Introducing a shrub species in a degraded steppe shifts fine root dynamics and soil organic carbon accumulations, in northwest China

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ABSTRACT

In the semiarid and arid regions of China, the introduction of shrubs into degraded steppe is generally considered a crucial tool to facilitate vegetation restoration and reduce desertification. However, the resultant changes in root dynamics, plant composition and soil carbon have not been completely evaluated, casting doubt on the ecological viability of this method. In this study, the fine root dynamics and soil organic carbon (SOC) of two land-use types, *Caragana microphylla* shrubland (CM-shrubland) and a natural restoration steppe (NR-steppe) in northwest China were compared. Fine root biomass and production of CM-shrubland were lower by 65.7% and 43.9%, respectively, than those in the NR-steppe, in soil depths down to 80 cm. Herbaceous fine roots in the CM-shrubland had the fastest turnover and decomposition rates, followed by herbaceous plants in the NR-steppe, and then by *C. microphylla*. Differences in SOC stocks between land-use types (including a decrease in the shrubland compared to the steppe) were reflected in the heavy fraction of SOC storage in the subsoil layer (60–80 cm), rather than in total and heavy fraction of SOC in the top soil layer (0–60 cm). Surprisingly, the light fraction of SOC increased slightly (8.7%) after *C. microphylla* introduction. Thus, changes in fine root dynamics contributed to differences in SOC and its fractions between the CM-shrubland and NR-steppe. These patterns suggest that, in terms of soil C sequestration, shrub restoration might not be an effective choice for land degradation control. Instead, a moderately protected steppe is a better approach for ecological restoration.

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1. Introduction

Despite efforts to control land desertification and degradation, 27.2% of land area of China still suffered from desertification. In northwest China, desertified steppes are the most common landscape (Wang et al., 2014; Zhang et al., 2014), constituting the regional vegetation of arid and semiarid regions (Niu et al., 2008). Introducing trees or shrubs into these degraded steppes is the primary approach currently used to reverse this trend of land degradation. The introduction of some leguminous shrubs has been favoured due to their adaptability to harsh environments and ability to fix nitrogen (N) (Lal, 2004). *Caragana microphylla*, for example,

has been widely planted (approximately $1.33 \times 10^6 \, \text{hm}^2$) in northwest China during the past few decades, to prevent wind erosion and restore the degraded steppe (Cao et al., 2008; Zhang et al., 2006). However, it is unclear if this type of land conversion is the most ecologically appropriate option for vegetation restoration in these areas.

Introducing woody plants usually changes herbaceous species composition (Buscardo et al., 2008). In grasslands, shrub introduction increases interspecific competition (Ludwig et al., 2004; Schenk, 2006), which then influences the patterns of plant litter and the amounts of carbon (C) added to the soil (Peichl et al., 2012). As the litter of herbaceous plants differs from that of shrubs in quantity and chemistry (Liao et al., 2014), the introduction of one group or the other affects nutrient cycling (Chapin et al., 2000) and soil microbial properties, such as biomass and activity (Zhou et al., 2012).

Fine roots (<2 mm) are an ephemeral part of root systems and have a high turnover rate (Jackson et al., 1997; Leppälammi-Kujansuu et al., 2014; Yuan and Chen, 2012; Wang et al., 2016), which makes them vulnerable to land-use changes (Upson and

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Burgess, 2013). The development of shrub root systems can lead to changes in fine root biomass and distribution, influencing the belowground competition between shrubs and herbaceous plants. Several studies have shown that fine roots are strongly affected by grassland afforestation (Peichl et al., 2012; Upson and Burgess, 2013; Zhou et al., 2012). In a mixed ecosystem, the shallow-root systems of herbaceous plants absorb the erratic and discontinuous water from upper soil profiles, whereas the deep-root systems of shrubs use the stable water resources located in deeper soil profiles (Ward et al., 2013). Studies evaluating belowground competition showed that mixed systems contain more herbaceous plants with fine roots in surface soil layers than pure grasslands (Ludwig et al., 2004; Schenk, 2006). Root biomass input via the extensive fine root systems of herbaceous plants is considered a major contributor of organic matter and nutrients in mixed ecosystems (Peichl et al., 2012).

A meta-analysis on 70 litter-manipulation experiments showed that aboveground litter affected soil organic C (SOC) accumulation in the top 10 cm of soil, and that dry ecosystems might show lower sensitivity to changes in litter inputs than other ecosystems (Xu et al., 2013). Limited soil resources in dryland ecosystems may cause plants to allocate more C toward root systems (Clark et al., 2010), producing a denser fine root network (Loiola et al., 2016). Although this increased fine root network could explain the low sensitivity to litter input changes observed in semiarid and arid regions, data on the effects of root systems on SOC are still scarce.

Land conversion also influences the cycles and stocks of soil C (Peichl et al., 2012; Wang et al., 2016). In semi-arid steppes, grassland afforestation is often accompanied by increased rates of C cycling (Zhou et al., 2012), and dryland soils have also shown great potential for SOC sequestration associated to changes in land-use and management (Lal, 2004). Tree or shrub plantations biomasses can accumulate considerable amounts of C (Strand et al., 2008), and some studies documented SOC increments in the top soil layers when grasslands or pastures were replaced by shrublands (Wheeler et al., 2007). In contrast, other studies showed that converting grasslands or steppes to woody plantations failed to change or decreased SOC storage (Wei et al., 2009; Zhou et al., 2012).

Overall, several studies have independently evaluated changes in the ecological and biochemical characteristics of fine roots or in SOC change due to shrub introduction (Guo et al., 2007; Lai et al., 2014). However, studies considering only fine root dynamics and their effects on SOC are not sufficient to completely evaluate the ecological effects of such changes in dry ecosystems. In order to approach such an evaluation, based on steppe and shrubland converted sites, the present study examined (1) fine root biomass distribution, lifetime, turnover rate, and decomposition following the conversion from steppe to shrubland; (2) changes in SOC stock and fraction after this land-use change; and (3) the effects of shrub and herbaceous fine root dynamics on SOC accumulation.

