Contribution of root to soil respiration and carbon balance in disturbed and undisturbed grassland communities, northeast China

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Changes in the composition of plant species induced by grassland degradation may alter soil respiration rates and decrease carbon sequestration; however, few studies in this area have been conducted. We used net primary productivity (NPP), microbial biomass carbon (MBC), and soil organic carbon (SOC) to examine the changes in soil respiration and carbon balance in two Chinese temperate grassland communities dominated by *Leymus chinensis* (undisturbed community; Community 1) and *Puccinellia tenuiflora* (degraded community; Community 2), respectively. Soil respiration varied from 2.5 to 11.9 g CO_2 m^{-2} d^{-1} and from 1.5 to 9.3 g CO_2 m^{-2} d^{-1}, and the contribution of root respiration to total soil respiration from 38% to 76% and from 25% to 72% in Communities 1 and 2, respectively. During the growing season (May–September), soil respiration, shoot biomass, live root biomass, MBC and SOC in Community 2 decreased by 28%, 39%, 45%, 55% and 29%, respectively, compared to those in Community 1. The considerably lower net ecosystem productivity in Community 2 than in Community 1 (104.56 *vs.* 224.73 g C m^{-2} yr^{-1}) suggests that the degradation has significantly decreased carbon sequestration of the ecosystems.

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1. Introduction

Global soil respiration is estimated to be 76.5 Pg C yr^{-1}, which is 30–60 Pg C yr^{-1} greater than the net primary productivity (NPP) (Raich and Potter 1995). Therefore, soil respiration is a major pathway for carbon to move from terrestrial ecosystems to the atmosphere and even small changes can strongly influence net ecosystem production (NEP) (Ryan and Law 2005). The potential switching of the terrestrial biosphere from its current role as a carbon sink to a carbon source is critically dependent upon the sensitivity of soil respiration to global warming (Cox *et al* 2000; Melillo *et al* 2002). Soil respiration is therefore a key process that improves our understanding of the terrestrial carbon cycle (Rustad *et al* 2000; Schlesinger and Andrews 2000).

Soil respiration consists mainly of root respiration (and associated mycorrhizal fungi) and microbial respiration in temperate grasslands. Although it has received considerable attention in recent decades, little is known about the contribution of root to total soil respiration, especially in China's grasslands (Jia *et al* 2006; Li *et al* 2002). Quantifying the contributions of these two major components to total soil respiration is critical to better modelling of the ecosystem carbon cycle (Kirschbaum 1995; Mizue *et al*

Keywords. Grassland ecosystem; root respiration; soil respiration; seasonal change; carbon sequestration.

Abbreviations used: ANPP, above-ground net primary productivity; BNPP, below-ground net primary productivity; MBC, microbial biomass carbon; MR, microbial respiration; NEP, net ecosystem production; NPP, net primary productivity; SOC, soil organic carbon

2000) and understanding the biological processes that control soil respiration (Ryan and Law 2005). This is not only because microbial decomposition of residual organic matter influences the amount of carbon stored in the soil, but also because microbial and root respiration may respond differently to changing temperature (Boone *et al* 1998) which, in turn, may induce a difference in the respiratory ratio between roots and microorganisms (Nina 2000).

In the present study, we compare root and microbial respiration in two grassland sites with the same climatic conditions. The studied grasslands are on the Songnen Plain, northeast China. They are the largest natural grasslands of *Leymus chinensis* on the Eurasian continent (Xiao *et al* 1995). Two perennial C_3-grasses, *L. chinensis* and *Puccinellia tenuiflora*, are the major dominant species in this area. Since the 1960s, increased needs for agriculture and livestock have led to serious salinization and, in turn, degradation of the grassland: the dominant *L. chinensis* has been replaced with *P. tenuiflora*, an indicator of a degraded grassland community (Wang and Earle 1997). However, the effect of the changes in species composition caused by the degradation on soil respiration and carbon sequestration remains unknown.

Accordingly, using two communities dominated by these two grass species, this study aimed to (i) compare seasonal changes in soil respiration, (ii) separate the contribution of root and microbial respiration from total soil respiration, and (iii) examine the changes in carbon sequestration associated with grassland degradation.

2. Materials and methods

2.1 *Study site*

The study site is located in the Yao Jingzi Grassland Nature Reserve (44º 45´N, 123 º 45´E, 160 m a.s.l.) in the southwestern region of the flat, low-lying Songnen Plain in northeast China. According to the local weather station (Changling), the area has a typical semi-arid temperate continental climate with an annual mean temperature of 4.9 ºC, annual precipitation of 470 mm, and actual annual evaporation of 1600 mm over the past 20 years. The concurrence of abundant summer heat and moisture favours plant growth, and grass shoots grow from May to September (growing season). The soil, chernozem in nature, results from blocked drainage and is characterized by a high content of sodic saline. The grassland mainly consists of *L. chinensis*, *P. tenuiflora*, *Calamagrostis epigeios*, *Chloris virgata* and *Suaeda glauca*. Two communities dominated by *L. chinensis* (Community 1) and *P. tenuiflora* (Community 2), which were close to each other (less than 500 m apart, to ensure identical climatic conditions), were selected for the experiment which ran from May to September 2002.

