and root nodules were carefully picked out by hand. All root samples were kept in zip polythene bags according to different soil layers to avoid dehydration and were stored in a cold room at –10 °C until measurement.

2.4. Soil water content

To test the effects of soil water content on fine root production, soil volumetric water content was determined by the soil cutting ring method. Soil profiles were divided into four 20-cm layers. Between May and September 2011, soil samples were collected from each layer 3 times each month. Three subsamples of soil were collected from the middle of every 20-cm layer. Soil samples were quickly transported to the laboratory for further analysis. These soil samples were weighed, dried for 72 h at 105 °C, and reweighed (± 0.01 g). Mass water content was transformed into volumetric water content using the volume of the soil cutting ring.

2.5. Quantitative parameters and image analysis of fine roots

In the laboratory, all roots from zip bags were washed free of soil and separated into grass fine roots, *C. microphylla* living fine roots, and dead fine roots based on color and luster, elasticity, toughness, smell, and appearance of phloem (Brassard et al., 2013). The roots of *C. microphylla* that were greater than 2 mm in diameter were discarded. All fine roots were washed with distilled water and allowed to dry at room temperature for 24 h. Roots were scanned using an automatic threshold method at 300 dpi (Expression 10000XL, EPSON). The resulting images were used to determine root length (cm) and diameter (mm). Root images were analyzed using calibrated WinRHIZO image analysis software (Regent Instruments Inc., Canada). After scanning, all roots were dried at 70 °C for

72 h and weighed (± 0.001 g) to determine oven-dried fine root biomass.

2.6. Statistical analysis

Two-way analysis of variance (ANOVA) was used to test the effects of soil depth and plant species as well as interactions between these and fine root distribution. Multiple comparison and one-way ANOVA were used to compare differences in fine root parameters (biomass and length density) between soil layers, and t-tests were used to compare differences between layers in the density of *C. microphylla* and grass fine roots. Fine root variables (biomass and length density) at 4 depth intervals were compared using a 2-sample paired t-test. Regression analyses were used to investigate the relationship between root density and soil water. To test the 2-layer hypothesis in the study silvopasture system, we compared the observed data using vertical cumulative fractions of *C. microphylla* and grass fine root biomass density and fine root biomass production density in the both plots. Statistical analysis was carried out using SPSS 18.0 (SPSS Inc., USA).

3. Results

3.1. Soil volumetric water content

In the silvopasture, soil volumetric water content was higher in the 20–60 cm soil layer than in the 0–20 and 60–80 cm layers (Figure 2). Between May and September 2011, soil water was consistent in the 20–40 and 40–60 cm layers. Soil water was almost depleted in the 60–80 cm soil layer, and this layer formed a dry sand layer in the silvopasture.

3.2. Fine root distribution

Fine root biomass density (FRBD; biomass per unit area; g m^{-2} ; Figure 3a) and fine root length density (FRLD; length per unit soil volume; cm m^{-3} ; Figure 3b) varied between

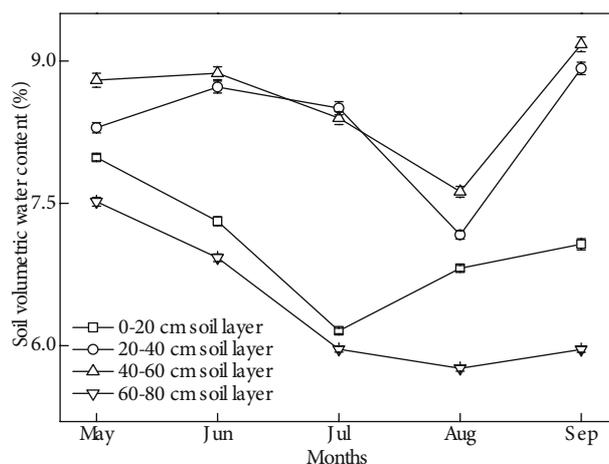


Figure 2. Seasonal variations in soil water content (mean \pm SD) in different soil layers in the silvopasture.