2. Methods and materials

2.1. Study site

The study site was located on the southern edge of the Mu Us desert, northwest China (37°04′ N–38°10′ N, 106°30′ E–107°41′ E; 1400–1800 m above sea level). This region experiences a semiarid continental climate, with an average annual temperature of 8.1 °C and an average frost-free period of 156 days (Jia et al., 2014). The mean annual precipitation is 287 mm, and 62% of the rainfall occurs between July and September (Liu et al., 2015). The potential mean annual evaporation exceeds 2000 mm. Soils in this region are classified as calciorthids, and the site is relatively flat with a slope of 1.2–2.0°. Since the 1980s, C. microphylla has been widely planted in

degraded steppes of northwest China to prevent soil erosion, using an alley cropping system (Lai et al., 2014; Zhang et al., 2006). The C. microphylla plantation (CM-shrubland) and neighbouring degraded steppe (natural restoration steppe, or NR-steppe) evaluated in the present study were fenced to exclude grazing and enable ecological restoration after planting. The physicochemical properties of the different soil layers in the NR-steppe and the CM-shrubland are shown in Table A.1. The dominant native grasses and forbs in the NR-steppe were Pennisetum centrasiaticum, Thermopsis shischkinii, Sophora alopecuroides, and Astragalus melilotoides, whereas CM-shrubland was co-dominated by Lespedeza davurica, Setaria viridis, and Artemisia scoparia (Table A.2). In the NR-steppe, the average plant height and cover were about 23.4 cm and 80%, respectively. In the CM-shrubland, C. microphylla mean density, height, and ground cover were 334 clusters ha^{-1}, 158.4 cm, and 8.4%, respectively; the average plant height and cover between C. microphylla belts were 12.4 cm and 40% (Table A.3).

The C. microphylla plantation and neighbouring NR-steppe had the same soil type and were both unfertilized. The two plots (50 × 50 m), one from each land-use type, selected for the present assessment had similar micro-physiographic features to enable comparisons of fine root dynamics and SOC accumulation.

2.2. Fine root distribution and production

To determine fine root biomass, soils were sampled during September 2011, after the wet season (July–September), using a cylindrical metal corer with a sharpened edge (diameter: 8.5 cm; height: 20 cm). In the CM-shrubland, four soil cores were taken at four perpendicular distances from the shrub row (1, 2, 3, and 4 m), and pooled into a composite sample (for method details, see Lai et al., 2014). Each 80-cm soil sample consisted of four soil cores taken at: 0–20, 20–40, 40–60, and 60–80 cm. Eighty-eight soil cores were collected in the CM-shrubland, providing 22 composite root samples per sampling depth. In the NR-steppe plot, 88 soil cores were randomly obtained (separated by 4–5 m) at the same depth ranges as CM-shrubland samples, and pooled into 22 composite samples per depth. All composite soil samples were sieved three times using 2-, 1-, and 0.5-mm meshes. After sieving, roots and root fragments were extracted with forceps and placed in a ziplock bag, which was kept on ice and immediately transported to laboratory for further analysis. In the lab, debris and attached soil particles were removed from the roots, which were cleaned with deionized water. Roots larger than 2 mm in diameter were discarded. In CM-shrubland root samples, roots of herbaceous plants and C. microphylla were separated based on their colour. To determine the biomass of dead fine roots, living and dead C. microphylla fine roots were separated based on colour, consistency, and smell (Brassard et al., 2011; Gwenzi et al., 2011). To distinguish the roots of different herbaceous plants, specimens of all herbaceous plants present in the plots were collected, classified, and labelled. In the lab, annual and perennial herbaceous plant roots were classified based on these root specimens.

After removing the roots, sieved soils were immediately transferred to nylon mesh bags (length: 80 cm; diameter: 8.5 cm; pore size: 0.5 mm), which were placed back at their corresponding sampling site and depth level. In September 2012, these 176 ingrowth cores (4 × 22 in CM-shrubland + 4 × 22 in NR-steppe) were collected and divided according to their soil depth: 0–20, 20–40, 40–60, and 60–80 cm. The subsequent handling and processing of the soil cores and roots were identical to that described for the original samples taken in September 2011.

To determine fine root dry mass, all fine roots were washed with deionized water, packed in paper bags, oven-dried for 72 h at 70 °C (Sariyildiz, 2015; Zewdie et al., 2008), and weighed. Fine root biomass density (FRBD, g m^{-2}) and fine root production
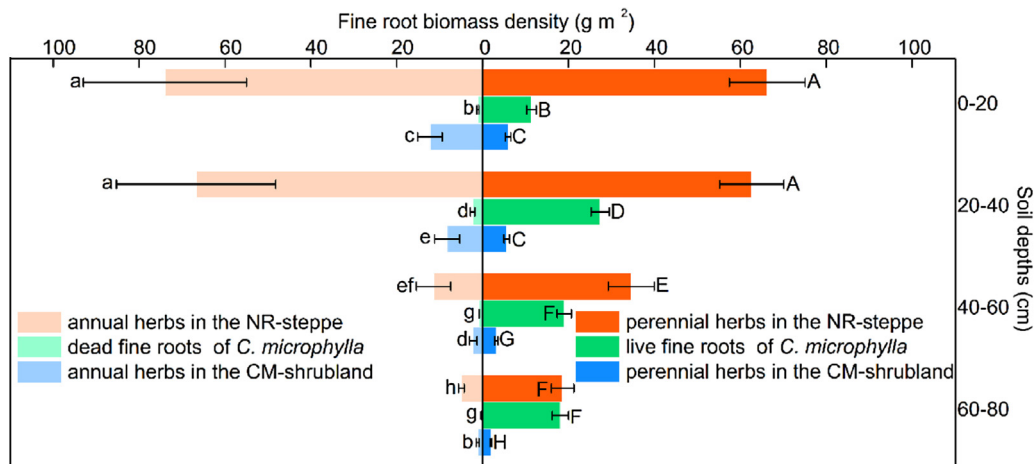
Fig. 1. Spatial distribution of fine root biomass in perennial herbs and *Caragana microphylla* (**right**), and in annual herbs and dead *C. microphylla* fine roots (**left**). Bars indicate the standard errors of the mean (*n* = 22). Bars with the same (upper- or lowercase) letter indicate a non-significant difference (*p* > 0.05).