2.2 *Methods*

The two communities cover approximately 20 000 m^2. The sample areas were 50 m ×50 m. Soil respiration, shoot biomass, root biomass, microbial biomass carbon (MBC) and soil organic carbon (SOC) were measured once or twice a month.

2.2a *Soil respiration, soil temperature and water content:* Twelve cylindrical chambers (13 cm × 23 cm) were randomly placed in each community. Each of them was inserted 3 cm into the mineral soil. Soil respiration was measured *in situ* using an alkali absorption method (Gupta and Singh 1981) during the growing season (May–September). All green vegetation above the ground was cleared one day before the chambers were fixed for the measurement of soil respiration. Although clipping shortly before measurement might have increased the exudation and respiration rates of roots (Fu and Cheng 2004), the water content and nutrient turnover were not affected (Kuzyakov 2006). CO_2 efflux was collected for reaction with 20 ml 1 mol l^{-1} NaOH for 24 h to avoid diurnal changes (Rochette *et al* 1992; Rochette and Flanagan 1997; Zhang *et al* 2003). NaOH solution was extracted for precipitation processing using saturated $BaCl_2$ solution. The amount of CO_2 absorbed was estimated by titration using 1 mol L^{-1} HCl solution and phenolphthalein as a visual indicator.

The soil temperature at 10 cm depth was measured adjacent to the location where soil respiration was measured, using a calibrated electronic thermometer equipped with an NTC probe (Testo 110, Lenzkirch, Germany). Gravimetric soil water content was determined by taking samples from the 0–10 cm deep soil layer next to the chambers and then weighing the samples against a constant weight.

2.2b *MBC:* The chloroform-fumigation extraction method was used to measure MBC (Vance *et al* 1987). Twelve replicate samples were taken from the 0–30 cm deep soil layer each time. Fumigated and unfumigated samples were extracted by 0.5 mol l^{-1} K_2SO4 for gravity filtering using presoaked Whatman 42 filter paper. The filtered samples were then vacuum filtered with a 0.45 μm Millipore filter. Organic carbon was analysed using the high-temperature combustion method with a Shimadzu TOC-500 Carbon Analyzer. A correction coefficient (0.45) was used while converting dissolved organic carbon to MBC when SOC was measured using a TOC auto-analyser (Joergensen 1996). The MBC was calculated by the following equation:

$$MBC = (C_f - C_n)/K_{EC}$$

where C_f – carbon in fumigated soil, C_n – carbon in non-fumigated soil, and K_{EC} – correction coefficient.

2.2c *SOC:* The soil samples from the 12 cores close to the soil respiration chambers for each time were dried at 31ºC for 72 h, crushed small enough to be passed through a 2 mm sieve, ground to 200 mm, and stored in glass bottles. SOC was determined by the dry combustion method *(*Nelson and Sommers 1982) using a Carlo Erba model NA 1500 automatic C/N analyser (Hake Buckler Instruments, Inc., Saddle Brook, NJ, USA).

2.2d *Shoot and root biomass:* Shoot biomass was measured by clipping vegetation samples from twelve quadrates along with measurement of soil respiration. Plant materials were divided into living and dead parts before they were oven dried at 65ºC for 48 h and then weighed. Root biomass was measured by collecting soil samples from depths of 0–30 cm from the twelve quadrates, at the same location of the chambers for the measurement of soil respiration. The soil samples were then further stratified into 3 layers according to the depths at which they were collected: 0–10, 10–20 and 20–30 cm. The roots were washed and oven dried for 24 h at 65ºC and then weighed. All sampled root biomass was less than 2 mm in diameter. As there is currently no effective method available for separating live and dead roots in field investigations, we distinguished live and dead roots with the naked eye based on colour and consistency. Live roots are far more resilient than dead ones and are not easily broken if twisted. In addition, live roots are light coloured, succulent and covered by root hair, whereas dead roots are dark red or brown-red. Live roots accounted for about 50% of the total root biomass.

2.2e *Root respiration:* CO_2 effluxes from the roots and microorganisms were separated using an inferred approach (Kucera and Kirkham 1971). According to this method, the linear relationship between root biomass and soil respiration rate is extrapolated to yield a y-intercept value, which can be used to indicate the minimum microbial respiration in the absence of root biomass (Kucera and Kirkham 1971). Root respiration can be estimated by subtracting the microbial respiration from the total soil respiration.

