

This article appeared in a journal published by Elsevier. The attached copy is furnished to the author for internal non-commercial research and education use, including for instruction at the authors institution and sharing with colleagues.

Other uses, including reproduction and distribution, or selling or licensing copies, or posting to personal, institutional or third party websites are prohibited.

In most cases authors are permitted to post their version of the article (e.g. in Word or Tex form) to their personal website or institutional repository. Authors requiring further information regarding Elsevier's archiving and manuscript policies are encouraged to visit:

<http://www.elsevier.com/copyright>



Contents lists available at SciVerse ScienceDirect

Soil Biology & Biochemistry

journal homepage: www.elsevier.com/locate/soilbio

Linking litter production, quality and decomposition to vegetation succession following agricultural abandonment

Kerong Zhang^a, Xiaoli Cheng^a, Haishan Dang^a, Chen Ye^a, Yulong Zhang^{a,b}, Quanfa Zhang^{a,*}^a Key Laboratory of Aquatic Botany and Watershed Ecology, Wuhan Botanical Garden, The Chinese Academy of Sciences, Wuhan 430074, PR China^b Graduate University of the Chinese Academy of Sciences, Beijing 100049, PR China

ARTICLE INFO

Article history:

Received 11 March 2012

Received in revised form

3 August 2012

Accepted 5 August 2012

Available online 17 August 2012

Keywords:

Litter

Fine root

Production

Decomposition

C and N input

Land use change

ABSTRACT

Agricultural land abandonment has been increasing worldwide for environmental and socio-economic reasons, and knowledge of its key ecological processes (e.g., carbon (C) and nitrogen (N) input and accumulation) in relation to vegetation succession can provide important information for ecosystem management and greenhouse gas emissions mitigation. In order to better understand the above- and belowground litter dynamics following agricultural abandonment, we simultaneously studied the litter and fine root production, quality, decomposition, C and N input in ecosystems along a secondary successional gradient (i.e., grassland, shrub-grass land, young secondary forest, and mature secondary forest) following agricultural abandonment in China's Qinling Mountains. Results showed that the significant increase of aboveground woody plant litter and decrease of grass litter during vegetation succession led little changes in total litter production and annual total C and N input in different succession stages, while the fine root production, fine root biomass, C input from fine root production increased significantly with stand age. The initial litter C concentration and fine root carbon: phosphorous ratio (C:P) were the main factors in explaining the variations of decomposition rates of litter and fine root, respectively. The increasing C concentration in litter and the increasing C:P ratio in fine root during vegetation succession had potentially driven the decreases in litter and fine root decomposition rate respectively. The accumulation of litter standing crop during vegetation succession could be attributed to the decreases in litter decomposition rate partly caused by changes in litter quality, rather than the increases in litter production. Our results imply that the changes in vegetation type have a much smaller role in the annual total litter production and the total litter C and N input than previously assumed, while the changes in quality and decomposition rate may have largely influenced C accumulation in stand floor and soil during secondary succession following agricultural abandonment.

© 2012 Elsevier Ltd. All rights reserved.

1. Introduction

Agricultural land abandonment has been increasing worldwide for environmental and socio-economic reasons such as soil degradation, market incentives, environmental protection programs, migration and rural depopulation (Rey-Benayas et al., 2007; Cramera et al., 2008). For example, the U.S. Conservation Reserve Program (established by the Food Security Act in 1985), one of the U.S. largest environmental programs targeting land use, removes almost 13.76×10^6 ha from crop production and establishes grass or tree covers under 10–15 year contracts (Roberts and Lubowski, 2007). China's 'Grain-for-Green' project (launched in 1999), one of the world's most ambitious ecological restoration programs, has

converted 9.26×10^6 ha former croplands to forests or grasslands until 2010. These abandoned agricultural lands are experiencing a change from crop to forest or other secondary vegetations, accompanied by ecosystem structure, processes and functions evolution (Davidson et al., 2007; Zhang et al., 2010). Knowledge of key ecological processes (e.g., carbon (C) and nitrogen (N) input and accumulation) in relation to vegetation succession following agricultural abandonment can provide important information for ecosystem management and greenhouse gas emissions mitigation (Lal, 2004; Chazdon, 2008; Ohtsuka et al., 2010; Yang et al., 2011).