biomass density (FRPBD, g m^{-2}) were computed by dividing fine root biomass (FRB) in the original samples and fine root biomass in ingrowth cores (FRPB) by the cross sectional area of soil cores (S), respectively.

2.3. Minirhizotron imaging of fine root turnover

In September 2011, three randomly selected *C. microphylla* clusters from the CM-shrubland and three locations from the NR-steppe were installed within a transparent acrylic tube (internal diameter: 5.08 cm; length: 100 cm), at a 45° angle from the soil surface. Seven months after installation, when the soil around the tubes became stable, a root scanner (CI-600 Root Scanner, CID Bio-Science, Inc., Camas, WA, USA) was inserted into the tubes to obtain digital images of fine root growth, at 10–20-d intervals from April 18, 2012 to September 28, 2013, excluding the frost period (early October to late April). The 312 captured images (width: 19.56 cm, length: 21.59 cm; 1.84 MB, 100 dpi) were used to analyse fine root turnover rates in WinRHIZOTron (Regent Instruments, Quebec, Canada). Black and wrinkled roots, or roots not appearing in subsequent viewings, were considered dead (Leppälammi-Kujansuu et al., 2014).

Based on the minirhizotron data, fine root turnover rate (TR; yr^{-1}) was calculated by dividing the annual fine root length pro-

duction (FRLP; cm cm^{-2} window area yr^{-1}) by average fine root length (cm cm^{-2}) (Guo et al., 2007).

2.4. Fine root decomposition

A 30 × 30 m plot was arbitrarily established near the research site in spring 2012. Fine root samples of *C. microphylla* and herbaceous plants were collected from six trenches near the soil sampling plots (three in the CM-shrubland and three in the NR-steppe; 0.5 m width × 1 m length × 0.4 m depth) in early March 2012. The sampled roots were placed on ice in a portable insulation can, immediately transported to the lab. After removing mineral soil particles with deionized water, fine roots were separated from coarse roots, sorted into >2-cm fractions, and dried at 70 °C to a constant weight (Sariyildiz, 2015; Zewdie et al., 2008). Dried fine roots were placed in 225 litterbags each containing *C. microphylla* root litter, herbaceous root litter from the CM-shrubland, or herbaceous fine root litter from the NR-steppe (three litter types × five replicates × 15 collection times; 10 × 10 cm; pore size: 0.5 μm). Each bag containing 5 g fine root litter was buried at 30 cm depth in the 30 × 30 m plot. Litterbags were harvested once a month during two growth periods: April 28 to October 28, 2012 and March 28 to October 28, 2013. Collected litterbags were immediately transported to the lab and the fine roots grown around litterbags were
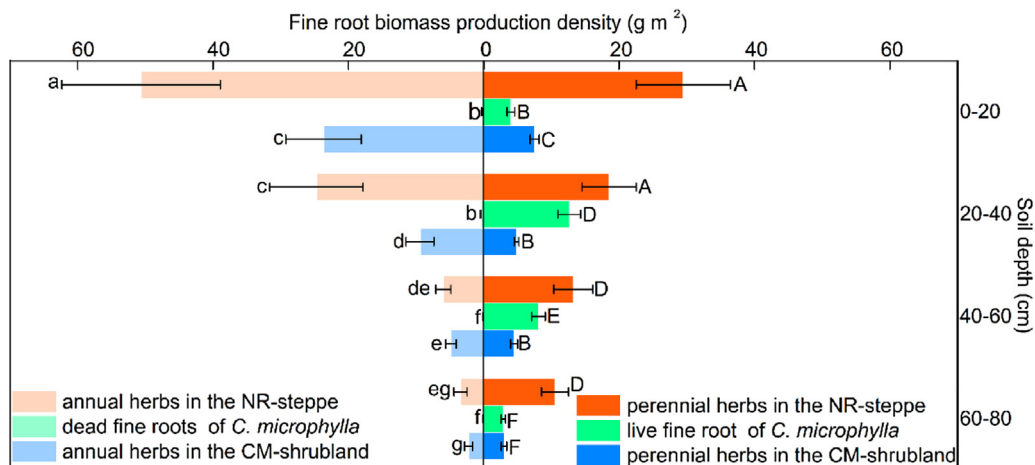

Fig. 2. Vertical distribution of fine root production in perennial herbs and *Caragana microphylla* (**right**) and in annual herbs and dead *C. microphylla* fine roots (**left**). Bars indicate the standard errors of the mean (*n* = 22). Bars with the same (upper- or lowercase) letter indicate a non-significant difference (*p* > 0.05).

gently removed. Fine root litter samples were cleaned of soil particles, dried for 72 h at 70 °C, and weighed (Sariyildiz, 2015; Zewdie et al., 2008). Fine root decomposition rates (mass recovery in%) were calculated using the average amount of dry mass calculated from five replications. In addition, the fine root decomposition rate (*k-value*) was estimated by fitting the exponential decay model $Y_t = b_0 e^{-kt}$ (Olson, 1963), where Y_t is the remaining fine root dry mass at time t (%), b_0 is the coefficient, k is the fine root decay rate (kg kg^{-1} month^{-1}), and t is the time (months).