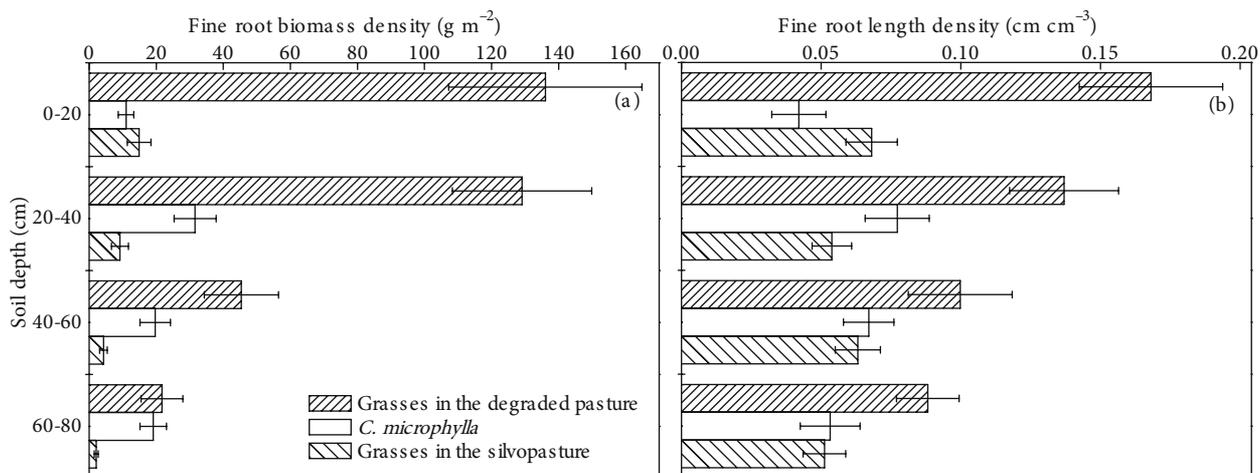


Figure 3. Vertical distribution of fine root biomass density (a) and fine root length density (b) in a degraded pasture and a silvopasture system (mean \pm SD). Each sample consisted of 1 soil core in the degraded pasture plot and 4 soil cores in the silvopasture system plot.

plots. Multiple comparison analysis showed that the fine roots of grasses in the degraded pasture were more abundantly distributed in the soil profile than all of the fine roots in the silvopasture ($P < 0.05$). Surprisingly, the FRBD of grasses in the degraded pasture was 332.3 g m^{-2} , 2.97 times the sum of grasses and *C. microphylla* in the silvopasture, whereas the FRLD was 0.13 cm m^{-3} , merely 1.14 times the sum of grasses and *C. microphylla* in the silvopasture. The biomass of *C. microphylla* fine roots and the *C. microphylla* FRLD were greater than those of grasses in the subsoil layers (20–80 cm) of the silvopasture; however, in the 0–20 cm soil layer, biomass of grass fine roots and FRLD were much greater than those of *C. microphylla* in the 0–20 cm soil layer (Figure 3). Grass fine root biomass in both plots sharply decreased with depth ($P < 0.05$), whereas *C. microphylla* fine root biomass peaked at a depth of 20–40 cm. Grass FRLD in the silvopasture tended to decrease with depth, but this decrease was not statistically significant (Figure 3b). Figure 4 shows that in both plots grass had similar fine root distributions. The top 40 cm of soil in the degraded pasture plot contained 79.8% of the grass fine root biomass, whereas that in the silvopasture contained 79.1% of the grass fine root biomass (Figure 4). The proportion of grass FRLD at the same soil layer was 61.9% and 57.2% in the degraded pasture and the silvopasture, respectively (Figure 3b). *C. microphylla* FRBD and FRLD were significantly related to soil water content, while the vertical variability of grass fine roots was negatively related to soil water content. Figure 4 shows that grass fine root distribution patterns were similar in both plots ($P < 0.05$) and grasses had more fine roots in the surface soil layer (0–20 cm) than *C. microphylla*.