The production and decomposition of above- and belowground litter (mainly fine root, Steinaker and Wilson, 2005) are key processes linking plant and soil in the terrestrial ecosystem (Cusack et al., 2009; Schindler and Gessner, 2009). Most of the terrestrial net primary production (e.g., more than 85% in temperate ecosystems) enters the detritus pool as dead organic matter (Swan et al., 2009), and the subsequent recycling of C and nutrients are

* Corresponding author. Tel.: +86 27 87510702; fax: +86 27 87510251.
E-mail address: qzhang@wbpcas.cn (Q. Zhang).

fundamentally important process which has major control over the fluxes of CO₂ from soils, buildup of soil organic matter, availability of N and other nutrients, with consequent feedbacks to vegetation growth (Hättenschwiler et al., 2005; Hättenschwiler and Gasser, 2005; Swan et al., 2009; Klotzbücher et al., 2011). The leaf litter and fine root are considered as 'fast C pools' (Meier and Leuschner, 2010). Annual C and nutrient inputs to the soil from fine roots frequently equal or exceed those from leaves (Jackson et al., 1997). In some semiarid and temperate ecosystems, belowground fine root production is even greater than aboveground production (Hibbard et al., 2001; Ruess et al., 2003; Steinaker and Wilson, 2005).

Changes in vegetation as a consequence of land-use change, e.g., agricultural abandonment, may affect litter and fine root dynamics through many potential factors and processes, including transformation of vegetation composition (Connin et al., 1997; Gill and Burke, 1999; Yang et al., 2010), improvement of soil fertility (Uselman et al., 2007), alteration of the needs in nutrient and water for plant growth (Uselman et al., 2007; Yang et al., 2010), etc. Although the litter and fine root production, decomposition and their influencing factors have been extensively investigated in various ecosystems worldwide (Bray and Gorham, 1964; Aerts, 1997; Matthews, 1997; Silver and Miya, 2001), few studies have simultaneously measured the above- and belowground litter production and decomposition in relation to vegetation succession following agricultural abandonment (Steinaker and Wilson, 2005; Yankelevich et al., 2006; Ostertag et al., 2008). Moreover, previous studies have mainly focused on the forest stage (Ruess et al., 2003; Yankelevich et al., 2006; Ostertag et al., 2008; Yang et al., 2010), and little attention has been paid to the early successional stages dominated by grass or shrub (Ostertag et al., 2008). The deficient knowledge in litter and fine root is still the main uncertainties in determining how C and N cycles respond to changes of vegetation or land-use (Matamala et al., 2003; Trumbore and Gaudinski, 2003).

In the present study, we investigated the production, quality and decomposition of litter and fine root in ecosystems along a successional gradient (i.e., grassland, shrub-grass land, young secondary forest, and mature secondary forest) following agricultural abandonment in the Qinling Mountains, China. We hypothesized that litter/fine root production had increased along with vegetation succession following agricultural abandonment, while decomposition rate decreased. We also explored the factors influencing production and decomposition of litter and fine root.

2. Materials and methods

2.1. Study site

This study was conducted in the Foping National Nature Reserve (FNNR, a member of UNESCO/MAB World Network of Biosphere Reserves), south aspect of China's Qinling Mountains. This region belongs to subtropical humid zone, and annual precipitation ranges from 950 to 1200 mm, most of which falls between July and September. Mean annual temperature is 11.8 °C, and the mean temperatures are −0.3 °C in January and 21.9 °C in July. Frost free days average 220. Natural vegetation of the study area is deciduous broad-leaved forests. The soil is yellow brown developed from granitic gneiss (Zhang et al., 2010).

