

# Responses of carbon transfer, partitioning, and residence time to land use in the plant–soil system of an alpine meadow on the Qinghai-Tibetan Plateau

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**Abstract** We conducted an in situ <sup>13</sup>C pulse-labeling experiment from July to September 2011, involving three land use types: native alpine meadow with winter grazing (native meadow), cultivated perennial *Elymus nutans* (perennial grass), and annual *Avena sativa* (annual grass) pastures in the Qinghai-Tibetan Plateau. Thirty-two days after labeling, 32, 23, and 43 % of recovered <sup>13</sup>C of native meadow, perennial grass, and annual grass, respectively, were released by shoot respiration, and 43, 34, and 22 % were allocated to belowground C pools. About half of <sup>13</sup>C allocated to belowground C pools was released by soil respiration. Mean residence time of net assimilate C in this ecosystem was 67, 118, and 43 days for native meadow, perennial grass, and annual grass, respectively. Our results imply that species abundance and root/shoot ratio are the major controlling factors of soil C stocks in high-altitude grassland ecosystems, explaining 35 and 73 %, respectively. We suggest that conversion to monoculture for food production on the Qinghai-Tibetan Plateau may deteriorate soil health through rapid loss of soil organic C. The main cause of C transfer reduction after conversion to monoculture is the change in species richness and root/shoot ratio. Together with previous research studies, our results also support the finding that moderate grazing benefits grassland C

transfer and stock, owing to higher species richness and root/shoot ratio.

**Keywords** Qinghai-Tibetan Plateau · Alpine meadow · Land use · Carbon transfer · <sup>13</sup>C pulse labeling

## Introduction

In terrestrial ecosystems, plants fix carbon dioxide (CO<sub>2</sub>) from the atmosphere, and this CO<sub>2</sub> is transferred to and accumulated in soil C pools (Bahn et al. 2010). Land use change alters the exchange of C between the atmosphere and terrestrial pools (including aboveground biomass, belowground biomass, and soil) and the rates of soil C accumulation and turnover (IPCC 2013). These processes vary greatly across plants and ecosystems (Bahn et al. 2009, 2010; Bruggemann et al. 2011; Comeau et al. 2013; Domanski et al. 2001; Kuzyakov and Domanski 2002; Zhao et al. 2005). Carbon partitioning varies with growth stages of plants (Grayston et al. 1997; Hafner et al. 2012; Meharg and Killham 1990a) and is influenced by nutrient (Kocyigit and Rice 2006; Kuzyakov 2001; Kuzyakov and Domanski 2002) and environmental conditions (Kocyigit and Rice 2006; Meharg and Killham 1990b; Sagar et al. 1999; Yao et al. 2012). However, studies on these processes in the most sensitive and fragile ecosystems such as those on the Qinghai-Tibetan Plateau are poorly known.

On the Qinghai-Tibetan Plateau, land use change includes two main processes: One is natural restoration of alpine meadows, and the other is the conversion of alpine meadows to cultivated pasture, because of the great requirement for livestock forage in the region. Alpine grasslands have been found to be a large C pool (4.4 Pg C in the top 30 cm of soil) (Yang et al. 2009) and moderate C sink (−58 to −192 g C m<sup>−2</sup> year<sup>−1</sup>) (Kato et al. 2006; Zhao et al. 2005,

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2006). Changes in land use and grassland management could switch from the C sink to the C source (Wang et al. 2011). Therefore, revealing the C dynamics of grasslands on the Qinghai-Tibetan Plateau, and determining the influence of various land uses and management practices on C are crucial to understand the regional and global C budget (Hafner et al. 2012).

Carbon transfer in different ecosystems has been extensively studied in recent decades. Nevertheless, many processes and plant–soil–atmosphere C fluxes are still not well understood (Bruggemann et al. 2011; Studer et al. 2014). Of special interest is the conversion from natural grassland to annual or perennial monoculture that alters the rate of C cycling, the C allocation patterns, and the C residence time of the different compartments of the plant–soil system, owing to changes in life form, community structure, and root/shoot ratio. These processes are not known which Qinghai-Tibetan Plateau biodiversity can have.

In this paper, we hypothesize that lower root biomass and plant biodiversity have negative effects on C sequestration after conversion of natural grassland to monoculture on the Qinghai-Tibetan Plateau following known processes: (1) After conversion, plants invest more C in the aboveground than in the belowground biomass and thus reduce root biomass and rhizodeposition and change their biodiversity (Wang et al. 2007); (2) a 2–2.5 times greater contribution of root-derived C to stable soil organic C (SOC) pools, compared with shoot-derived C (Rasse et al. 2005); and (3) responses of C cycling to changes in plant community structures (Zou et al. 2014). We tested our hypothesis by examining the partitioning pattern of C flux using an in situ  $^{13}\text{C}$  pulse-labeling experiment during the 2011 growing season, for three land use types: native alpine meadow with winter grazing (native meadow), perennial *Elymus nutans* (perennial grass), and annual oat (*Avena sativa*) pasture (annual grass). The aims were to (i) determine the partitioning of recently fixed C among shoot, root, and soil pools and fluxes in the atmosphere–plant–soil system, (ii) estimate differences in the partitioning pattern of recent assimilates for different land use types, and (iii) estimate the effect of land use change on C input to soil.