2.5. Soil sampling and analysis

During root sampling, all soils from different layers were sieved to collect roots and the four soil samples were pooled into a composite sample, yielding 176 soil samples from the two land-use types (see 2.2.). Soil bulk density was determined at the time of sampling. All soil samples were air-dried at room temperature, finely ground, and then sieved (0.1 mm).

SOC was determined following Liu et al. (2014). Air-dried bulk soil comprising aggregates <2 mm diameter was separated into light and heavy fractions. 10 g of soil was suspended in 50 ml NaI solution (density 1.8 g cm^{-1}) for 10 min, before centrifuging for 1 h. The supernatant was decanted in vacuum using nylon filter paper (pore diameter: 0.45 μm), dried, and sieved as described in the previous paragraph. The residue on the second filter paper represented the light fraction of SOC (LF-SOC). It was washed off with CaCl$_2$ (0.01 mol L^{-1}) and distilled water into a vial, and oven-dried at 60 °C for 72 h to constant weight (Walkley and Black, 1934; Zhang et al., 2014). The soil residue left in the centrifuge tube was extracted with NaI, washed, oven-dried to constant weight, and weighed; it was then mixed with the sample on the filter paper. The LF-SOC residue was ground, sieved through a <0.075-mm mesh, and analysed for SOC concentration (%) using an Elemental CHNS analyser (Vario EL III, Elementar Analyser systeme, GmbH, Hanau, Germany). The heavy fraction of SOC (HF-SOC) and total SOC were determined by the K$_2$Cr$_2$O$_7$-H$_2$SO$_4$ oxidation method (Walkley and Black, 1934)

2.6. Statistical analysis

The effects of land-use type, soil layer, and fine root parameters (including biomass, production, length, and necromass [from minirhizotrons and destructive samplings]) on SOC were analysed using a repeated-measures one-way analysis of variance (rmANOVA), followed by a least-significant difference (LSD) test. A two-way ANOVA accompanied by Holm's test was used to examine the effects of land-use type, soil layer, and their interaction on fine root parameters, SOC, and SOC fractions. Differences among means values were evaluated using the LSD test, and significance was set at $p < 0.05$.

3. Results

3.1. Spatial distribution of fine root biomass and production

Fine root biomass and production density differed significantly between CM-shrubland and NR-steppe.

Fine-root biomass density in the NR-steppe was 339.2 g m^{-2}, split into 157.2 and 182.0 g m^{-2} for annual and perennial herbs, respectively (Fig. 1). Additionally, annual herbs exhibited higher fine root concentrations than perennial herbs in the topsoil layer (0–40 cm), whereas this pattern was reversed in the subsoil layer (40–80 cm). The topsoil contained 89.5% and 70.8% of the annual and perennial herbs fine root biomass, respectively.

In the CM-shrubland, *C. microphylla* fine root biomass and necromass were 75.8 and 4.7 g m^{-2}, respectively, accounting for 62.5% and 3.9% of the total fine root biomass. The fine root biomass of
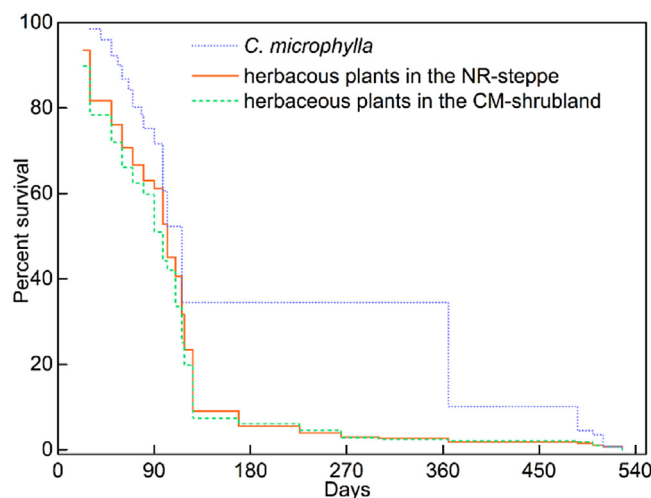

Fig. 3. Fine root survival curves of *Caragana microphylla* (*n* = 886) and in herbaceous plants in the CM-shrubland (*n* = 1622) and NR-steppe (*n* = 2320).

annual herbs (24.1 g m^{-2}) accounted for 59.1% of the total herbaceous fine root biomass. Annual herbs had more fine roots in the topsoil (85.7% of their total fine root biomass) than *C. microphylla* (51.1%) or perennial herbs (69.4%). In addition, 74.7% of dead fine roots occurred in the topsoil.

Taken together, CM-shrubland and NR-steppe data indicated a continuous decrease of herbaceous fine root biomass with increasing soil depth.

The overall fine root production in the NR-steppe was 1.8 times higher than in the CM-shrubland (*C. microphylla* and herbaceous plants included; Fig. 2). Herbaceous fine root production in the NR-steppe was 156.7 g m^{-2} yr^{-1}, or 78.8% of the total fine root production. For annual and perennial herbs, 88.9% and 66.8% of fine root production occurred in the topsoil, respectively. In the CM-shrubland, herbaceous plants exhibited 60.2 g m^{-2} yr^{-1} fine root production (40.3 and 19.9 g m^{-2} yr^{-1} for annual and perennial herbs, respectively), accounting for 67.7% of total fine root production. Annual herbs tended to have higher fine root production in the topsoil (82.2% of the total annual fine root production) than *C. microphylla* (62.2%) and perennial herbs (60.2%).