2.2f *Estimation of annual soil respiration:* Annual soil respiration rate (g CO_2 m^{-2} yr^{-1}) (R_{ann}) was estimated from Q_{10} models between soil respiration rate and soil temperature as follows:

$$R_{ann} = \sum_{j=1}^{365} \beta_0 e^{\beta_1 T_j}$$

where *Tj* represents the mean daily soil temperature at 10 cm soil depth for j days of the year.

Ten-day mean soil temperature at 10 cm depth (1982–2002) was obtained from the local weather station. Daily soil temperature (T_j) was calculated using the relationship between the 10-day mean soil temperature at 10 cm (T) and Julian day (t) (figure 1) as follows:

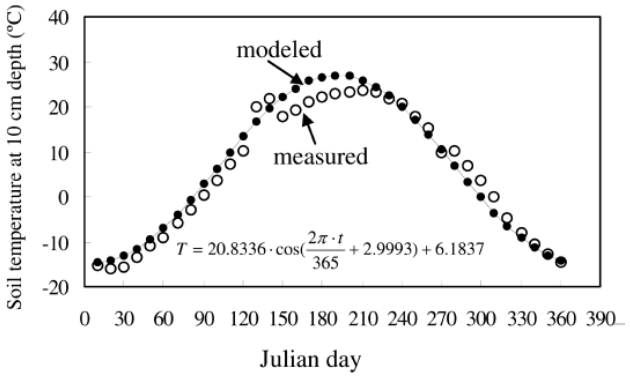

Figure 1. Relationship between ten-day mean soil temperature at 10 cm depth and Julian day

$$T = 20.8336 \cdot \cos(\frac{2\pi \cdot t}{365} + 2.9993) + 6.1837$$

($R^2 = 0.98$; $P<0.001$).

2.2g *Estimation of carbon balance*: The maximum (living and newly formed) shoot biomass measured during the growing season (May–September) was taken as the annual above-ground net primary productivity (ANPP). The below-ground net primary productivity (BNPP) was estimated using the annual increment of growth, as defined by Dahlman and Kucera (1965). A coefficient (0.45) was used to convert the dry mass to carbon content (Li *et al* 2004). The annual carbon output was estimated by multiplying the annual soil respiration by the proportion of microbial respiration in soil respiration. NEP was determined as the difference between the NPP and annual carbon output.

2.2h *Statistical analysis:* Kolmogorov–Smirnov statistics showed that all the data sets measured are normally distributed (P = 0.91). The difference of means of soil temperature, water content, SOC, root biomass, MBC and shoot biomass between the two communities were assessed using a *t*-test and ANOVA. Linear regression was used to evaluate the relationship between soil respiration and root biomass. Step-wise multiple linear regression was used to identify the most influential abiotic and biotic factors for controlling soil respiration. All statistical analyses were performed with a significance level of 0.05 with StatView 5.0 (SAS Institute, Inc., Cary, NC, USA).

3. Results

3.1 *Soil respiration, soil temperature, soil water content, MBC, SOC, shoot biomass and root biomass*

Soil respiration in the *L. chinensis* community (Community 1) ranged from 2.5 to 11.9 g CO_2 m^{-2} d^{-1} with higher values in the summer and lower values in the spring and autumn (figure 2c). Soil respiration in the *P. tenuiflora* community (Community 2) showed a similar pattern, ranging from 1.5 to 9.3 g CO_2 m^{-2} d^{-1}. During the entire experimental period, the soil respiration in Community 2 decreased by 28%, compared with Community 1 (pair comparison, $P<0.001$). Soil temperature and water content over the entire course of soil respiration measurements ranged from 8.3 to 29.3 °C, and from 8% to 21% in Community 1, respectively (figures 2a, b) and did not differ significantly between the two communities. This suggests that soil temperature and water content may not exert a significant effect on seasonal change in soil respiration between the two communities.

The MBC in both communities showed a similar seasonal pattern: increasing from May to July and decreasing in September in an inverted V-shape (figure 2d). The MBC ranged from 0.3 to 1.5 g m^{-2} and from 0.2 to 0.5 g m^{-2} for Communities 1 and 2, and the SOC averaged 31 and 22 g kg^{-1}, respectively (figure 2e). Live root biomass varied from 0.55 to 0.9 kg m^{-2}, with a maximum in early June (0.9 kg m^{-2}) in Community 1, and from 0.25 to