The natural successional pathway after agricultural abandonment in the region follows grassland, shrub-grass land, young secondary forest, and mature secondary forest (Zhang et al., 2010). Thus, nineteen stands including 5 grasslands, 6 shrub-grass lands, 4 young secondary forest forests, and 4 mature secondary forest (with stand age older than 50 years) were selected in this study (Table 1). We inferred that the stands were derived from croplands according to abandoned irrigation ditches and ridges (Ren et al., 1998). The years since abandonment (stand age) was sought from landowners or estimated from the tree-rings of the oldest pioneer trees. A comprehensive survey of vegetation and soil was carried

Table 1
Site characteristics and the relative proportion of the dominant litter species used in decomposition experiment.

Site	Stand age (yr)	Altitude (m)	Vegetation type	Dominant litter species	Proportion of litter used in experiment (%)
H1	1	1250	Grassland	<i>Artemisia lavandulaefolia</i> ; <i>Polygonum alatum</i> ; <i>Elsholtzia ciliata</i>	50:25:25
H2	4	1130	Grassland	<i>A. lavandulaefolia</i> ; <i>Pennisetum alopecuroides</i>	75:25
H3	5	1233	Grassland	<i>A. lavandulaefolia</i> ; <i>Cucubalus baccifer</i>	75:25
H4	5	1284	Grassland	<i>A. lavandulaefolia</i> ; <i>Cynoglossum zeylanicum</i> ; <i>P. alatum</i>	75:12.5:12.5
H5	8	1135	Grassland	<i>A. lavandulaefolia</i> ; <i>P. alopecuroides</i>	87.5:12.5
S1	5	1098	Shrub-grass land	<i>A. lavandulaefolia</i> ; <i>Pueraria lobata</i>	62.5:37.5
S2	6	1290	Shrub-grass land	<i>A. lavandulaefolia</i>	100
S3	7	1250	Shrub-grass land	<i>A. lavandulaefolia</i> ; <i>P. lobata</i> ; <i>Pteridium aquilinum</i> ; <i>Rhus chinensis</i>	37.5:37.5:12.5:12.5
S4	7	1095	Shrub-grass land	<i>Populus purdomii</i> ; <i>A. lavandulaefolia</i>	50:50
S5	11	1253	Shrub-grass land	<i>A. lavandulaefolia</i> ; <i>P. lobata</i>	62.5:37.5
S6	12	1260	Shrub-grass land	<i>Castanea mollissima</i> ; <i>Juglans regia</i> ; <i>R. chinensis</i> ; <i>P. lobata</i> ; <i>Prunus tomentosa</i>	60:12.5:12.5:10:5
N1	15	1280	Young secondary forest	<i>Broussonetia papyrifera</i> ; <i>Actinidia chinensis</i> ; <i>Picrasma quassioides</i>	50:25:25
N2	20	1140	Young secondary forest	<i>C. mollissima</i> ; <i>Platycarya strobilacea</i>	50:50
N3	≈ 30	1111	Young secondary forest	<i>Quercus variabilis</i>	100
N4	≈ 45	1301	Young secondary forest	<i>C. mollissima</i> ; <i>Carpinus turczaninowii</i> ; <i>Rhus punjabensis</i> var. <i>sinica</i> ; <i>Quercus serrata</i> var. <i>brevipetiolata</i> ; <i>Picrasma quassioides</i>	30:25:15:15:15
N5	≈ 50	1298	Mature secondary forest	<i>C. mollissima</i> ; <i>Carpinus turczaninowii</i> ; <i>Actinidia chinensis</i> ; <i>Corylus heterophylla</i> ; <i>Litsea tsinlingensis</i>	30:25:15:15:15
N6	≈ 70	1276	Mature secondary forest	<i>C. mollissima</i> ; <i>Q. serrata</i> var. <i>brevipetiolata</i> ; <i>Bashania fargesii</i> ; <i>Dendrobenthamia japonica</i> var. <i>chinensis</i> ; <i>Acer palmatum</i>	50:17.5:17.5:10:5
N7	≈ 80	1277	Mature secondary forest	<i>C. mollissima</i> ; <i>Carpinus turczaninowii</i> ; <i>Q. serrata</i> var. <i>brevipetiolata</i> ; <i>D. japonica</i> var. <i>chinensis</i> ; <i>B. fargesii</i>	50:17.5:17.5:7.5:7.5
N8	≈ 100	1257	Mature secondary forest	<i>C. mollissima</i> ; <i>B. fargesii</i> ; <i>Juglans mandshurica</i>	50:25:25