3.2. Fine root longevity and turnover rate

During the monitoring period, 2320 herbaceous root segments were observed in the NR-steppe, while 1622 and 886 fine root segments of herbaceous plants and *C. microphylla*, respectively, were observed in the CM-shrubland. Fine root longevity varied among plant groups (Fig. 3). Herbaceous plants and *C. microphylla* displayed similar root growth patterns throughout the growing season, with a peak during summer, corresponding to root emergence. Median longevity was 98 d for herbaceous plants in the CM-shrubland, 102 d for herbaceous plants in the NR-steppe, and 116 d for *C. microphylla* (Table 1). Consequently, fine root turnover rates ranged from 1.08 to 2.70 year^{-1} (Fig. 4), with *C. microphylla* fine roots exhibiting the slowest turnover rate among plants present in both plots.

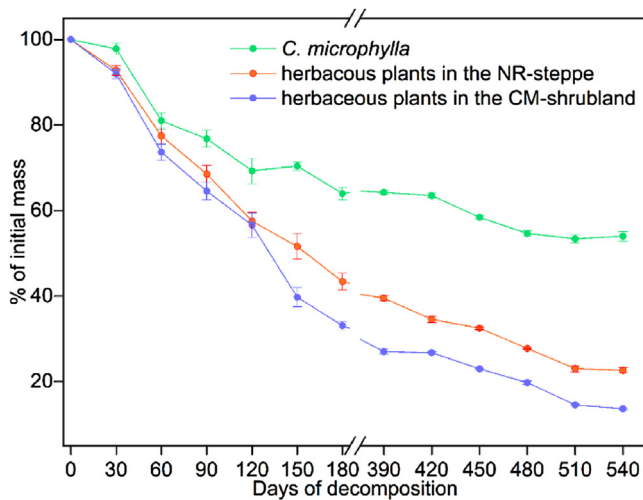### 3.3. Fine root decomposition

Although fine root decay rates varied dramatically across root types, all fine roots experienced faster mass loss in the first year and slower mass loss in the second year (Fig. 5). In the first year, about 57% and 67% of the total herbaceous fine root litters in the CM-shrubland and NR-steppe were lost, respectively; *C. microphylla*

Table 1
Fine root lifespan (days) of *Caragana microphylla* and herbaceous plants in both plots, based on Kaplan–Meier analyses, n = number of fine root segments.

Species	n	Mean	Error	Median	Error
Caragana microphylla	886	197.6	5.2	116	1.1
Herbaceous plants in shrubland	1622	98.7	2.0	98	1.4
Herbaceous plants in the degraded pasture	2320	103.1	1.6	102	1.0

Table 2
Olson exponential regression equations for fine root decomposition rates in herbaceous plants and *Caragana microphylla*.

Species	Model function	R^2	k (month^{-1})	Observed value of y_{18}	Theoretical value of y_{18}	$T_{50\%}$ (month)	$T_{95\%}$ (month)
Caragana microphylla	$y = 87.44e^{-0.028x}$	0.811	0.028	54.00	52.82	20.0	102.2
Herbaceous plants in the NR-steppe	$y = 86.87e^{-0.071x}$	0.924	0.071	24.20	22.65	7.8	40.2
Herbaceous plants in the CM-shrubland	$y = 85.75e^{-0.095x}$	0.924	0.095	15.51	13.65	5.7	29.9

Note: y_{18} is the fine root dry mass remaining (%) in the first 18 months; $T_{50\%}$ is the time required for 50% mass loss; $T_{95\%}$ is the time required for 95% mass loss.
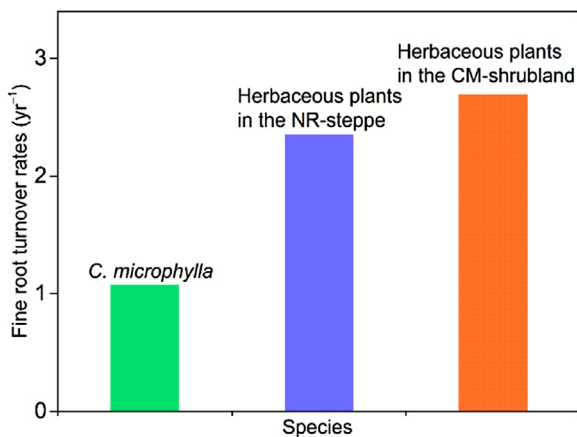
Fig. 4. Fine root turnover rates of *Caragana microphylla* and herbaceous plants in the CM-shrubland and NR-steppe.

Fig. 5. Fine root dry mass remaining (%) for *Caragana microphylla* and herbaceous plants in the CM-shrubland and NR-steppe during two years of decomposition. Bars are the standard errors of the mean (*n* = 5). The break on the x-axis represents frost periods.

fine root litter decayed by only 34%. After the 540-d decomposition period, herbaceous fine roots in the CM-shrubland decomposed significantly faster (86% mass loss) than *C. microphylla* fine roots (46%; p < 0.001) and herbaceous fine roots in the NR-steppe (77%; p < 0.01), on average. The mass loss pattern shown in all fine-root decomposition data was characterized using Olson's decay model (a negative exponential equation) (Table 2). The average

decomposition rate constant (k) of herbaceous fine root litter (CM-shrubland: 0.095 month^{-1}; NR-steppe: 0.071 month^{-1}) was higher than in *C. microphylla* (k = 0.028 month^{-1}). Therefore, herbaceous fine root litter in the CM-shrubland reached a 95% mass loss significantly faster (2.5 years) than in the NR-steppe (3.3 years), or *C. microphylla* fine roots (8.5 years).

3.4. Spatial distribution of total SOC and SOC fractions

Total SOC and HF-SOC did not significantly differ among land-use plots or soil depths, except in the 60–80 cm soil layer, where total SOC and HF-SOC levels in the NR-steppe were significantly higher than in the CM-shrubland (Fig. 6). Total SOC and SOC fractions did not exhibit distinct spatial patterns, although LF-SOC tended to decrease with increasing depth. The 0–20 and 40–60 cm soil layers exhibited slightly higher LF-SOC in the CM-shrubland than in the NR-steppe. Additionally, the 60–80 cm soil layer had significantly higher HF-SOC in the NR-steppe (52.6%) than in the CM-shrubland.