## Materials and methods

### Site description

The experimental site is at the Haibei Alpine Meadow Ecosystem Research Station (37° 37' N, 101° 12' E), a facility run by the Northwest Institute of Plateau Biology, Chinese Academy of Sciences. The station lies in the northeastern portion of the Qinghai-Tibetan Plateau, within a large valley surrounded by the Qilian Mountains. Annual average temperature and precipitation in the 1981–2010 period were  $-1.7\text{ }^{\circ}\text{C}$  and

561 mm, respectively (Zhao and Zhou 1999; Zhao et al. 2010). The soil is clay loam, with average thickness of 65 cm. The top 5–10 cm of surface soil, which is classified as a Mat-Gryic Cambisol according to the classification system of the Chinese National Soil Survey, is wet and rich in organic matter. The study site is grazed by yaks and sheep every winter.

The native alpine meadow at the experimental site is dominated by *Kobresia humilis*, *Festuca ovina*, *Elymus nutans*, *Poa pratensis*, *Carex scabrostris*, *Scripus distigmaticus*, *Gentiana straminea*, *Gentiana farreri*, *Leontopodium odiumnanum*, *Blvsmus sinocompressus*, *Potentilla nivea*, and *Dasiphora fruticosa*. Average biomasses of aboveground and belowground (0–40 cm) were about 350 and 3000  $\text{g m}^{-2}$ , respectively, and belowground biomass of surface soil (0–10 cm) amounted to 85–95 % of the total biomass of soil at 0–40-cm depths (Zhao and Zhou 1999). Basic soil properties are organic C 55.8  $\text{g kg}^{-1}$ , K 13.0  $\text{g kg}^{-1}$ , total P 0.70  $\text{g kg}^{-1}$ , total N 5.37  $\text{g kg}^{-1}$ , pH 8.2, and bulk density 1.05  $\text{g cm}^{-3}$  at 10-cm depth (Zhang et al. 2012).

### Land use experiment

The entire experimental area was 100 m  $\times$  100 m. A completely randomized design was used, with four replicated plots for each of the three land use types: (i) natural native alpine meadow (native meadow), (ii) perennial grass, and (iii) annual grass (600 kg seeds  $\text{ha}^{-1}$ ) pastures tilled at the end of May with tillage, from 2006 to 2011 (annual grass). Each plot (4.0 m  $\times$  4.5 m) was separated by a 2-m buffer zone. Further details are given in Zhang et al. (2012).

### Aboveground and belowground biomass measurement

Peak aboveground biomass was sampled by clipping a 1 m  $\times$  1 m quadrat in each plot during late August each year. At the same time, plant diversity was monitored in the same quadrat. At the center of each quadrat, four soil cores of 0–20-cm depth were collected using an 8-cm diameter soil auger. Root samples were washed to remove soil, for estimating belowground biomass in the laboratory. All samples were oven-dried at 65  $^{\circ}\text{C}$  to constant weight.

### Pulse labeling

We carried out the  $^{13}\text{C}$  pulse-labeling experiment on 21 July 2011, which was a clear day. Four replicates were selected for each land use type. Each plot was pulse-labeled in a closed chamber consisting of a stainless steel base (1 m  $\times$  1 m, 10-cm height) with a channel on top and a PVC cover (1 m  $\times$  1 m, 45-cm height, with transparent polyethylene film with more than 96 % transmittance of photosynthetically active radiation). The bases were installed in the soil at 10-cm depth on the

day before the pulse labeling. When the pulse-labeling experiment began, the PVC covers were inserted into the top channel of bases and sealed with water. <sup>13</sup>CO<sub>2</sub> was released by carefully injecting 10 mL 10 % H<sub>2</sub>SO<sub>4</sub> into the container with 2.0 g Na<sub>2</sub><sup>13</sup>CO<sub>3</sub> in each chamber. The containers were connected to the chambers by tubing and were placed at the center of plots before the chambers were sealed. To guarantee uniform distribution of <sup>13</sup>CO<sub>2</sub>, a 5-V fan was used inside the chamber. The <sup>13</sup>CO<sub>2</sub> was present almost simultaneously (with 4–6-min difference) in each chamber. The chambers were removed after 2 h. Before opening them, chamber air was injected into 1 M NaOH, using syringes so as to facilitate the absorption of the unassimilated <sup>13</sup>CO<sub>2</sub> (Zou et al. 2014). As references of <sup>13</sup>C photosynthesized, we used <sup>13</sup>C recovered in all considered C pools 3 h after labeling in every replicated plot (83, 78, and 89±9 % <sup>13</sup>C of total added for the native meadow, perennial grass, and annual grass land uses, respectively).

**Sample collection**

After pulse labeling, the samples were collected at eight times (0, 3, and 6 h and 1, 4, 11, 18, and 32 days) in each replicated plot of the three treatments. At each sampling time, the plant–soil system was separated into shoots (live shoots were separated from the dead ones, and oven-dried and grounded), roots (washed with deionized water and carefully dabbed with a tissue), and rhizosphere soil (visible roots removed with tweezers). To estimate soil CO<sub>2</sub> efflux, a chamber (8 cm in diameter and 10 cm in height) covered the ground after removing shoots. CO<sub>2</sub> trapped in NaOH solution (inside the chamber) was precipitated with 2 M BaCl<sub>2</sub> solution, and the NaOH was titrated with 0.1 M HCl using phenolphthalein as an indicator (Lundegardh 1921; Singh and Gupta 1977; Werth and Kuzyakov 2008). Ten-milliliters of SrCl<sub>2</sub> (2 M) was added to 10 mL NaOH solution to produce SrCO<sub>3</sub> precipitate. The SrCO<sub>3</sub> precipitates were washed with degassed water and oven-dried for <sup>13</sup>C measurements. Further details are from Hafner et al. (2012) and Zou et al. (2014).