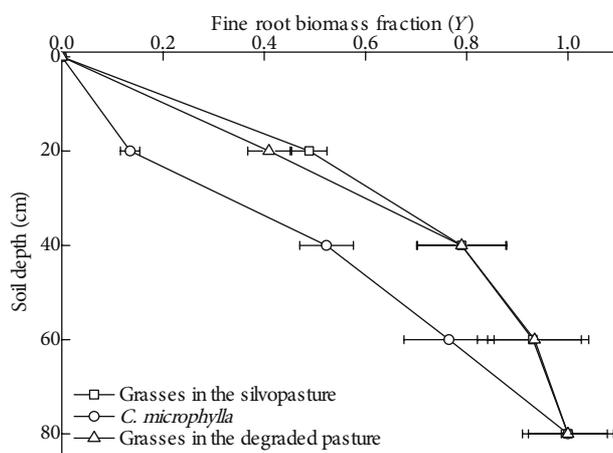


Figure 4. Depth distribution of fine root biomass fraction (Y) of grasses and *C. microphylla* in a silvopasture system and a degraded pasture.

3.3. Fine root production

Distinct differences in grass fine root biomass production density (FRBPD; biomass production per unit area; g m^{-2} ; Figure 5a) and fine root length production density (FRLPD; length per unit soil volume; cm cm^{-3} ; Figure 5b) were found between the degraded pasture and the silvopasture ($P < 0.05$). The FRBPD of *C. microphylla* and grass (0–80 cm layer) was 25.6 g m^{-2} and 51.3 g m^{-2} , respectively, in the silvopasture. In the degraded pasture, the FRBPD of grasses was 149.1 g m^{-2} . Fine root production of grasses in both plots decreased with soil depth. In the silvopasture, *C. microphylla* invested greatly in fine roots in the 20–60 cm soil layer, where FRBPD was similar between *C. microphylla* and grasses ($P < 0.05$) while the FRLPD of

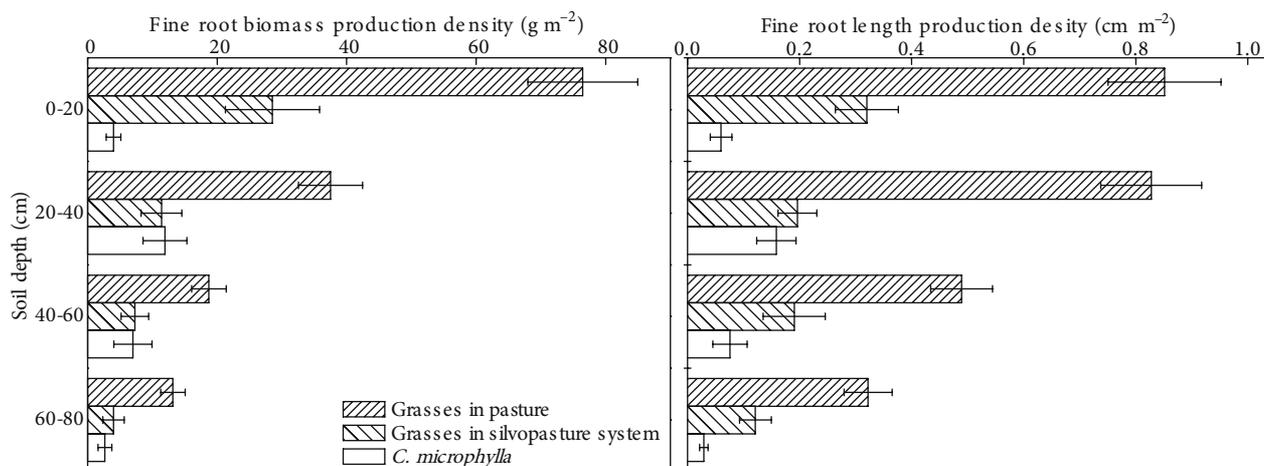


Figure 5. Vertical distribution of fine root biomass production density (a) and fine root length density (b) in a degraded pasture and a silvopasture system (mean \pm SD). Each sample consisted of 1 ingrowth core in the degraded pasture plot and 4 ingrowth cores in the silvopasture system plot.

grass was greater than that of *C. microphylla* ($P < 0.05$). In all soil layers, all fine root parameters were remarkably greater in the degraded pasture than in the silvopasture system (Figure 5). In both plots, grasses were prevalent in the top 40 cm of soils, which contained 77% of the fine root biomass (Figure 6).