4. Discussion

4.1. Fine root dynamics in the *C. microphylla* shrubland and degraded steppe

Fine root biomass and production were both higher in the NR-steppe than in the CM-shrubland (Figs. 1 and 2). Mixed stands, such as the plots examined in this study, seem to have higher fine root biomass and productivity rates than monoculture stands (Brassard et al., 2011). This positive outcome of mixed stands is attributed to contrasting but complementary root traits in species assemblages (Brassard et al., 2011) or to the resultant root system plasticity, which allows the full use of soil space (Rolo and Moreno, 2012). Furthermore, root systems can continuously adjust to changes in soil conditions and to the introduction of new species (Ward et al., 2013). Overall, herbaceous fine roots occupy more surface soil layers than woody vegetation roots (Jackson et al., 1997), although the latter exhibit a relatively higher ability to explore belowground soil resources (Pinno and Wilson, 2013). Despite these characteristics, fine-root biomass decreased after converting the degraded steppe to a *C. microphylla* plantation (Fig. 1), in agreement with that found in previous studies (Guo et al., 2008; Peichl et al., 2012), where the introduction of shrubs and trees in dry areas significantly reduced fine root biomass and production (Guo et al., 2007; Pinno and Wilson, 2013). For example, fine root biomass was reduced by 26% in a 16-year old *Pinus radiata* plantation that replaced a pasture (Guo et al., 2007). Increases in interspecific competition intensity might explain these negative changes (Ward et al., 2013).

Herbaceous fine root biomass and production decreased with increasing soil depth (Figs. 1 and 2), but their vertical
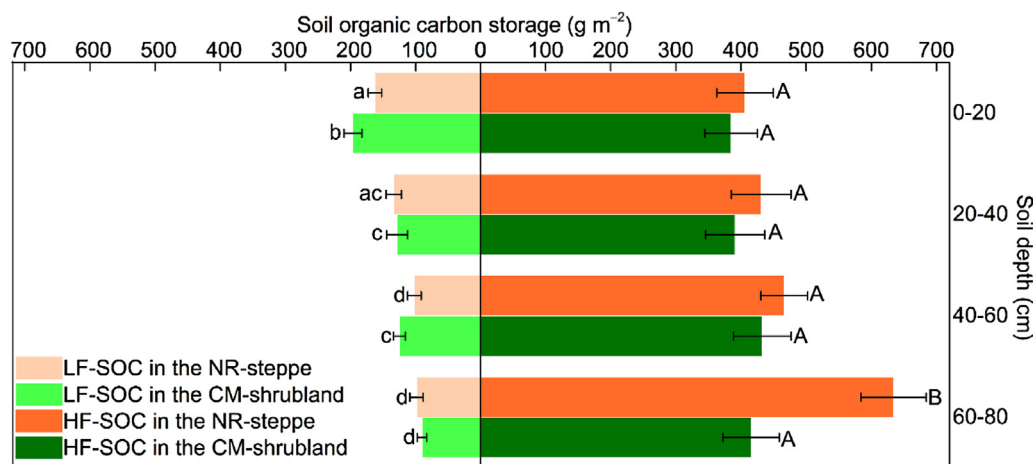
Fig. 6. Spatial distribution of soil organic carbon (SOC) high fraction (HF; **right**) and low fraction (LF; **left**) in CM-shrubland and NR-steppe. Bars indicate the standard errors of the mean ($n = 22$). Bars with the same (upper- or lowercase) letter indicate a non-significant difference ($p > 0.05$).

distribution patterns were similar in both land-use plots. This contradicts a previous study showing that herbaceous root distribution patterns were markedly modified by the presence of shrubs (*Retama sphaerocarpa* and *Cistus ladanifer*) (Pinno and Wilson, 2013). Indeed, herbaceous species usually avoid competition with neighbouring woody species, either by occupying more resource-poor patches (Kambatuku et al., 2012) or by withdrawing from occupied soil spaces (Ward et al., 2013). As a result, herbaceous fine root productivity is likely to decrease after introducing woody plants into steppes.

The faster decomposition of fine roots in steppe species than in shrubland species (Fig. 5) was consistent with invasion of woody plants with long-lived fine root systems reportedly leading to a remarkable extension of fine root longevity, and thus to a decrease in fine root turnover (Pinno and Wilson, 2013). In turn, the input of fine root litter is also reduced (Guo et al., 2007). Furthermore, fine root litter in a *P. radiata* plantation decayed far more slowly than in the original pasture (Guo et al., 2008).

The C-loss rate of herbaceous plants in the CM-shrubland was significantly faster than in the NR-steppe. Planting leguminous shrubs might have resulted in a proportional increase of annual herbaceous plants that decomposed faster than perennial herbaceous plants. Moreover, recent studies have shown that the initial C/N ratio of fine root litter plays an important role in root decomposition (Sariyildiz, 2015; Solly et al., 2014), and that root decay rates are positively affected by soil N concentration (Sariyildiz, 2015). Indeed, the observed C loss in the CM-shrubland may actually be underestimated in our study. Under natural soil conditions, the root litter of *C. microphylla* (an N-fixing shrub with high root N concentration in roots) and herbaceous plants would mix and interact during decomposition, thus increasing root decay and C loss. However, the experimental procedures in this study isolated the fine root litters of shrubland species during decomposition. Future studies should pay more attention to the effects of exogenous N addition (i.e., from N deposition and litter input) on root decomposition rates.