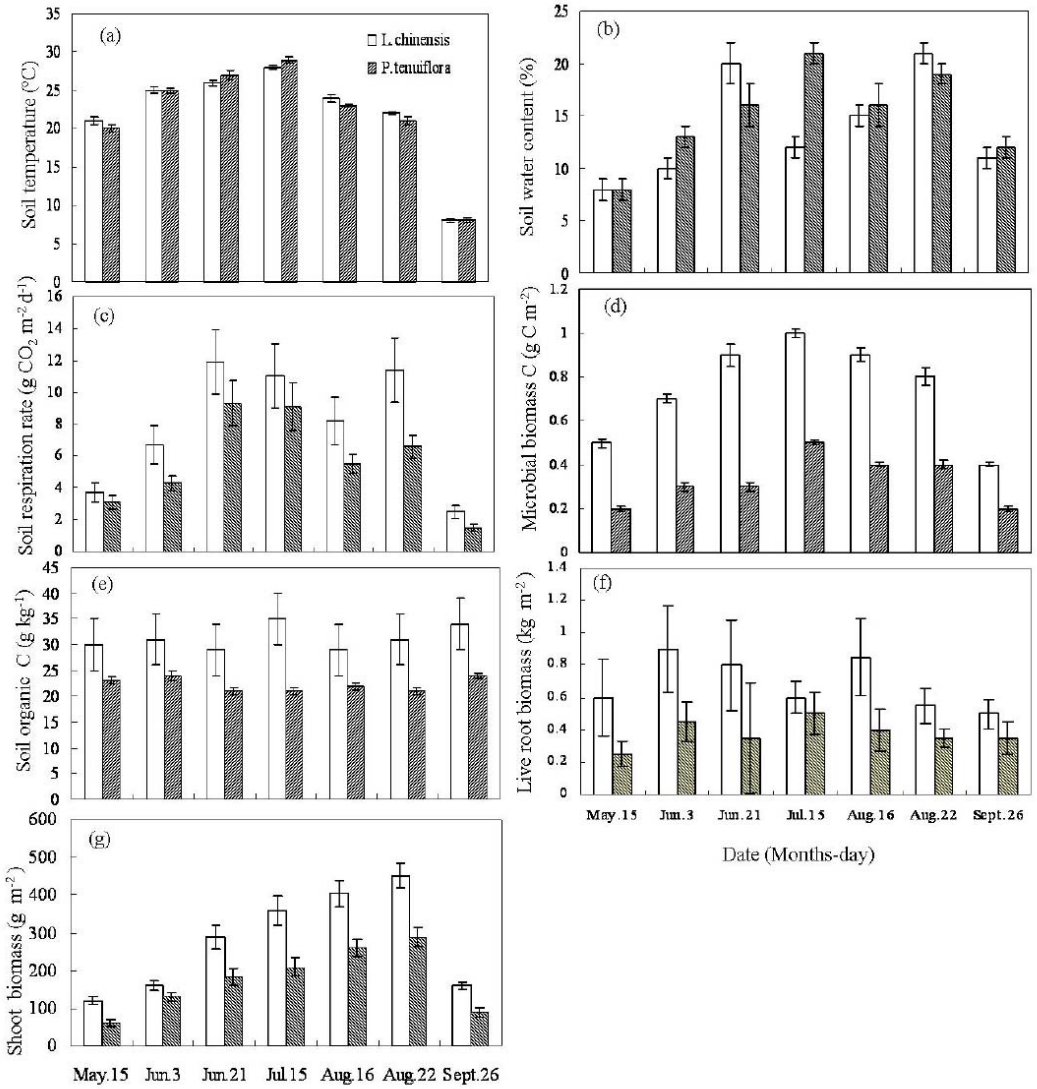

Figure 2. Comparisons of soil temperature **(a)**, soil water content **(b)**, soil respiration rate **(c)**, microbial biomass carbon **(d)**, soil organic carbon **(e)**, live root biomass **(f)** and shoot biomass **(g)** between *L. chinensis*- and *P. tenuiflora*-dominated communities at different observation times. Bars indicate the standard deviation of the mean (n=12).

0.5 kg m^{-2} without significant seasonal change in Community 2 (figure 2f). Shoot green biomass increased from May, reaching its maximum of 452 g m^{-2} in late August in Community 1, while a much smaller shoot biomass with a maximum of 289 g m^{-2} in late August was seen in Community 2 (figure 2g).

In summary, the MBC, SOC, live root biomass and shoot green biomass in Community 2 decreased by 55%, 28%, 45% and 37%, respectively, compared with Community 1 (figures 2d–g). There were high within-site variations of root biomass in the two communities; the highest coefficient of variation was 33% in Community 1 in May and 25% in Community 2 in mid-August (data not shown).