4. Discussion

4.1. Fine root distribution and belowground interactions

We found that grass fine roots were significantly affected by the establishment of *C. microphylla* (Figure 3), whereas the grass fine root behaviors were not influenced by *C. microphylla* (Figure 4). This indicated that there was competition between grasses and *C. microphylla*. Other

studies (Eastham and Rose, 1990; Mordelet et al., 1997; Jurena and Archer, 2003) also indicated that grass roots systems are affected by the introduction of trees or shrubs. Eastham and Rose (1990) found that grass root density decreased with decreasing density of established *Eucalyptus grandis*. Mordelet et al. (1997) reported that although grass fine root phytomass distribution in open sites was less than half of that beneath tree canopies in a humid savanna, the grass rooting patterns were similar in both areas. Jurena and Archer (2003) showed that herbaceous root biomass was significantly decreased by the establishment of *Prosopis* seedlings.

We found that the fine roots of grass and *C. microphylla* had different vertical spatial patterns in the silvopasture (Figure 4). Grass fine roots were mostly distributed in the surface soil layer (0–20 cm), while *C. microphylla* fine roots occupied the deeper soil layer (20–60 cm). This pattern was particularly evident for root biomass (Figure 3a). Some researchers (Mordelet et al., 1997; Scholes, 1997; Ward et al., 2013) documented that trees or shrubs have different rooting patterns than grasses or herbs in mixed tree/shrub–grass systems. Such results correspond with other competition experiments on water partitioning between grasses and shrubs in the 2-layer hypothesis (Walter, 1971; Hipodonka et al., 2003; Ludwig et al., 2004b), which states that grasses acquire water and soil nutrients only from the upper soil layer, while woody vegetation has exclusive access to the deeper soil layer (Roux et al., 1995). This hypothesis has not been consistently supported (Roux et al., 1995; Mordelet et al., 1997; Reynolds et al., 2000, 2004). Schenk and Jackson (2002) found that there was no strict spatial partitioning of shrub and grass fine roots in the soil in ecosystems with summer or nonseasonal precipitation.

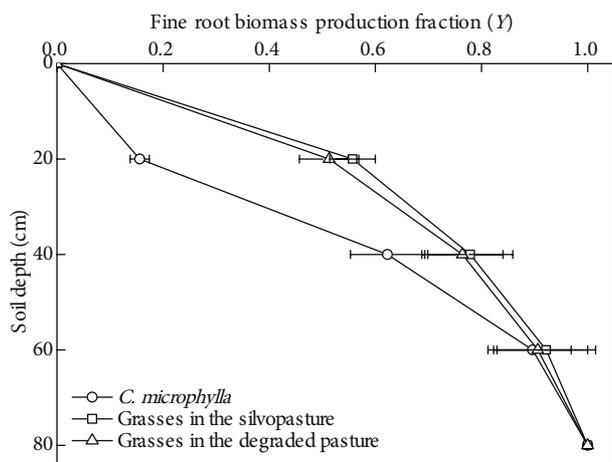


Figure 6. Depth distribution of fine root biomass production fraction (Y) of grasses and *C. microphylla* in a silvopasture system and a degraded pasture.

In our study, the spatial partitioning of *C. microphylla* and grass fine root length was not as distinct as the spatial partitioning of fine root biomass in the silvopasture. These results might be explained by a deeper rooting system in some herbaceous plants (i.e. perennials).