4.2. SOC storage and distribution in the C. microphylla shrubland and degraded steppe

Introducing *C. microphylla* decreased SOC stocks by 11.1% compared to the NR-steppe (Fig. 6). This result is supported by previous SOC storage decrease when grasslands were converted to shrub or tree plantations in semiarid and arid areas (Jiao et al., 2009; Wei et al., 2009; Zhou et al., 2012). The reduced SOC stock could be

partially attributed to changes in the amount and patterns of litter-derived organic materials across land-use types (Wei et al., 2009). Afforestation disturbances accompanied by soil C losses from the original vegetation might also play a role as well (Berthrong et al., 2012). Both herbaceous plant abundance and species composition were altered by land-use change, leading to changes in litter quantity and quality. Site preparation can also result in a rapid C loss (Don et al., 2009) by accelerating organic C decomposition rates, increasing soil erosion, reducing plant inputs (Guo and Gifford, 2002), and disrupting soil aggregates, which exposes previously protected organic matter to decomposition (Cotrufo et al., 2013; Solly et al., 2014). Additionally, the transition from grassland to a woody plantation may cause shifts in stand and soil microenvironments (Bárcena et al., 2014), influencing organic matter decomposition rates (Guo and Gifford, 2002), or reallocating aboveground C to belowground (Peichl et al., 2012). Finally, ecosystem biochemical cycles are likely affected after afforestation, due to the replacement of ground cover (Poeplau et al., 2011). Specifically, the lack of woody plant cover can increase soil temperature, accelerating SOC loss via microbial decomposition (Laganière et al., 2010).

In this study, the NR-steppe had a slightly higher soil bulk density than the *C. microphylla* plantation. The association between land conversion and the decline in soil bulk density might be due to root growth-induced soil compression and increased soil water use, which lower soil water content and alter soil leaching (Upson and Burgess, 2013). Some studies demonstrated that soil leaching can directly cause SOC loss (Berthrong et al., 2012; Jiao et al., 2009). Specifically, C leaching into deep soil layers played a role in SOC reduction (Guo and Gifford, 2002). Therefore, the observed decrease in SOC following the conversion from steppe to *C. microphylla* plantation might be partially attributed to a decline of soil bulk density.

There were no significant differences in total SOC and HF-SOC in the upper 0–60 soil layer (Fig. 6). Land use exerts a predominant influence on SOC fractions (Liu et al., 2014; Poeplau and Don, 2013; Zhang et al., 2014), suggesting that SOC fractions are appropriate early indicators of land-use change (Leifeld and Kögel-Knabner, 2005). The light fraction of SOC, with a turnover time of years to decades (Liu et al., 2014; Zhang et al., 2014), is generally thought to be plant material at an earlier stage of decomposition (Leifeld and Kögel-Knabner, 2005). Therefore, LF-SOC stocks and its depth distribution are more sensitive to land-use changes than HF-SOC (Liu et al., 2014). However, in the present study, HF-SOC in the deep soil layer (60–80 cm; Fig. 6) accounted for most of

the discrepancies in total SOC observed among land-uses. A possible explanation might be that the higher soil water content in the NR-steppe increased SOC decomposition rates (see data from Lai et al., 2014), by influencing SOC sequestration rates (Haden and Dornbush, 2014; O'Brien et al., 2010).

Our findings were generally in agreement with previous work showing that a grassland-to-forest conversion usually reduces, or does not affect, SOC stocks and distributions (Don et al., 2009; Guo and Gifford, 2002; Laganière et al., 2010; Poeplau et al., 2011). More specifically, grassland afforestation only caused a slight decrease in SOC, even after 140 years of forest growth (Poeplau et al., 2011). A review of afforestation effects on SOC revealed that grassland afforestation negatively affects SOC stocks in Northern Europe (Bárcena et al., 2014).

However, there was a positive effect of the steppe-to-shrubland conversion on SOC storage, at least for the topsoil layer. Given that woody plants have deeper root systems than herbaceous plants, topsoil assessment alone may be an incomplete evaluation of how change in land-use influence SOC. Furthermore, the relative distribution of SOC in grasslands (42% in the 0–20 cm soil layer) and in forests (50% in the 0–20 cm soil layer) indicated it can be found deeper in the former (Jobbágy and Jackson, 2000). Thus, to improve data quality, samples should be collected from deeper soil layers (Don et al., 2009).

Overall, the different effects of grassland afforestation on SOC stocks can be attributed to five major factors: 1) site preparation during afforestation (Don et al., 2009); 2) changes in herbaceous aboveground litter and root litter C inputs (Bárcena et al., 2014); 3) soil-biota-induced bioturbation (Cotrufo et al., 2013); 4) discrepancies in sampling design (Don et al., 2009); and 5) plantation age (Berthrong et al., 2012; Guo and Gifford, 2002). Unlike broadleaf and coniferous trees, shrub-generated floor litter C may not offset SOC losses after afforestation of former grasslands (Poeplau et al., 2011). As a result, SOC amount between the shrubland and the original grassland may increasingly differ with time. Taken together, these factors highlight the crucial influence of C input patterns in different stand conditions on SOC changes following land-use conversion.

4.3. Effects of fine root dynamics on SOC

Despite the changes in herbaceous species compositions in the CM-shrubland, the annual fine root biomass and productivity were higher in the NR-steppe than in the CM-shrubland (Figs. 1 and 2). Arid and semiarid steppes that have erosion-induced low SOC concentration are likely to sequestrate C after afforestation (Bárcena et al., 2014). In addition, woody plantations are thought to have larger net primary production rates than pastures or grasslands, and thus higher SOC levels. When compared to former pastures, forests have higher above- to belowground biomass ratios, suggesting that belowground root C input is more important for SOC accumulation than aboveground C inputs (Peichl et al., 2012). However, in our results, higher overall plant C stocks did not yield higher soil C sequestration in the form of SOC. Because fine roots always remain in the soil (Uselman et al., 2007), their biomass and turnover rate might be better predictors of SOC accumulation than aboveground litter inputs (Leppälammi-Kujansuu et al., 2014). While most of the biomass of woody plants corresponds to trunk biomass, herbaceous plants allocate more biomass to root systems (Berthrong et al., 2012). Moreover, a large portion of the woody-plant root system is long-lived and has a lower turnover rate than herbaceous roots, causing faster root turnover in grasslands than in forests (Guo et al., 2007), also indicating that woody plant roots may be a less important SOC source than herbaceous roots (Guo and Gifford, 2002). Therefore, the higher litter input in the NR-steppe resulted in higher SOC accumulation rates than in the C. microphylla

plantation, possibly explaining some of the differences in the fine root and SOC patterns found between the two land-use types.