out to ensure the comparability (e.g., similar soil type, parent material, topography, and disturbance regime) among the sampling plots. Also the samplings were carried out within a distance of 4 km (107°49'–107°51'E, 33°32'–33°35'N) in a small watershed. There were no fertilization, cutting, insect pest control and human disturbance in all stands. The mature secondary forests were deciduous broad-leaved forests dominated by *Quercus serrata* var. *brevipetiolata*, *Castanea mollissima*, *Dendrobenthamia japonica* var. *chinensis*, *Bashania fargesii*, etc., with well-developed understory. The young secondary forests were dominated by deciduous broad-leaved trees, e.g., *C. mollissima*, *Broussonetia papyrifera*, *Platycarya strobilacea*, etc. The shrub-grass lands were dominated by *Pueraria lobata*, *Rhus chinensis*, *Artemisia lavandulaefolia* etc., while the dominant herbs in grasslands were *A. lavandulaefolia*, *Polygonum alatum*, *Pennisetum alopecuroides* etc. The stand characteristics and vegetation composition were previously reported (Zhang et al., 2010).

2.2. Measurement of litter production, litter standing crop, litter quality, decomposition, C and N input

In each shrub and forest stand, five litter traps were randomly set approximately 0.3 m above the ground for litter collecting. The litter traps were made from nylon window screening (1 mm mesh) with a size of 100 cm × 80 cm. Litter was collected monthly for two years beginning in July 2008 (litter collecting in two stands, i.e., N3 and N7, began in July 2009). Five 1 m × 1 m quadrats were set in each stand for grass harvesting in the end of September (i.e., the peak value of grass biomass). Because almost all aboveground biomass of grass dies in winter, we estimated its annual litter production using the peak value of biomass. All litter was dried at 65 °C and sorted into leaves, twigs, bark, flower, fruit and others. We used the mean value of annual production in 2009 and 2010 in the following analysis because statistical analysis showed that there were no significant differences between the two years. The C and N input from aboveground litter production ($\text{Mg ha}^{-1} \text{y}^{-1}$) was calculated by multiplying the annual production by their C and N concentration (as Steinaker and Wilson, 2005). Litter standing crop was sampled in the mid of October (i.e., one month before the peak of litter fall) by collecting litter from the surface of the floor (L and F horizons). Five 1 m × 1 m quadrats were set randomly in each stand for litter standing crop collecting.

A preliminary analysis indicated that leaf litter accounted for 81.5% of the total litter production in secondary forests (Zhang, 2011). Thus, only leaf litter was employed in litter decomposition experiment for secondary forests. We collected freshly senesced leaf of main woody species in each stand in the end of October as litter material for decomposition experiment. For grassland, all senescent aboveground biomass was collected, and then cut the stem into 5 cm sections together with leaf as material for decomposition. Recent studies have showed that single species litter decomposition may not represent natural ecosystems where multiple species decompose together (Hättenschwiler and Gasser, 2005; Hui and Robert, 2009), thus, experiments of mixed litter decomposition was conducted. For each stand, mixed litter was weighed according to the proportion of each dominant litter species in corresponding stands, assumed to represent the average litter production in the stands (Table 1). Four gram air-dried and well mixed litter was placed into nylon litterbags (20 cm × 16 cm, with a top mesh of 1 mm and a bottom of 55 μm mesh) with unique plastic tag. Twenty gram mixed subsamples for each stand was dried at 65 °C for determining the residual moisture content of the air-dried material, and then ground for measuring initial chemical characteristics. Total C and total N concentrations of litter were measured by C/N Analyzer (Flash, EA, 1112 Series, Italy). Total