Scholes (1997) demonstrated that the fibrous root systems of grasses intensively exploit a relatively small proportion of the soil profile, whereas woody plants extensively exploit a larger volume. We found that, in deeper soil profiles, the FRLD of grasses was lower than that of *C. microphylla* and the fine root biomass of grasses was absolutely lower than that of *C. microphylla* in the silvopasture (Figure 3). The difference in root length between shrubs and grasses growing in the same soil volume can be used as an indicator of each plant type's proportional share of the soil resources and competitive power (Bowen, 1985). Grasses use the growth and length of fine roots to compete with trees for water and soil nutrient resources in the same soil volume. Therefore, root density tends to be more important for acquisition of belowground resources than the physiological characteristics of roots (Clarkson, 1985). Roots of established *C. microphylla* are densely branched in each soil layer. Grass seedlings must compete with *C. microphylla* for resources during their early development, especially in the upper horizon. This explains why grasses exploited water in the deeper soil patches by root elongation and why grass FRBD was lower than grass FRBPD in the silvopasture.

4.2. Fine root production and belowground interactions

Our root exclusion experiments demonstrated that the establishment of *C. microphylla* in the degraded pasture strikingly influenced grass fine root production (Figure 5). This confirms the importance of belowground competition between grasses and *C. microphylla* in our study sites. *C. microphylla* and grass had 2 clearly different forage strategies for soil resources through fine roots (Figure 6), which supported the 2-layer hypothesis. Our results confirmed some findings (Breshears and Barnes, 1999; Kambatuku et al., 2013) that woody plant and grass roots occupied different vertical niches for acquiring essential resources such as water and nutrients. By injecting denatured water into different soil depths, Kulmatiski et al. (2010) found that trees and grasses absorbed soil water from different soil layers. There are many studies in which the vertical resource partitioning or the 2-layer hypothesis was assessed based on root excavations and measurements of soil water or plant water potentials, soil water content, or stable isotope ratios (Ward et al., 2013). However, there are few based on root exclusion, which is a better method because grass and woody plant roots can occupy the same soil patches simultaneously. Our results also showed that the differences in fine root biomass and production between *C. microphylla* and grasses were

converse (Figures 3 and 5), indicating the effect of fine root competition between *C. microphylla* and grasses through root excavations and exclusion.

Experimental studies of competitions between trees and grasses in arid and semiarid regions have consistently indicated that root production is affected by root competition (Ludwig et al., 2004a; Rodríguez et al., 2007; Riginos, 2009). Fine root growth and the distribution of trees and grasses are directly related to the amount of resources available to them, especially in competitive situations (Wilcox et al., 2004; Schenk, 2006; Kalliokoski et al., 2010). All of these studies support Fowler's (1986) hypothesis that competition is a relatively frequent plant-plant interaction in arid and semiarid plant communities. Soil water availability is likely the main factor influencing changes in root growth strategies (Kätterer et al., 1995). This explains why *C. microphylla* roots mainly occupied the 20–60 cm soil layer, which had the highest soil water content (Figure 5). The intensity of belowground competition for water between shrubs and native grasses seems to depend on the level of resource availability in the soil profile. *C. microphylla* produced fewer fine roots in the periodically dry topsoil (0–20 cm) and subsoil layer (60–80 cm) than in the relatively moisture-rich layer (20–60 cm). Knoop and Walker (1985) suggested that tree roots predominantly grew in the subsoil because of periodically dry topsoil rather than because of competition with grasses. Competition may be a minor factor in seasons of low precipitation or in very dry soil layers (60–80 cm) because of limitation due to lack of water. Schwinning et al. (2002) found that *Artemisia filifolia* and *Coleogyne ramosissima* were not able to maintain active fine roots in the upper soil during some drought periods but did develop an opportunistic active shallow-fine root system after water pulses. Our results indicated that grass forage strategy was not changed by belowground competition caused by the establishment of *C. microphylla*.