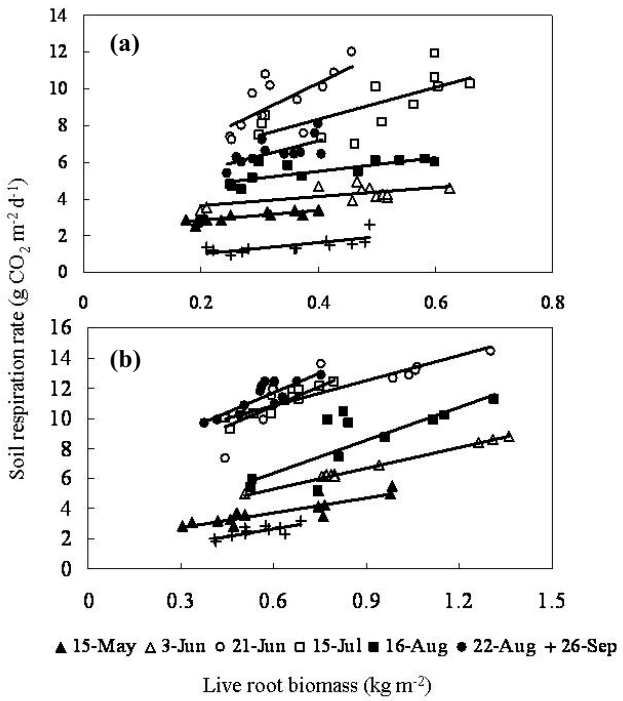

Figure 3. Linear regression lines between soil respiration rates and live root biomass in **(a)** *L. chinensis*- and **(b)** *P. tenuiflora*-dominated communities.

Multiple step-wise regression between soil respiration and soil temperature, water content, shoot biomass, root biomass, MBC and SOC showed that soil temperature was the primary factor affecting seasonal variation for both communities (R^2 was 0.68 and 0.75 for Communities 1 and 2, respectively).

3.2 *Estimation of root respiration*

In terms of the soil respiration rates and their corresponding root biomass, a set of linear regressive relationships between soil respiration (y) and live root biomass (x) were developed on each measuring date (e.g. 15 May, 3 June, 21 June, 15 July, 16 August, 22 August and 26 September; figure 3). Fifty-nine to 90% of the variation in soil respiration could be explained by the root biomass for Community 1, and 44–71% for Community 2 (table 2).

Microbial respiration rate ranged from 0.7 to 7.43 g CO_2 m^{-2} d^{-1} and from 0.42 to 4.83 g CO_2 m^{-2} d^{-1} in Communities 1 and 2, respectively (figure 4). The mean microbial respiration rates during the entire experiment were 3.78 and 3.23 g CO_2 m^{-2} d^{-1} for the two communities, respectively. The root respiration rate ranged from 0.78 to 5.26 g CO_2 m^{-2} d^{-1} in Community 2 (figure 4), decreasing by 41% compared with Community 1. There was a significant difference (paired t-test of monthly means, n=7, P<0.001) in the root respiration rate between the two communities, but not for the microbial respiration rate (paired t-test of monthly means, n=7, P>0.05).

Specific root respiration rate (root respiration rate normalized with root biomass) was higher in July (8.61 mg CO_2 g^{-1} d^{-1}) and late August (8.81 mg CO_2 g^{-1} d^{-1}) in Community 1 and in late June (15.65 mg CO_2 g^{-1} d^{-1}) in Community 2 (figure 4), but they were not significantly different as a whole during the study period (paired t-test of monthly means, n=7, P>0.05).

The contribution of root to soil respiration ranged from 38% to 76%, and from 25% to 72% for Communities 1 and 2, respectively (figure 4). The ratio of root respiration to total soil respiration averaged 56% and 43% in the two communities, respectively.

Table 1. Temperature-based Q_{10} models ($y=\beta_0 e^{\beta 1 T}$). R^2 is the coefficient of determination.

Community	Q_{10} model	R^2	Q_{10}	Basal soil respiration (g CO_2 m^{-2} d^{-1})	Annual soil respiration (g C m^{-2} yr^{-1})
L. chinensis	$Y=1.282\ e^{0.077x}$	0.69	2.16	2.77	360.6
P. tenuiflora	$Y=0.741e^{0.086x}$	0.83	2.36	1.75	239.5

In this model, y and T are soil respiration (g CO_2 m^{-2} d^{-1}) and soil temperature (°) at 10 cm soil depth; Q_{10} and basal soil respiration (t= 10°) were calculated using the formula $e^{10\beta 1}$ and $\beta_0 e^{10\beta 1}$, respectively.

Table 2. Regression of soil respiration Y (g CO_2 m^{-2} d^{-1}) as a function of live root biomass x (kg m^{-2}).