phosphorus (P) concentration was measured using Molybdenum Yellow method (Lu, 2000). Klason lignin concentration was measured as dry weight of solids after hydrolysis with 72% (w/w) H_2SO_4 (Kirk and Obst, 1988). Total tannin concentrations were estimated by using a radial diffusion assay of tannin-mediated protein precipitation (Hagerman, 1987), and tannin concentrations were expressed as the amount of tannic acid standard needed to precipitate the same amount of protein on a per dry weight litter mass basis (as described by Huang et al., 2010).

At each stand, 20 litterbags were randomly placed on the floor at the end of November in 2009. Four litter bags were retrieved from each stand after 73, 146, 219, 292, and 365 days. The retrieved litter was removed from litterbags, weighed and taken subsamples for measuring moisture content (dried at 65 °C). The proportion of initial mass was calculated by dividing the mass at any harvest date by the initial mass. Decomposition rates were calculated from percent mass remaining material by using the negative exponential decay constants (k) (Olson, 1963):

$$y = e^{-kt}$$

where y is the fraction of mass remaining at a given time, t (year) (Bontti et al., 2009).

2.3. Measurement of fine root biomass, production, quality, decomposition, C and N input

Ten soil cores were collected randomly for measuring the fine root vertical distribution in each stand. The soil cores were cut into four segments according to the soil layers, 0–10, 10–20, 20–30, and 30–40 cm (about half of the soil layers were shallower than 40 cm in our sampling stands). The H horizon (comprised of well-decomposed plant residues), if existed, was included in the surface layer of 0–10 cm. Considering most fine root distributed in 0–20 cm (according to the results of vertical distribution investigation), we only studied the fine root production in the depth of 0–20 cm. Sequential soil core method was carried out to estimate changes in live/dead fine root standing stocks over time (King et al., 2002; Silver et al., 2005; Jha and Mohapatra, 2010). Bimonthly, about twelve soils cores were collected randomly by using 5.4 cm diameter core sampler in the depth of 0–20 cm at each stand. A total of 1368 soil cores were taken out from 19 stands during August 2009 to August 2010. Roots in each soil cores were washed free of soil and separated into live/dead fine root (diameter ≤ 2 mm) according to a catalogue of color, luster and elasticity (Yang et al., 2010). All roots were dried at 65 °C and weighted.

We determined the belowground litter production by measuring fine root production (as Steinaker and Wilson, 2005). The compartment flow model was used to estimate the fine root production as described by Ostertag (2001) and Silver et al. (2005):

$$P_t = \text{LFR}_t - \text{LFR}_{t-1} + M_t,$$

$$M_t = \text{DFR}_t - \text{DFR}_{t-1} + D_t,$$

$$D_t = \text{Dss} \left(1 - e^{-kt} \right),$$

$$\text{Dss} = (\text{DFR}_t + \text{DFR}_{t-1})/2$$

where P_t is fine root production, LFR is live fine root mass, DFR is dead fine root, t and $t - 1$ is the time interval, D is the mass of root decayed over the interval, Dss is the mean dead fine root standing stock over the interval, $1 - e^{-kt}$ is the fraction of mass of roots that have decomposed over the time interval calculating from the root

litter bags incubation experiment (McClagherty et al., 1982; Silver et al., 2005).