Although most of the grass fine roots were concentrated in the top soil layer (0–40 cm) in the present study, some roots of herbaceous plants extended deeper into the subsoil layer in the silvopasture system (Figure 5b). In mixed tree-grass systems, some grasses may fully occupy a patch using a broad and uniform rooting distribution regardless of soil resource distribution. This is because nonperennial grasses would have to wait until the following year if they missed a growth season for proliferation (Schenk, 2006). Some plants may have both high root concentration in the topsoil and some roots in deeper soil layers. This root distribution may reduce their susceptibility to drought (Schroth, 1999). Scholes and Zech (1995) found that grass roots may be more abundant, in absolute terms, than tree roots to depths of up to 1 m. We also found that, in the

silvopasture, grass fine roots were more abundant in the deepest soil layer (60–80 cm) than those of *C. microphylla* due to pressure from the competition for the limited water in the study area. Studies conducted by Eissenstat (1992), Ryser and Lambers (1995), and Livesley et al. (2000) demonstrated that plants with small-diameter roots tend to have greater physiological capacity for resource uptake and greater ability to respond to changes in their resource environment than those with large-diameter roots. Some plants must allocate more photosynthates in order to acquire a limiting resource than similar plants would in the absence of competition (Craine, 2006). Therefore, plants with high FRLD are likely to be more competitive than plants with low FRLD (Schroth, 1999).

In this study, we confirmed that *C. microphylla* and indigenous grasses in the silvopasture underground compete for limited water. This competition was indicated by the influence of the establishment of *C. microphylla* on the belowground fine root production of the system. However, the vertical distribution patterns of grass fine roots were scarcely affected by established *C. microphylla*. The rooting behavior of grasses was the same

in both degraded pasture and silvopasture. The fine root distribution of *C. microphylla* was not vertically changed by competition with grasses, the roots of which mostly occupied the relatively wet middle soil layer. Although Walter's 2-layer model of soil depth partitioning appears appropriate for explaining the belowground interactions between *C. microphylla* and native grasses in sandy soil, the belowground productions of the system were greatly changed by the establishment of shrubs. Therefore, we suggest that, if introduced into degraded pastures, *C. microphylla* should be spaced farther apart than at present in order to reduce the belowground competition between *C. microphylla* and local grasses.

Acknowledgments

This research was supported by the National Key Technology Research and Development Program of China for the 12th Five-Year Plan (2012BAD16B02). We thank Huishu Shi, Yuming Zhang, Jinhong Zhao, Xuewu Yang, and other staff of the research station for their help with sampling in the field. We appreciate Graham Forbes' editing of this paper.