	L. chinensis-dominated community			*P. tenuiflora*-dominated community		
Date	*a*	*b*	R^2	*a*	*b*	R^2
15 May	1.82±0.33	3.21±0.54**	0.84	2.32±0.14	2.70±0.62**	0.71
3 June	2.54±0.23	4.58±0.32**	0.94	3.11±0.34	2.56±0.80*	0.47
21 June	7.43±1.17	5.61±1.24**	0.65	4.04±1.12	15.65±2.4*	0.49
15 July	5.63±0.3	8.61±0.56**	0.91	4.83±1.05	8.71±1.26*	0.53
16 August	1.94±0.45	7.30±1.86*	0.59	4.04±0.38	3.66±1.04**	0.62
22 August	6.42±0.57	8.81±0.98**	0.73	3.81±0.54	8.43±1.56*	0.44
26 September	0.70±0.04	3.33±0.44*	0.60	0.42±0.08	3.02±0.76*	0.55

The equation for predicting soil respiration from root biomass can be expressed as $Y=a+bx$, where a represents microbial respiration and b is specific respiration rate of roots (mg CO_2 g^{-1} d^{-1}) (per milligram mass of live roots). Data are expressed as mean ± standard deviation. Degrees of freedom for all the above equations were 11. * Indicates the values different from zero (P<0.05) and ** means P<0.01.

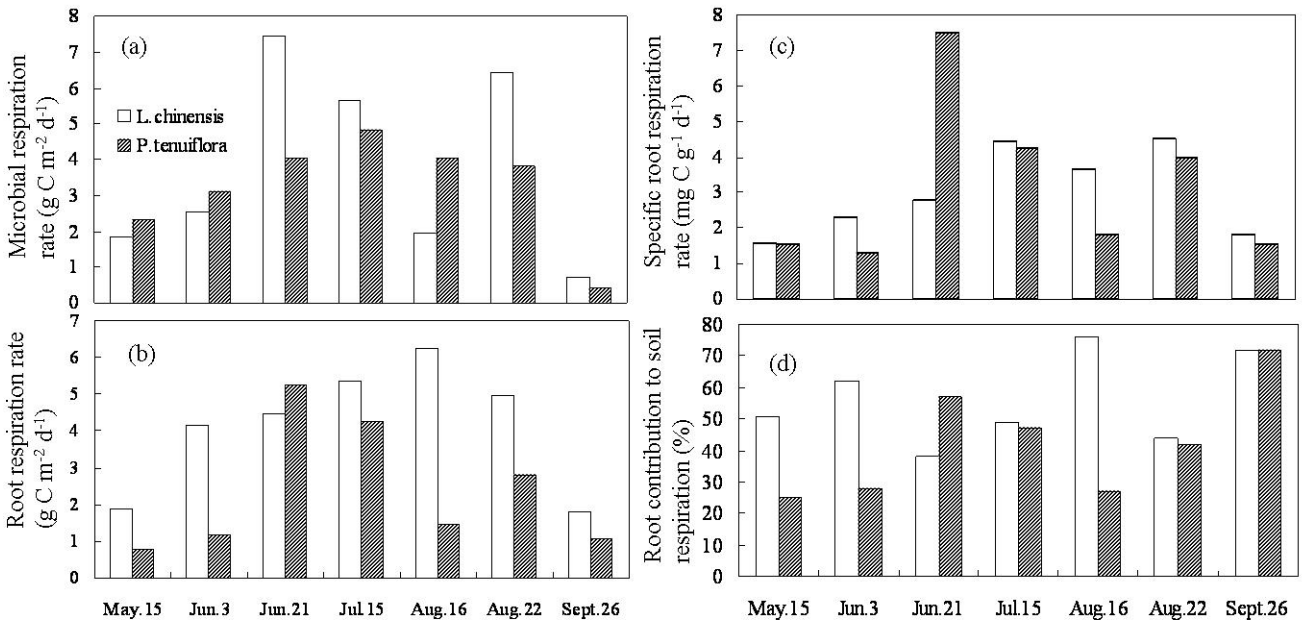

Figure 4. Seasonal changes in microbial respiration rate **(a)**, root respiration rate **(b)**, specific root respiration rate **(c)** and the contribution of root to soil respiration **(d)** in *L. chinensis*- and *P. tenuiflora*-dominated communities.

3.3 *Soil carbon balance*

The carbon input and output of Community 1 decreased by 34% and 12%, compared with Community 2 (table 3). The BNPP accounted for 47% and 46% of the NPP in the two communities, respectively. NEP was 54% lower in Community 2 than in Community 1, primarily due to its lower NPP (243.5 *vs* 383.4 g C m^{-2} yr^{-1}).

4. Discussion

4.1 *Effect of degradation on grassland biomass*

As shown in figure 2g, the maximum biomass in the disturbed community (Community 2) was considerably lower than that in the undisturbed community (Community 1) (291 *vs* 452 g m^{-2}), suggesting that degradation significantly decreases

Table 3. Soil carbon balance estimated for the two grassland communities.