**Measurement and calculations**

Isotopic ratios were expressed as delta (δ) compared to the international standard Vienna Pee Dee Belemnite (VPDB, <sup>13</sup>C/<sup>12</sup>C=0.0111802). The <sup>13</sup>C data were determined with a MAT 253 stable isotope ratio mass spectrometer system coupled to an elemental analyzer (Thermo Finnigan, USA). The excess atom fraction  $x^E(^{13}C)_P/reference$  within a plant–soil compartment was

calculated according to Coplen (2011) and used to calculate mass balances. Then, we calculated the total mass of label recovered in excess  $m^E(^{13}C)$  (in mg <sup>13</sup>C) of plant tissues, soil samples, and respired CO<sub>2</sub>. This was done by multiplying the excess atom fraction by the C pool size or C flux and considering the change in molar C weight owing to the addition of the <sup>13</sup>C tracer (Eqs. 1 and 2), as suggested by Brand and Coplen (2012). The percentage of <sup>13</sup>C incorporated into C pools was calculated by Eq. 3 at a special time *t* after labeling:

$$m^E(^{13}C)_{PT,S}[\text{mg}] = \frac{x^E(^{13}C)_{PT,S} \cdot m(C)_{PT,S} \cdot M(^{13}C)}{x^E(^{12}C)_{PT,S} \cdot M(^{12}C) + x^E(^{13}C)_{PT,S} \cdot M(^{13}C)} \quad (1)$$

where  $m(C)_{PT,S}$  is the C mass (in mg) of plant tissue (PT) or soil organic matter (S),  $x^E(^{12}C)_{PT,S}$  and  $x^E(^{13}C)_{PT,S}$  are the respective <sup>12</sup>C and <sup>13</sup>C atom fractions, and  $M(^{12}C)$  and  $M(^{13}C)$  are the molar weights (mg mol<sup>-1</sup>) of <sup>12</sup>C and <sup>13</sup>C, respectively:

$$m^E(^{13}C)_{SR}[\text{mg day}^{-1}] = \frac{x^E(^{13}C)_{SR} \cdot F(C)_{SR} \cdot M(^{13}C)}{x^E(^{12}C)_{SR} \cdot M(^{12}C) + x^E(^{13}C)_{SR} \cdot M(^{13}C)} \quad (2)$$

Where  $F(C)_{SR}$  is the soil respiration rate (in mg C day<sup>-1</sup>) extrapolated to 24 h:

$$\% \text{ of recovered } ^{13}C = \frac{^{13}C_{t,amount}}{^{13}C_{0,amount}} \cdot 100 \quad (3)$$

Here <sup>13</sup>C<sub>0, amount</sub> represents the weight (mg m<sup>-2</sup>) of <sup>13</sup>C in the pool 3 h after the labeling.

Shoot respiration was calculated as reported by Hafner et al. (2012) according to the following equation:

$$^{13}C_{\text{shootrespiration}} = 100 - (^{13}C_{\text{shoot}} + ^{13}C_{\text{belowground}}) \quad (4)$$

where <sup>13</sup>C<sub>shootrespiration</sub> is the % of recovered <sup>13</sup>C of shoot respiration, and <sup>13</sup>C<sub>shoot</sub> is the % of recovered <sup>13</sup>C in shoots <sup>13</sup>C<sub>belowground</sub> is the % of recovered <sup>13</sup>C in the belowground C pool (including soil <sup>13</sup>CO<sub>2</sub> efflux); shoot respiration is presented for the first time 6 h after the labeling. Mean residence time (MRT) is the average time of a C atom remaining in a compartment and is defined as the ratio of the holding capacity (pool size) and (net) C flux through the pool (Studer et al. 2014). MRT was determined by Eqs. 5 and 6 (Hafner et al. 2012):

$$m(^{13}C)_t = m(^{13}C)_{max} \cdot e^{-kt} \quad (5)$$

where  $m(^{13}C)_t$  is the mass (in mg) of C present in the plant–soil compartment at *t* time,  $m(^{13}C)_{max}$  is the amount of <sup>13</sup>C at the peak, *t* is the time after labeling:

$$MRT = 1/k \quad (6)$$

## Statistical analysis

Normality of aboveground and belowground plant biomass and SOC stocks were tested by the Kolmogorov–Smirnov test. The significance of differences among the three treatments considering the aboveground and belowground plant biomass and SOC stocks was tested by ANOVA, which was calculated separately for each layer;  $P < 0.05$  was considered statistically significant for treatment means. We used nonlinear least squares (function “nls”) to fit Eq. 5. Statistical analysis was done with SAS 9.2 for Windows.

## Results

### Carbon stocks

To study the partitioning of recently fixed C among pools and C fluxes in the plant–soil system, it is necessary to know vegetative composition. Species richness and aboveground and belowground C stocks for the various land use types are presented in Table 1. After conversion of native alpine grassland to monoculture for 6 years, aboveground shoot C stocks significantly increased (Table 1). In contrast, root C stock of native meadow was significantly greater than those of perennial grass and annual grass. The major difference of root C stocks was in the upper 10 cm of the soil profile. Converting native meadow to monoculture reduced root C stocks by 50–63 % in the 0–10-cm layer after 6 years (Table 1). In deeper layers, root C stocks were not significantly different among the three land use types (Table 1). After conversion to monoculture, SOC stocks decreased and C stocks showed significant differences between perennial grass and annual grass (Table 1).