References

- Bartelheimer M, Steinlein T, Beyschlag W (2006). Aggregative root placement: a feature during interspecific competition in inland sand-dune habitats. *Plant Soil* 280: 101–114.
- Bowen GD (1985). Roots as a component of tree productivity. In: Cannell MGR, Jackson JE, editors. *Attributes of Trees as Crop Plants*. Huntingdon, UK: Institute of Terrestrial Ecology, pp. 303–315.
- Brassard B, Chen HYH, Cavard X, Laganière J, Reich PB, Bergeron Y, Paré D, Yuan Z (2013). Tree species diversity increases fine root productivity through increased soil volume filling. *J Ecol* 101: 210–219.
- Breshears DD, Barnes FJ (1999). Interrelationships between plant functional types and soil moisture heterogeneity for semiarid landscapes within the grassland/forest continuum: a unified conceptual model. *Landsc Ecol* 14: 465–478.
- Caldwell MM, Dawson TE, Richards JH (1998). Hydraulic lift: consequences of water efflux for the roots of plants. *Oecologia* 113: 151–161.
- Cao CY, Jiang DM, Teng XH, Jiang Y, Liang WJ, Cui ZB (2008). Soil chemical and microbiological properties along a chronosequence of *Caragana microphylla* Lam. plantations in the Horqin sandy land of Northeast China. *Appl Soil Ecol* 40: 78–85.
- Clarkson DT (1985). Factors affecting mineral nutrient acquisition by plants. *Ann Rev Plant Physiol* 36: 77–115.
- Craine JM (2006). Competition for nutrients and optimal root allocation. *Plant Soil* 285: 171–185.
- Dawson LA, Duff EI, Campbell CD, Hirst DJ (2001). Depth distribution of cherry (*Prunus avium* L.) tree roots as influenced by grass root competition. *Plant Soil* 231: 11–19.
- Eastham J, Rose CW (1990). Tree/pasture interactions at a range of tree densities in an agroforestry experiment. I. Rooting patterns. *Aust J Agric Res* 41: 683–695.
- Eissenstat DM (1992). Costs and benefits of constructing roots of small diameter. *J Plant Nutr* 15: 763–782.
- Fernández ME, Gyenge JE, Schlichter TM (2006a). Growth of the grass *Festuca pallescens* in silvopastoral systems in a semi-arid environment, Part 1: positive balance between competition and facilitation. *Agroforest Syst* 66: 259–269.
- Fernández ME, Gyenge JE, Schlichter TM (2006b). Growth of the grass *Festuca pallescens* in silvopastoral systems in a semi-arid environment, Part 2: parameterization of models of stomatal conductance and leaf photosynthesis. *Agroforest Syst* 66: 271–280.
- Fowler NL (1986). The role of competition in plant communities in arid and semiarid regions. *Annu Rev Ecol Syst* 17: 89–110.
- Hipodonka MHT, Aranibar JN, Chirara C, Lihavha M, Macko SA (2003). Vertical distribution of grass and tree roots in arid ecosystems of Southern Africa: niche differentiation or competition? *J Arid Environ* 54: 319–325.
- Jurena PN, Archer S (2003). Woody plant establishment and spatial heterogeneity in grasslands. *Ecology* 84: 907–919.