	L. chinensis	*P. tenuiflora*
ANPP (g C m^{-2} yr^{-1})	203.4	130.9
BNPP (g C m^{-2} yr^{-1})	180.0	112.5
NPP (g C m^{-2} yr^{-1})	383.4	243.4
MR (g C m^{-2} yr^{-1})	158. 7	138.9
NEP (g C m^{-2} yr^{-1})	224.7	104.6

ANPP, above-ground net primary productivity; BNPP, below-ground net primary productivity; NPP, net primary productivity; MR, microbial respiration; NEP, net ecosystem productivity.

the shoot biomass of the grassland ecosystem. A similar conclusion was also drawn in a grazed *L. chinensis* steppe in Inner Mongolia (Li *et al* 2004) and in an alpine meadow on the Tibetan Plateau (Cao *et al* 2004). On the other hand, in grasslands, the below-ground biomass is generally 5–10 times higher than the shoot biomass (Iwaki 1973). In our study area, the ratio of below-ground to shoot biomass averaged 4:1 and 3:1 in Communities 1 and 2, respectively, close to the ratio of 4:1 in a grazed *L. chinensis* steppe (Li *et al* 2004) and 5:1 in a light grazing alpine meadow on the Tibetan Plateau (Cao *et al* 2004). Root biomass at 30 cm depth is usually 85% of that of the whole depth in temperate grasslands (Jackson *et al* 1996). The actual ratio thus may be somewhat higher because roots deeper than 30 cm were not included.

4.2 *Factors controlling soil respiration*

Soil temperature and water content are known to have a pronounced influence on the seasonal dynamics of soil respiration (Fang and Moncrieff 2001; Reichstein *et al* 2003). The physical and chemical properties of soil such as SOC, root density and MBC may also affect the magnitude of soil respiration (Raich and Tufekcioglu 2000). Our study showed that the soil temperature at 10 cm was the main factor affecting the seasonal change of soil respiration (P=0.02). Similar results were also found in a typical steppe of Inner Mongolia and an alpine meadow on the Tibetan plateau (Li *et al* 2000; Cao *et al* 2004).

The reported Q_{10} values vary widely from 1.5 to 5.6 in grasslands (Rey *et al* 2002). Our estimates (2.16–2.36 in table 1) were very close to the value obtained (2.0–3.0) in an *L. chinensis* steppe in Inner Mongolia (Li *et al* 2000), but lower than that for an alpine meadow on the Tibetan plateau (Cao *et al* 2004). The higher Q_{10} value in the latter may be a result of the colder climate in Tibet because soil respiration is shown to be more sensitive to soil temperature in cold areas than in warm regions (Kirschbaum 1995). However, the Q_{10} value calculated by field data is affected by many other factors, such as microbial and soil chemical properties, and varies even at the same site at different times (Kirschbaum 1995). Therefore, estimates of the Q_{10} value derived from a short-term observation should be considered with caution.

4.3 *Requirements and limitations of the inferred approach*

The inferred approach used in the present study was first proposed by Kucera and Kirkham (1971). This approach has the following shortcomings. First, large variations in root biomass and soil respiration could lead to a relatively low R^2 (Kucera and Kirkham 1971). Second, this method assumes that microbial respiration is estimated as the respiration rate when the root biomass is zero (in fact, at this point, microbial respiration is minimum). Consequently, the root respiration derived by this method is based on the minimum microbial respiration, ignoring root biomass; however, this subtraction in some cases may not be valid as it is based on the minimum root activity (i.e. minimum root biomass). Finally, plants will allocate available photosynthates, i.e. whenever there is plenty of sugar (photosynthate) available, all roots get more; otherwise, only some get more. Consequently, microbes might get plenty of sugar only when there is a threshold value of soluble carbohydrates in roots (i.e. increased root exudation). Despite these shortcomings, this method is relatively simple and has been widely used in recent studies (e.g. Gupta and Singh 1981; Behera *et al* 1990; Hill *et al* 2004; Wang *et al* 2005; Jia *et al* 2006). In his most recent review, Kuzyakov (2006) concluded that this approach, compared with other methods, has the lowest disturbance and highest universality for separating the sources of CO_2 efflux from soil.

4.4 *Seasonal changes in microbial and root respiration*

Microbial respiration depends on temperature, moisture, substrate quality and quantity, maximum activity of respiratory enzymes and demand for respiratory products (Ryan and Law 2005). In our study, microbial respiration in both communities showed similar patterns (figure 4a); higher in the summer and lower in the spring and autumn, which corresponded to the change in soil temperature (figure 2a).