### Mass excess $^{13}\text{C}$ ( $m^E$ ) dynamics in the plant–soil system

The expression of  $m^E$  takes into account present pool size and shows the total amount of  $^{13}\text{C}$  distributed in the plant–soil system. The  $m^E$  of shoots followed an exponential decrease during the chase period (Fig. 1a), and the decline reflected reallocation of assimilated  $^{13}\text{C}$  in belowground pools and C loss by shoot respiration (Fig. 1).  $^{13}\text{C}$  allocated to belowground C pools and shoot respiration between 3 h and 32 days after labeling amounted to 57, 38, and 51 % of recovered  $^{13}\text{C}$  under annual grass, perennial grass, and native meadow, respectively.  $^{13}\text{C}$  turnover rates ( $k$ , in Eq. 5) of shoots for annual grass, perennial grass, and native meadow were respectively  $0.043 \pm 0.025$ ,  $0.014 \pm 0.007$ , and  $0.035 \pm 0.014 \text{ day}^{-1}$ , which were similar across all land use types ( $F_{(2,9)} = 2.38$ ,  $P = 0.1468$ , Fig. 1b). These results confirm that the recovery of  $^{13}\text{C}$  in shoots did not vary significantly by land use type.

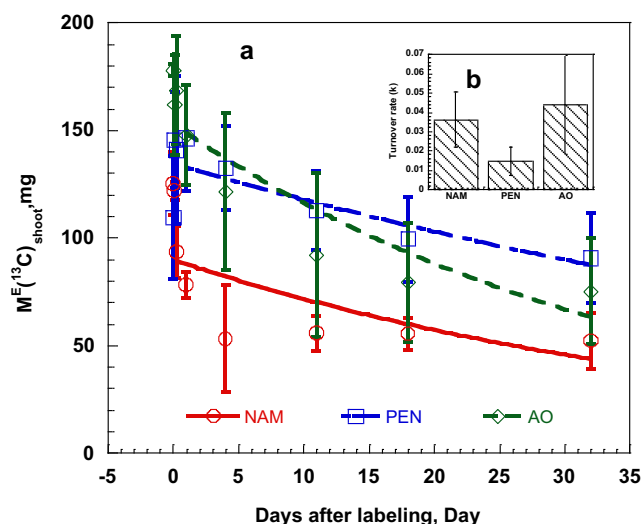
The amount of  $^{13}\text{C}$  transferred to belowground pools was greatest for native meadow, and differences were significant between native meadow and annual grass at 0.25, 4, 18, and 32 days. No significant difference was found between native meadow and perennial grass at any sampling time (Fig. 2a and Table 2). Carbon loss by shoot respiration for native meadow was greater at the beginning of the chase period (Fig. 2b), and maximum loss of  $^{13}\text{C}$  by shoot respiration was 4 days after labeling in native meadow (Fig. 2b).  $^{13}\text{C}$  loss by shoot respiration remained constant for perennial grass and annual grass during the later chase period (4–32 days after labeling; Fig. 2b). The amount of  $^{13}\text{C}$  lost by shoot respiration was significantly greater at each sampling time for annual grass; yet,  $^{13}\text{C}$  reallocation to belowground C pools was significantly greater for perennial grass than for annual grass (Fig. 2a, b and Table 2).

Figure 3a shows that 4 days after labeling, assimilated  $^{13}\text{C}$  of roots for native meadow, perennial grass, and annual grass

**Table 1** Dominate species, species diversity, and aboveground and belowground C stocks ( $\text{kg C m}^{-2}$ ) for the three land use types

Treatment	Depth (cm)	NAM	PEN	AO
Dominate species		<i>Kobresia</i>	<i>Elymus nutans</i>	<i>Avena Sativa</i>
Planting year			2006	2006
Soil C	0–10	3.42 (0.18) <sup>a</sup>	2.74 (0.24) <sup>b</sup>	2.20 (0.40) <sup>c</sup>
	10–20	2.92 (0.39) <sup>a</sup>	3.11 (0.23) <sup>a</sup>	2.42 (0.65) <sup>b</sup>
Soil N	0–10	0.38 (0.00) <sup>a</sup>	0.38 (0.00) <sup>a</sup>	0.29 (0.01) <sup>b</sup>
	10–20	0.31 (0.01) <sup>a</sup>	0.26 (0.00) <sup>a</sup>	0.18 (0.01) <sup>b</sup>
Roots	0–10	0.65 (0.03) <sup>a</sup>	0.33 (0.18) <sup>ab</sup>	0.24 (0.13) <sup>b</sup>
	10–20	0.07 (0.03)	0.05 (0.03)	0.06 (0.03)
Shoot		0.10 (0.05) <sup>b</sup>	0.20 (0.08) <sup>a</sup>	0.17 (0.07) <sup>ab</sup>
Species richness		19 (0.24) <sup>a</sup>	1.00 (0.00) <sup>b</sup>	1.00 (0.00) <sup>b</sup>

Numbers in the parentheses are standard deviation ( $n=4$ ,  $P < 0.05$ ). Different superscript letters indicate significant difference among the three land use types *NAM* native meadow, *PEN* perennial grass, *AO* annual grass



**Fig. 1** Mass excess  $^{13}\text{C}$  ( $m^E$ ) dynamics (a) and turnover rate ( $k$ , in Eq. 6) (b) in shoots during the chase period. *NAM* natural meadow, *PEN* perennial grass, *AO* annual grass. Mean±standard deviation ( $n=4$ ) are given

was 5, 3, and 4 %, respectively. During subsequent weeks, the percentage of  $^{13}\text{C}$  for native meadow and perennial grass gradually increased to 11 and 13 % at 32 days, respectively, whereas the percentage for annual grass remained constant at 5 % (Fig. 3a).