- Kalliokoski T, Pennanen T, Nygren P, Sievänen R, Helmisaari HS (2010). Belowground interspecific competition in mixed boreal forests: fine root and ectomycorrhiza characteristics along stand developmental stage and soil fertility gradients. *Plant Soil* 330: 73–89.
- Kambatuku JR, Cramer MD, Ward D (2013). Overlap in soil water sources of savanna woody seedlings and grasses. *Ecohydrology* 6: 464–473.
- Kätterer T, Fabião A, Madeira M, Ribeiro C, Steen E (1995). Fine-root dynamics, soil moisture and soil carbon content in a *Eucalyptus globulus* plantation under different irrigation and fertilization regimes. *Forest Ecol Manag* 74: 1–12.
- Knoop WT, Walker BH (1985). Interactions of woody and herbaceous vegetation in a southern African savanna. *J Ecol* 73: 235–253.
- Kulmatiski A, Beard KH, Verweij RJT, February EC (2010). A depth-controlled technique measures vertical, horizontal and temporal patterns of water use by trees and grasses in a subtropical savanna. *New Phytol* 88: 199–209.
- Livesley SJ, Gregory PJ, Buresh RJ (2000). Competition in tree row agroforestry systems. 1. Distribution and dynamics of fine root length and biomass. *Plant Soil* 227: 149–161.
- Ludwig F, Dawson TE, De Kroon H, Berendse F, Prins HHT (2003). Hydraulic lift in *Acacia tortilis* trees on an East African savanna. *Oecologia* 134: 293–300.
- Ludwig F, Dawson TE, Prins HHT, Berendse F, Kroon HD (2004a). Below-ground competition between trees and grasses may overwhelm the facilitative effects of hydraulic lift. *Ecol Lett* 7: 623–631.
- Ludwig F, Kroon HD, Berendse F, Prins HHT (2004b). The influence of savanna trees on nutrient, water and light availability and the understory vegetation. *Plant Ecol* 170: 93–105.
- Mommer L, van Ruijven J, Jansen C, van de Steeg HM, de Kroon H (2012). Interactive effects of nutrient heterogeneity and competition: implications for root foraging theory? *Funct Ecol* 26: 66–73.
- Mordelet B, Menaut JC, Mariotti A (1997). Tree and grass rooting patterns in an African humid savanna. *J Veg Sci* 8: 65–70.
- Reynolds JF, Kemp PR, Ogle K, Fernandez RJ (2004). Modifying the 'pulse-reserve' paradigm for deserts of North America: precipitation pulses, soil water, and plant responses. *Oecologia* 141: 194–210.
- Reynolds JF, Kemp PR, Tenhunen JD (2000). Effects of long-term rainfall variability on evapotranspiration and soil water distribution in the Chihuahuan desert: a modeling analysis. *Plant Ecol* 150: 145–159.
- Reynolds JF, Smith DMS, Lambin EF, Turner BL 2nd, Mortimore M, Batterbury SPJ, Downing TE, Dowlatabadi H, Roberto JE, Herrick JE et al. (2007). Global desertification: building a science for dryland development. *Science* 316: 847–851.
- Ridenour WL, Callaway RM (2003). Root herbivores, pathogenic fungi, and competition between *Centaurea maculosa* and *Festuca idahoensis*. *Plant Ecol* 169: 161–170.
- Riginos C (2009). Grass competition suppresses savanna tree growth across multiple demographic stages. *Ecology* 90: 335–340.
- Rodríguez MV, Bertiller MB, Bisigato A (2007). Are fine roots of both shrubs and perennial grasses able to occupy the upper soil layer? A case study in the arid Patagonian Monte with non-seasonal precipitation. *Plant Soil* 300: 281–288.
- Roux XL, Bariac T, Mariotti A (1995). Spatial partitioning of the soil water resource between grass and shrub components in a West African humid savanna. *Oecologia* 104: 147–155.
- Ryser P, Lambers H (1995). Root and leaf attributes accounting for the performance of fast- and slow-growing grasses at different nutrient supply. *Plant Soil* 170: 251–265.
- Schenk HJ (2006). Root competition: beyond resource depletion. *J Ecol* 94: 725–739.
- Schenk HJ, Jackson RB (2002). Rooting depths, lateral root spreads and belowground/aboveground allometries of plants in water-limited ecosystems. *J Ecol* 90: 480–494.
- Scholes RJ (1997). Tree-grass interactions in savannas. *Annu Rev Ecol Syst* 28: 517–544.
- Schroth G (1999). A review of belowground interactions in agroforestry focusing on mechanisms and management options. *Agroforest Syst* 43: 5–34.
- Schroth G, Zech W (1995). Root length dynamics in agroforestry with *Gliricidia sepium* as compared to sole cropping in the semi-deciduous rainforest of West Africa. *Plant Soil* 170: 297–306.
- Schwinning S, Davis K, Richardson L, Ehleringer JR (2002). Deuterium enriched irrigation indicates different forms of rain use in shrub/grass species of the Colorado Plateau. *Oecologia* 130: 345–355.
- Segarra J, Acevedo M, Raventós J, García-Núñez C, Silva JF (2009). Coupling soil water and shoot dynamics in three grass species: a spatial stochastic model on water competition in Neotropical savanna. *Ecol Model* 220: 2734–2743.
- Ward D, Wiegand K, Getzin S (2013). Walter's two-layer hypothesis revisited: back to the roots! *Oecologia* 172: 617–630.
- Walter H (1939). Grasland, Savanne und Busch der arideren Teile Afrikas in ihrer ökologischen Bedingtheit. *Jahrb Wiss Bot* 87: 750–860 (in German).
- Walter H (1971). *Ecology of Tropical and Subtropical Vegetation*. Edinburgh, UK: Oliver & Boyd.
- Wilcox CS, Ferguson JW, Fernandez GCJ, Nowak RS (2004). Fine root growth dynamics of four Mojave Desert shrubs as related to soil moisture and microsite. *J Arid Environ* 56: 129–148.
- Zhang YG, Xu ZW, Jiang DM, Jiang Y (2013). Soil exchangeable base cations along a chronosequence of *Caragana microphylla* plantation in a semi-arid sandy land, China. *J Arid Land* 5: 42–50.