Root respiration exhibited a markedly different seasonal pattern from that of microbial respiration in the two communities (figure 4b). From May to early June, root respiration increased by a factor of 2.2 in Community 1 and from May to late June, by a factor of 6.74 in Community 2 (figure 4). The higher root respiration in early summer may

have resulted from the associated high physiological activity of the roots (Li *et al* 2002). The higher root respiration in early June in Community 1 may be due to higher root biomass (0.9 kg m^{-2}) and the highest net photosynthesis rates. For Community 2, rapid increase of root respiration in late June was probably due to the higher specific respiratory activities of roots (15.65 mg C g^{-1} d^{-1}) (figure 4d).

The seasonal differences in pattern between microbial and root respiration may be resulting from the different sensitivity of microorganisms and roots to environmental factors (Kirschbaum 1995). Phenological processes are also likely to constrain the response of root growth and respiration to environmental changes (Oleksyn *et al* 2000). Root respiration rates have been reported to be correlated with tissue nitrogen concentrations (Kelliher *et al* 2004; Ryan *et al* 1996) and nitrogen has the potential to alter whole-plant source–sink relationships, and root and mycorrhizal biomass because of reduced allocation of carbon to roots (Ryan *et al* 2004). In addition, acclimation generally limits the response of autotrophic respiration to temperature and reduces carbon loss at sustained high temperatures (Bolstad *et al* 2003). However, because of the limited sampling frequencies (7 times) in our study, it is difficult to arrive at a general conclusion about the dependence of root respiration on environmental factors. Our results toward this objective are preliminary, and need further investigation in the future.

4.5 *Contribution of root to soil respiration*

Contribution of root to soil respiration varies widely among different studies, ranging from 15% to 90% in grassland ecosystems (Norman *et al* 1992; Dugas *et al* 1999; Wang *et al* 2005; Li *et al* 2002). At our study site, the contribution in the growing season ranged from 38% to 76% and from 25% to 72% in Communities 1 and 2, respectively. Our estimate was consistent with the results obtained from a tallgrass prairie grassland in Missouri (40%, Kucera and Kirkham 1971), a tropical grassland at Kurukshetra (42%, Gupta and Singh 1981) and a C_3/C_4 mixed grassland in Japan (31–51%, Wang *et al* 2005), but was higher than that in a semi-arid grazed grassland in China (15–37%, Li *et al* 2002).

4.6 *Annual soil respiration rate and grassland carbon sequestration*

Our estimate (239.5–360.6 g C m^{-2} yr^{-1}) of the annual soil respiration rate in the two communities (table 1) fell within the reported range (132–830 g C m^{-2} yr^{-1}) for world temperate grasslands (Raich and Schlesinger 1992), and close to the value (271.3 g C m^{-2} yr^{-1}) in a grazed *L. chinensis* grassland in Inner Mongolia (Li *et al* 2004).

NEP is the difference between NPP and heterotrophic respiration, and is taken as a measure of sink or source strength (Schulze *et al* 2002). Using existing management conditions, most temperate grasslands worldwide are considered to be C sinks. Our estimate (104.6–224.7 g C m^{-2} yr^{-1}) of NEP fell within the reported carbon sequestration rates of temperate grassland, ranging from 45 to 640 g C m^{-2} yr^{-1} (Jones and Donnelly 2004). The amount of SOM retained in grassland soils is strongly influenced by management (Conant *et al* 2001; Zan *et al* 2001; Schuman *et al* 2002). Our results strongly suggest that degradation has decreased grassland carbon sequestration in the long term. The potential switching of the grassland ecosystem from its current role as a carbon sink to a carbon source is critically dependent upon the degree of degradation. A net carbon release of 75.1 g C m^{-2} yr^{-1} was reported in a grazed *L. chinensis* steppe in Inner Mongolia (Li *et al* 2004). A decrease in soil C close to 60% was observed for the degradation induced by the transition from grassland to arable land (Guo and Gifford 2002).

Although some evidence suggests that temperate grassland soils can sequester relatively large amounts of C, there is still uncertainty as to how long this can remain and whether there is an upper limit to C storage (Frank 2002). Grassland degradation influences both the above- and below-ground processes which drive the C cycle, and ultimately determine how much C is sequestered in grassland soils. Therefore, it is crucial to understand how degradation regulates these processes and affects the capacity to sequester amounts of C in grassland soils in the future.

5. Conclusions

By comparing the seasonal changes in soil respiration, shoot and below-ground biomass, MBC and SOC between an undisturbed and a degraded community, we demonstrated that grassland degradation significantly alters soil respiration rates and carbon sequestration. Such degradation significantly decreases the productivity of grassland ecosystems (via shoot and below-ground production). No significant change occurred for annual CO_2 release from the soil to the atmosphere. Although the two communities at present serve as a carbon sink, our results strongly suggest that degradation will decrease grassland carbon sequestration in the long term.

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