Fine root samplings were collected in November 2009 for decomposition experiment. Collecting and identifying recently senesced roots from field is impractical (Steinaker and Wilson, 2005), thus we collected the mixed fine roots at the time after leaf abscission. The fine roots were washed, air-dried, cut into 5 cm sections. Four gram well mixed fine roots were placed into each nylon bags (20 cm × 16 cm, with a top mesh of 1 mm and a bottom of 55 μm mesh) with unique plastic tag. The fine root was tiled evenly in order to get in touch with soil. At each stand, 20 root bags were randomly buried vertically into the soil to a depth of 20 cm at the end of November 2009. The retrieved date, number of root bags, treatment and decomposition rate measurement for fine root bags were similar to the aboveground litter bags. In addition, 20 g mixed initial subsamples for each stand was dried at 65 °C for determining the residual moisture content of the air-dried material, and then ground for measuring initial chemical characteristics. The total C, N, P, tannin and lignin concentrations of fine root were measured using the method in accordance with litter. The C and N input from fine root ($\text{Mg ha}^{-1} \text{y}^{-1}$) was determined by multiplying the fine root production by their C and N concentrations (as Steinaker and Wilson, 2005).

2.4. Soil physico-chemical properties and net N mineralization rate

Three quadrats were selected randomly in each stand for soil sampling. Soil samples were taken at a depth of 0–20 cm in each stand for physico-chemical properties analyses. All soil sampling was carried out within two days at end of July, the vegetation growing season. The air-dried subsamples were passed through 1.0 and 0.25 mm sieves for chemical analyses. The methods described by Lu (2000) were used to determine the following variables in each soil sample: total P, molybdenum blue colorimetry; total potassium (K), flame photometry; available P, colorimetric method (by 0.5 M NaHCO_3 extraction); available K, flame photometry; soil moisture content, dried at 105 °C. The $\text{NO}_3\text{--N}$ was extracted from fresh soil samples with pure water (with CaSO_4) and measured by phenol disulfonic acid spectrophotometric method, and the $\text{NH}_4\text{--N}$ was extracted from fresh soil samples with a 2 M KCl solution and its concentration was determined by indophenol blue colorimetry (Lu, 2000). An aliquot (about 10 g) of dried soil was treated with 1 M HCl for 24 h at room temperature to remove inorganic carbon, then the residue was washed, dried at 65 °C, and analyzed for soil organic C (SOC) (as described by Cheng et al., 2006). An aliquot (about 10 g) of dried soil was hydrolyzed with H_2SO_4 at 105 °C to obtain recalcitrant C (RC) as described by Rovira and Vallejo (2007). Soil total C (TC), SOC, RC, and total N (TN) were measured using a C/N Analyzer (Flash, EA, 1112 Series, Italy) (Cheng et al., 2006). Additional samples, six soil cores per stand, were taken by a core sampler for bulk density measurement. All results of soil variables were expressed on a dry weight basis. The soil C and N storages were calculated using the following equations (Guo and Gifford, 2002),

$$\text{Soil C or N storage} = (\text{soil C or N concentration}) \\ \times (\text{soil bulk density}) \times (\text{soil depth})$$

We performed *in situ* incubations of soil cores in July–August in 2009 to assess rates of net soil N mineralization as indices of N availability, using the method described by Yan et al. (2009). Five paired soil cores (positioned in pairs) were taken using PVC tubes (20 cm in length, 5 cm in diameter) from five randomly chosen quadrats in each stand at end of July. One soil core from each pair was taken to laboratory as the unincubated sample to measure

initial $\text{NH}_4\text{--N}$ and $\text{NO}_3\text{--N}$ concentrations. The other core of each pair was wrapped with low-density polyethylene on the top and with gauze under the bottom, and then inserted into its original position. After 30 days field incubation, the incubated samples were taken to laboratory to determine $\text{NH}_4\text{--N}$ and $\text{NO}_3\text{--N}$ concentrations. The changes in inorganic-N concentration during the incubation period represented net N mineralized from organic sources.