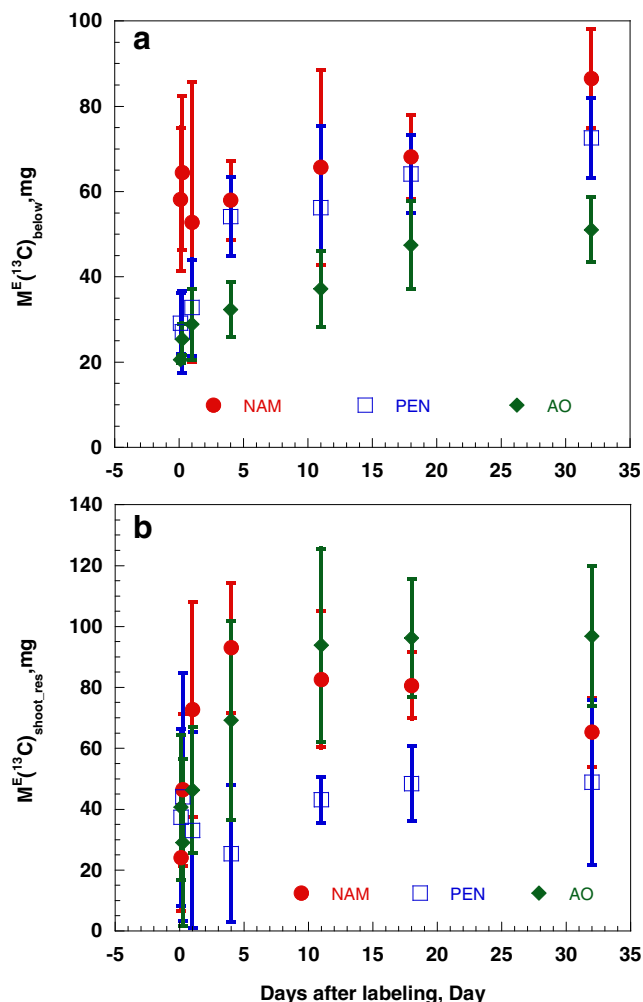
The native meadow retained more  $^{13}\text{C}$  in the soil than perennial grass and annual grass at all sampling times (Fig. 3b). However, there was a significant change in soil  $^{13}\text{C}$  content for the native meadow during the experimental period (Fig. 3b).

The accumulated  $^{13}\text{C}$  in soil respiration increased during the chase period;  $^{13}\text{C}$  recovered in soil respiration leveled off faster for native meadow and perennial grass than for annual grass, increasing from 5 % at 4 days to 17 % at 32 days (Fig. 3c).  $^{13}\text{C}$  recovered in soil respiration for annual grass was significantly less than those for native meadow and perennial grass at each sampling time (Fig. 3c).

### Mass excess $^{13}\text{C}$ ( $m^E$ ) partitioning

$^{13}\text{C}$  partitioning within the plant–soil compartments is shown in Fig. 4. Thirty-two days after labeling, a total of 43 and 32 % of recovered  $^{13}\text{C}$  were respectively transferred to belowground C pools, and due to shoot respiration for native meadow, the ratio (below- $^{13}\text{C}$ /shoot respired  $^{13}\text{C}$ ) was about 1.3:1. For perennial grass, the values were, respectively, 34 and 23 %, and the ratio was about 1.5:1. Reallocation percentages for annual grass were 22 and 43 %, respectively, and the ratio was about 1:2. Compared with annual grass, belowground C pools were significantly greater for native meadow and perennial grass (Fig. 4).

To assess belowground C partitioning, sampling time is of great importance. At the end of labeling, 23–43 % of the  $^{13}\text{C}$  recovered was detected belowground for native meadow, and,



**Fig. 2**  $^{13}\text{C}$  allocation to belowground C pools (roots, soil, and soil respiration) (a) and  $^{13}\text{C}$  losses by shoot respiration (b) during 32 days after labeling. *NAM* native meadow, *PEN* perennial grass, *AO* annual grass. Mean±standard deviation ( $n=4$ ) are given

on this basis, most of the  $^{13}\text{C}$  recovered for native meadow was released as  $\text{CO}_2$  (42 %), followed by 33 % remaining in soil and 25 % in the root; however, there were no differences among the three values. Carbon allocated to soil respiration, roots, and soil were respectively 53, 38, and 9 % for perennial grass, and 57, 26, and 17 % for annual grass.

Thirty-two days after labeling,  $50\pm 5$ ,  $42\pm 13$ , and  $56\pm 11$  % of recovered  $^{13}\text{C}$  was relocated to ecosystem respiration (shoot respiration+soil respiration) for native meadow, perennial grass, and annual grass, respectively. Distribution percentages did not vary with land use type, and about 50 % of net assimilated C was released by ecosystem respiration.

### Mass excess $^{13}\text{C}$ ( $m^E$ ) turnover rate and residence time

To evaluate the lifetime of assimilates in the ecosystem, MRT of net assimilate C in the ecosystem was determined. MRT was calculated as the inverse of the rate

**Table 2** Carbon partitioning to belowground and shoot respiration indicated by the relative  $^{13}\text{C}$  distribution (in %) at different sampling dates after pulse labeling