Results from this study showed that SOC spatial distribution was not significantly correlated with fine root traits (biomass, necromass, and production), instead decreasing with increasing soil depth in both land-use types. This pattern was not consistent with previous findings that suggested soil C was positively related to fine root biomass density across all soil layers (0–40 cm) (Liao et al., 2014). However, the distribution patterns of SOC concentrations observed in the present study support data showing that sandy soil negatively contributes to SOC protection and sequestration (Adhikari and Bhattacharyya, 2015). In sandy soils, the spatial heterogeneity of SOC stocks is easily affected by soil moisture (Adhikari and Bhattacharyya, 2015; Haden and Dornbush, 2014), which could cause losses in dissolved SOC.

Although the land-use conversion from a degraded steppe to a C. microphylla plantation resulted in a significant drop of total SOC concentration, LF-SOC was slightly higher in the CM-shrubland and decreased with soil depth (Fig. 6). This is consistent with the findings of Poeplau and Don (2013), who showed that LF-SOC storage increased following grassland afforestation. Other studies also found that LF-SOC stocks increased after grassland afforestation, especially under broadleaf trees (Guo and Gifford, 2002; Poeplau et al., 2011). One possible explanation for our results might be that soil organic matter and the LF-SOC fraction decayed faster in the NR-steppe than in the shrubland. Microbial products of decomposition from labile plant material (e.g., fine root litter) may be the main precursor of stable soil organic matter due to organo-mineral interactions (Cotrufo et al., 2013). In the same study site, Lai et al. (2014) found that soil moisture was lower in the C. microphylla plantation than in the NR-steppe, especially at 20 and at 70 cm soil depths. This low moisture might lead to a slower decomposition of soil organic matter in the CM-shrubland, while the higher soil temperatures of the NR-steppe (without canopy protection) could accelerate decomposition. The combined effects of soil moisture and temperature on SOC dynamics may have partially contributed to the LF-SOC discrepancy between the two land-use patterns. With the available data, it is difficult to disentangle the exact mechanism responsible for the SOC decrease in the CM-shrubland and the remarkable loss of LF-SOC in the NR-steppe. However, variation in soil microbial activities is likely important (Clemmensen et al., 2015; Moore et al., 2015).

4.4. Research limitations

Although our soil sample depths were deeper than that shown in previous studies, the possibility of underestimating SOC accumulation in the entire soil profile remains. Similarly, the spatial distribution of fine roots did not reflect SOC distribution in either land-use patterns, suggesting that free or dissolved SOC fractions were transported to the subsoil stratum through leaching. In addition, we might have underestimated SOC accumulation in the NR-steppe. Therefore, collecting deeper soil samples should be considered in further studies to acquire a complete and accurate evaluation of SOC stocks and their spatial dynamics.

Similar to other studies (e.g. Wei et al., 2009; Zhou et al., 2012), the data presented here derived from paired sites, which are most commonly used for assessing afforestation effects on soil properties such as SOC, N, phosphorous, and potassium (Laganière et al., 2010). We were unable to acquire SOC stocks before shrubs were introduced in the steppe, which precluded being able to determine whether soil C had reached equilibrium after land-use conversion. The estimation of post-land-conversion SOC changes might therefore be biased. In future research, soils should be periodically sampled after planting, which allows for retrospective

estimations of how land-use changes affect SOC storage and dynamics (Laganière et al., 2010).

In general, the invasion of woody species into grassland can lead to changes in plant root traits and soil C dynamics, while the effect of this land-use change on ecological process still remain unclear. In our study, although the steppe showed more SOC accumulation and herbaceous plant compositions compared with *C. microphylla* plantation, we can not concluded that the degraded steppe has restored to its normal state. In future research, what is the normal state when the degraded steppe is restored, should be paid more attention during ecological restoration.

5. Conclusions

The natural restoration of a degraded steppe resulted in higher rates of SOC accumulation than the establishment of a *C. microphylla* plantation, which was accompanied by a remarkable reduction of fine root quantity and productivity. Differences in SOC storage between the two land-use types increase with time and cannot be reversed by the faster rates of herbaceous fine root turnover and decomposition in the *C. microphylla* plantation. The higher fine root abundance and production in the NR-steppe primarily explained its higher SOC accumulation compared to the CM-shrubland. Although the latter exhibited a slight increase in labile SOC storage, the NR-steppe accumulated more recalcitrant SOC, suggesting a less dynamic SOC pool. More research is necessary to fully explain why the NR-steppe had a higher SOC accumulation than the CM-shrubland, especially in terms of recalcitrant SOC. Overall, our analysis suggests that excessive shrub planting may not be a sustainable management practice for low-nutrient and arid sites, at least considering C sequestration. Instead, we propose that shrubs like *C. microphylla* should be planted in steppes as shelterbelts with a wider row distance. Additionally, regional shrub or tree planting should consider landscape design, taking into account the landscape phytosociology. In conclusion, our results provide some evidence and technical support for the selection of appropriate ecological management practices in drylands.

Acknowledgments

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ecoleng.2017.01.001.

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