2.5. Statistical analyses

We used one-way ANOVA to determine whether the studied variables exhibited significant variation among grassland, shrub-grass land, young secondary forest forests, and mature secondary forest. The litter/fine root production and litter standing crop were expressed as the amount of biomass dry weight per area (ha). We estimated the relationships among the studied variables with stand age using curve estimation. We used the Pearson correlation analysis and stepwise regression analyses to explore correlations among two or more variables. All statistical analysis was carried out using SPSS 13.0. All differences reported were significant at $P < 0.05$ unless otherwise stated.

3. Results

3.1. Aboveground litter production, decomposition rate and litter standing crop

Annual aboveground litter production from woody plants increased significantly with stand age ($R^2 = 0.60$, $P = 0.0001$), while the litter from grass decreased significantly ($R^2 = 0.85$, $P < 0.0001$) (Fig. 1). However, total aboveground litter production (including woody plants and grass) had no significant relationship with stand age ($P > 0.05$), and there were no significant differences among grassland, shrub-grass land, young secondary forest, and mature secondary forest (Table 2, Fig. 1).

Litter standing crop increased significantly with stand age, and decreased significantly with increasing decomposition rate, but had no significant relationship with annual litter production (Fig. 2). Litter standing crop in mature secondary forest was significantly greater than in grassland and shrub-grass land (Table 2).

The litter decomposition rate was significantly lower in mature secondary forest than grassland (Table 2), and it decreased significantly with stand age (Fig. 3). Linear correlation analysis showed that litter decomposition rate was negatively correlated with initial C concentration ($r = -0.78$, $P < 0.0001$), lignin concentration ($r = -0.49$, $P = 0.034$), and lignin:P ($r = -0.48$, $P = 0.0036$). The litter C concentration was significantly positively correlated with lignin concentration ($r = 0.54$, $P = 0.017$). Stepwise regression analyses showed that initial C concentration in litter was the main factor in explaining the variation of litter decomposition rates ($R^2 = 0.61$, $P < 0.0001$) (Fig. 3).

3.2. Fine root biomass, production, and decomposition rate

Most fine root was distributed in the 0–20 cm soil layer, and the proportion of surface fine root biomass (in 0–20 cm) in total fine root (in 0–40 cm) was 84.9% in grassland, 74.3% in shrub-grass land, 79.0% in young secondary forest, and 69.5% in mature secondary forest. The fine root biomass in mature secondary forest was significantly greater than those in grassland, shrub-grass land, and young secondary forest (Table 2). The fine root biomass and production both increased significantly with increasing stand age (Fig. 4). Fine root production was significantly greater in mature secondary forest than in grassland (Table 2). There were no significant differences in dead fine root production among

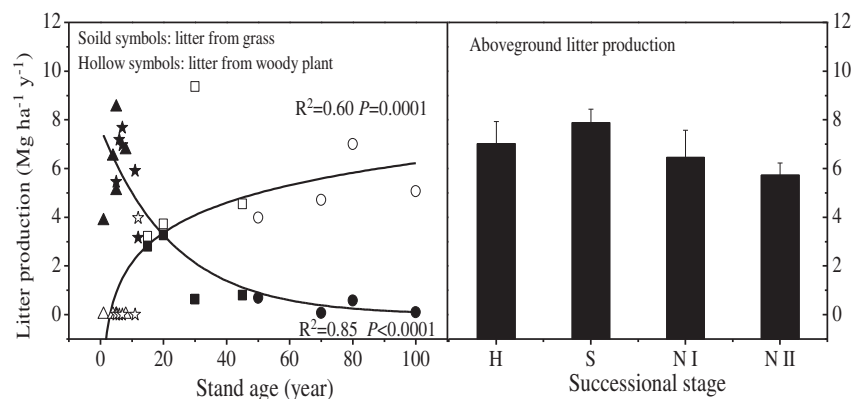


Fig. 1. Litter production in different successional stages (H = Grassland, S=Shrub-grass land, NI = Young secondary forest, NII = Mature secondary forest), and its relationship with stand age. In the left panel, each symbol represents the average of five repetitions from each of the 19 different stands. Triangle: Grassland; Star: Shrub-grass land; Square: Young secondary forest; Circle: Mature secondary forest.

grassland, shrub-grass land, young secondary forest, and mature secondary forest (Table 2).