Pool	Sampling dates (days)	Treatment		
		NAM	PEN	AO
Belowground allocation	0.125	28.50 (8.25) <sup>a</sup>	13.71 (3.33) <sup>b</sup>	9.23 (0.30) <sup>b</sup>
	0.25	31.55 (8.81) <sup>a</sup>	12.78 (4.53) <sup>b</sup>	11.36 (1.65) <sup>b</sup>
	1	26.12 (15.75)	15.45 (5.33)	12.93 (3.72)
	4	28.41 (4.50) <sup>a</sup>	25.53 (4.32) <sup>a</sup>	14.49 (2.85) <sup>b</sup>
	11	32.19 (11.16)	26.49 (8.98)	16.66 (4.01)
	18	33.37 (4.86) <sup>a</sup>	30.22 (4.31) <sup>ab</sup>	21.26 (4.61) <sup>b</sup>
	32	42.40 (5.67) <sup>a</sup>	34.23 (4.43) <sup>a</sup>	22.89 (3.40) <sup>b</sup>
Shoot respiration	0.125	11.79 (8.53)	17.61 (13.65)	18.21 (10.65)
	0.25	22.76 (12.22)	20.74 (19.15)	13.03 (12.36)
	1	35.66 (17.30)	15.58 (15.12)	20.75 (9.29)
	4	45.57 (10.48) <sup>ab</sup>	11.98 (10.57) <sup>a</sup>	31.00 (14.68) <sup>b</sup>
	11	40.48 (10.97) <sup>ab</sup>	20.31 (3.58) <sup>b</sup>	42.07 (14.23) <sup>a</sup>
	18	39.50 (5.31) <sup>a</sup>	22.85 (5.85) <sup>b</sup>	43.10 (8.69) <sup>a</sup>
	32	32.00 (5.56) <sup>ab</sup>	23.03 (12.79) <sup>b</sup>	43.37 (10.30) <sup>a</sup>

Numbers in the parentheses are standard deviation ( $n=4$ ,  $P<0.05$ ). Different superscript letters indicate significant difference among the three land use types at each sampling date

NAM native meadow, PEN perennial grass, AO annual grass

constant (Eq. 6) of the exponential model between ecosystem net fixed  $^{13}\text{C}$  (shoot recovered  $^{13}\text{C}$ +root recovered  $^{13}\text{C}$ +soil recovered  $^{13}\text{C}$ ) and days after labeling. The longest MRT was detected in perennial grass (118 days), followed by native meadow (67 days) and for annual grass (43 days). Therefore, the ecosystem C turnover increased after conversion to annual grass but decreased after conversion to perennial grass.

## Discussion

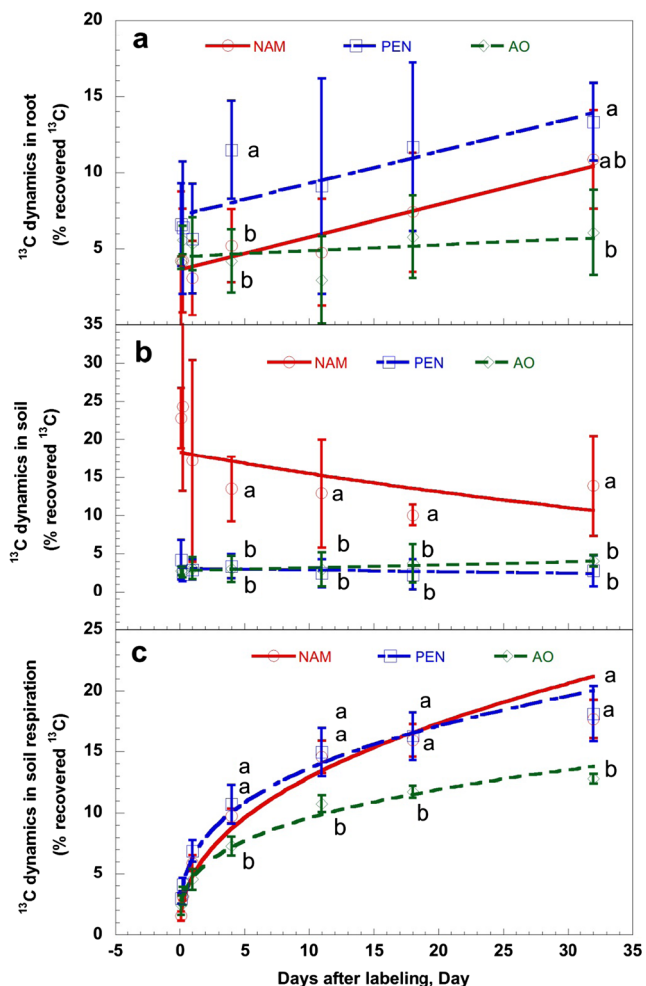
Some studies have reported significant effects of land use change on the exchange and sequestration of ecosystem C (Hafner et al. 2012; Wu et al. 2009; Zou et al. 2014). Likewise, our results indicate that the responses of C partitioning and residence time to conversion of native meadow to monoculture varied during the experimental periods. Although there was no significant difference in the amount of assimilated  $^{13}\text{C}$  among the three land use types, the C allocation percentages to belowground and aboveground pools differed. The ecosystem had higher aboveground C partitioning and lower belowground C allocation after conversion to monoculture. These results imply that C transfer is controlled by changes in plant growth, species richness, and root/shoot ratio induced by land use change.

## Effect of land use on dynamics of $m^E$

Assimilated  $^{13}\text{C}$  was recovered in shoots (59–73 %), roots (4.2–6.5 %), and soil (3–22 %) and lost by soil respiration (1.5–2.9 %) 3 h after labeling for all land use types (Table 2 and Fig. 3). Loss or export of recently fixed C to shoots was 61.7, 31.0, and 33.7 % in the first 24 h for native meadow, perennial grass, and annual grass, respectively, and the values are within the reported range of 32–77 % loss (Johnson et al. 2002; Ostle et al. 2000; Wu et al. 2009). Peak loss by respiration occurred within the first day after the pulse labeling (Fig. 3), and the maximum translocation rate to belowground was between 0 and 6 h after labeling (Fig. 2). These results are similar to those of Butler et al. (2004) and Wu et al. (2009), who found export of  $^{13}\text{C}$  from the assimilating shoot initiated within 3 h after the labeling start (Bruggemann et al. 2011).

Loss through shoot respiration, which increased between 3 h and 18 days, did not change significantly during the rest of the chase period (Fig. 2). This is consistent with Hafner et al. (2012), who found significant losses via shoot respiration after labeling.

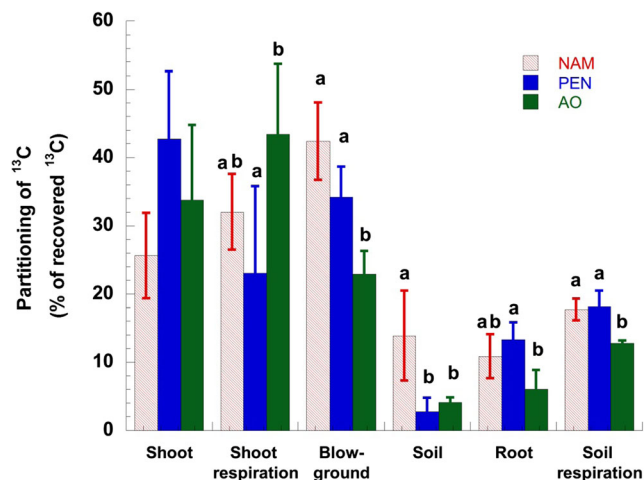
The  $m^E$  in the plant–soil system showed a similar translocation tendency during the chase period, and turnover rates of  $^{13}\text{C}$  in shoots did not vary with land use type (Fig. 1). However, two main characteristics were found for the C allocation pattern from shoots to shoot respiration and belowground. More  $^{13}\text{C}$  was allocated to belowground pools for both native meadow and perennial grass, and  $^{13}\text{C}$  remaining within the



**Fig. 3**  $^{13}\text{C}$  allocation to roots (a), soil (b), and soil respiration (c) during 32 days after labeling. *NAM* native meadow, *PEN* perennial grass, *AO* annual grass. Mean  $\pm$  standard deviation are given. Different letters indicate significant difference among the three land use types at each sampling date ( $n=4$ ,  $P<0.05$ )

shoots for annual grass was mainly consumed by shoot respiration (Fig. 2 and Table 2). These differences reflect that plant life form influences the incorporation of C into the plants organs. The annual grass depends on seed breeding and directs more energy to shoots, whereas the native meadow and perennial grass with perennial species mainly depend on asexual reproduction, and direct more energy to roots. Moreover, long-term selection toward an increase in the aboveground yield, which changes the natural ratio of biomass between belowground and aboveground organs of annual plants, favors the latter.

Large differences were found in the partitioning of  $^{13}\text{C}$  into belowground C pools among native meadow, perennial grass, and annual grass. For native meadow and perennial grass, there was a significantly greater percentage of recently assimilated  $^{13}\text{C}$  in belowground C pools (native meadow, 43 %; perennial grass, 34 %), than for annual grass (22 %). By evaluating various studies, Kuzyakov (2001) showed that the



**Fig. 4** Partitioning of  $^{13}\text{C}$  32 days after assimilating. *NAM* native meadow, *PEN* perennial grass, *AO* annual grass. Mean  $\pm$  standard deviation are given. Different letters indicate significant difference among the three land use types at each sampling date ( $n=4$ ,  $P<0.05$ )

average long-term C sequestration in meadow plants was about 30–50 % of assimilated C, which matches the data of both native meadow and perennial grass. The partitioning percentage of native meadow was within ranges observed in other pulse-labeling studies of similar nearby grassland (Hafner et al. 2012; Wu et al. 2009; Zou et al. 2014); in particular, it is close to the 40 % reported by Hafner et al. (2012), but smaller than data of similar alpine *Kobresia* (58.7–61 %) with winter grazing (Wu et al. 2009; Zou et al. 2014). Probably it depended on the variability of C partitioning with species positively influencing ecosystem (this study, 19 species; Wu et al. (2009) and Zou et al. (2014), 39 species). According to niche complementary hypothesis, higher species richness will benefit ecosystem function (Tilman et al. 1997). This is confirmed by our results in which  $^{13}\text{C}$  recovered by belowground C pools was increased with species richness ( $\% \text{ recovered}_{\text{Root}}^{13}\text{C} = 6.43 + 0.32 \times \text{Species richness}$ ,  $R^2 = 0.41$ ,  $P < 0.05$ ;  $\% \text{ recovered}_{\text{Soil}}^{13}\text{C} = 1.75 + 0.46 \times \text{Species richness}$ ,  $R^2 = 0.41$ ,  $P < 0.05$ ;  $\% \text{ recovered}_{\text{Soil respiration}}^{13}\text{C} = 13.41 + 0.25 \times \text{Species richness}$ ,  $R^2 = 0.47$ ,  $P < 0.05$ ;  $n = 12$ ; data was pooled together of the native meadow and the perennial grass).

$^{13}\text{C}$  partitioning patterns in belowground C pools were similar among the land use types. Most (44–57 %) of the assimilated C was released as  $\text{CO}_2$  because of root respiration and microbial degradation of exudates, followed by roots (26–38 %) and soil (9–31 %, including microbial biomass C and humus substances in the soil). This result indicates that about half the  $^{13}\text{C}$  allocated to belowground C pools was released by soil respiration, and roots are considered as the major C sink within the belowground pools (Table 3), which agrees with Domanski et al. (2001) and Wu et al. (2009).

By comparing allocation patterns of belowground C pools for the three land use types, we found that the main difference

**Table 3** Published C translocation into belowground C pool (as percentage of assimilated  $^{13}\text{C}$ ) in published study sites under field conditions compared with our data

Grassland type	Harvest day (days)	Roots (%)	Soils (%)	Soil respiration (%)	Total translocation to the soil	Source
Alpine Kobresia meadow under enclosure condition	27	0.6 (3 %) <sup>a</sup>	10.4 (52 %)	9 (45 %)	20 (100 %)	Hafner et al. 2012
Alpine Kobresia meadow under moderate grazing condition	27	1.5 (4 %)	18 (45 %)	20 (50 %)	40 (100 %)	Hafner et al. 2012
Alpine Kobresia meadow under winter pasture condition	32	34.2 (58 %)	7.3 (12 %)	17.2 (29 %)	58.7 (100 %)	Wu et al. 2009
Alpine Kobresia meadow under moderate grazing condition	32	11 (26 %)	14 (33 %)	19 (44 %)	43 (100 %)	This study
Perennial <i>Elymus nutans</i> grassland	32	13 (38 %)	3 (9 %)	18 (53 %)	34 (100 %)	This study
Annual <i>Avena Sativa</i> pasture	32	6 (26 %)	4 (17 %)	13 (57 %)	23 (100 %)	This study

<sup>a</sup>The  $^{13}\text{C}$  allocation in the belowground C pool

in photosynthetic C allocation at the current development stage of the grasses was in soil and soil respiration (Fig. 3b, c). For natural grassland (e.g., native meadow), soil pools were higher than for single-species grassland (e.g., perennial grass and annual grass). Carbon allocation to soil respiration for perennial grass was smaller than that for native meadow and annual grass. The higher  $^{13}\text{C}$  percentage in soil and root–soil respiration for native meadow indicated that these roots may produce more exudates and increase rhizodeposition and decompose faster than those of monoculture (Figs. 2 and 3), probably because of the higher root/shoot ratio and species richness of native meadow (Table 1,  $\% \text{ recovered}_{\text{Soil}}^{13}\text{C} = 0.44 + 1.84 \times \text{Root/Shoot Ratio}$ ,  $R^2 = 0.73$ ,  $P < 0.01$ ;  $n = 12$ ). The pattern illustrates that native meadow with its higher root/shoot ratio and species richness would increase exudates and rhizodeposition, thus enhancing SOM turnover (Johnson and Matchett 2001; Li et al. 2014; Sousa et al. 2012).

### Effects of land use change on C stocks

We found that plants allocated less C to belowground pools, and 21–35 % of soil C stocks were in the upper 10-cm soil, which significantly declined 6 years after converting natural grassland to monoculture. These findings are consistent with what reported in bibliography that land use change from native vegetation (usually fertile soil) to monoculture reduced soil C stocks by about 37–44 % (Li et al. 2006; Li 2008), and this may be due to the decreased root biomass and the belowground C input (Table 1 and Fig. 4). Therefore, conversion from natural grassland to monoculture for food production in areas such as the Qinghai-Tibetan Plateau may deteriorate soil health through rapid loss of SOC.

As mentioned, the effect of land use change on long-term C stock was confirmed by the partitioning of recent assimilates, revealing that the portion of plant-derived C remaining in soil was higher in natural grassland (native meadow, 14 %) than in annual single-species grassland (annual grass, 4 %); the

former value is similar to 13 % of assimilates C already reported (Hafner et al. 2012; Zou et al. 2014). Our results indicate that MRT of ecosystem C for native meadow was 1.6 times longer than that of annual grass. Our findings indicate that natural grassland was more resistant to degradation than that of annual monoculture. In addition, there was a significant difference in the amount of root residues between native meadow and annual grass, depending on life form rather than assimilate partitioning. After maturation, annual grass died completely, including its belowground organs. On the contrary, growth and development of the native meadow root system continued after grazing by increasing rhizodeposition into soil.

Overall, our results indicate that land use change affected C transfer in particular, by altering species composition, life forms, and the root/shoot ratio. The results further show a relationship between root/shoot ratio and soil C stocks with moderate grazing. Moderate grazing, which could maintain a higher species richness and root/shoot ratio than no-grazing or over-grazing (Dong et al. 2011; Fensham et al. 2014; Wang et al. 2010; Zhou et al. 2008). These results support Hafner et al. (2012) and Zou et al. (2014).

### Conclusion

Our results support the hypothesis that conversion from natural vegetation to artificial pasture lands caused SOC loss on the Qinghai-Tibetan Plateau. The main reason for reduced C transfer after conversion to monoculture was the altered life form, species richness, and root/shoot ratio. We found that (1) 32, 23, and 43 % of recovered  $^{13}\text{C}$  were released by shoot respiration for native meadow, perennial grass, and annual grass respectively; (2)  $^{13}\text{C}$  allocated to belowground C pools for native meadow, perennial grass, and annual grass was 43, 34, and 22 %, respectively, 32 days after the labeling; (3) about half of  $^{13}\text{C}$  allocated to belowground C pools was



released by soil respiration; and (4) MRT of net assimilated C in the ecosystem was 67, 118, and 43 days for native meadow, perennial grass, and annual grass, respectively. Our results suggest that species richness and root/shoot ratio are the major controls on soil C stocks, explaining 35 and 73 % of soil C pool variation, respectively. Conversion to single-species artificial grassland on the Qinghai-Tibetan Plateau for food production may deteriorate soil health through rapid loss of SOC. Our results support the finding that moderate grazing will benefit grassland C transfer and stock, owing to greater species richness and root/shoot ratio. Manipulated experiment with different species richness or combinations should be conducted to explore the effect of plant diversity on C transfer.

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