Fine root decomposition rate decreased significantly with stand age (Fig. 3), and it was significantly higher in grassland and shrub-grass land than in mature secondary forest (Table 2). Linear correlation analysis showed that fine root decomposition rate was negatively correlated with initial lignin concentration ($r = -0.48$, $P = 0.038$), lignin:N, C:N ($r = -0.55$, $P = 0.02$), and C:P ($r = -0.56$, $P = 0.02$), while positively correlated with root initial P and N concentration ($P < 0.05$). Regression analyses showed that the initial C:P ratio in fine root was the main factor in explaining the variation of fine root decomposition rate ($R^2 = 0.41$, $P = 0.003$) (Fig. 3).

3.3. Litter and fine root quality

The litter C concentration increased significantly with stand age (Fig. 3), and it was significantly higher in mature secondary forest than that in grassland (Table 3). Litter tannin concentrations in secondary forests were significantly higher than that in grassland and shrub-grass land (Table 3). The C:P ratio in fine root increased significantly with stand age (Fig. 3), and it was significantly higher in mature secondary forest than that in grassland (Table 3). Fine root C concentration increased significantly with stand age ($R^2 = 0.33$, $P = 0.01$), and it was significantly lower in grassland than that in secondary forests (Table 3). Fine root lignin concentrations in young and mature secondary forests were significantly higher than that in grassland (Table 3). There were no significant

differences in litter and fine root N concentration among grassland, shrub-grass land, young secondary forest, and mature secondary forest (Table 3). The N, P, lignin and tannin concentration in litter and fine root had no significant relationship with stand age ($P > 0.05$, data not shown).

3.4. C and N input from litter and fine root

There were no significant differences in C input from above-ground litter among grassland, shrub-grass land, young secondary forest, and mature secondary forest (Table 2). The annual C and N inputs from litter had no significant relationship with stand age ($P > 0.05$), while the C input from annual fine root production increased significantly with stand age (Fig. 5). For total C input from the combination of litter and fine root, there were no significant differences among grassland, shrub-grass land, young secondary forest, and mature secondary forest (Table 2). For N input from litter, fine root, litter and fine root (together), there were no significant differences among the four vegetation types (Table 2). There was no significant relationship between annual N input from fine root production and stand age ($P > 0.05$, Fig. 5).

3.5. Soil properties and net N mineralization

The SOC storage, RC storage, $\text{NH}_4\text{-N}$ concentration, and net N mineralization rate increased significantly with stand age (Figs. 5 and 6). The soil TC storage, SOC storage, RC storage, $\text{NH}_4\text{-N}$ concentration, and net N mineralization rate in mature secondary

Table 2

Production, C/N input and decomposition rate (mean \pm SE) of litter and fine root in different successional stages (Different letters behind data indicated statistically significant differences among successional stages. **n.s.**, means no significant difference, $P > 0.05$). All biomasses were expressed dry weight per area.

	Grassland	Shrub-grass land	Young secondary forest	Mature secondary forest
Litter production ($\text{Mg ha}^{-1} \text{y}^{-1}$) (n.s.)	6.137 \pm 0.79	6.719 \pm 0.35	7.086 \pm 1.03	5.550 \pm 0.69
Mass remaining after 1-year of decomposition (litter) (%)	22.36 \pm 2.02 b	28.87 \pm 3.22 ab	33.12 \pm 7.54 ab	43.23 \pm 7.54 a
Litter decomposition rate k (y^{-1})	1.59 \pm 0.10 a	1.31 \pm 0.11 ab	1.48 \pm 0.20 ab	0.91 \pm 0.20 b
C input from litter ($\text{Mg ha}^{-1} \text{y}^{-1}$) (n.s.)	2.845 \pm 0.34	3.237 \pm 0.18	3.415 \pm 0.54	2.739 \pm 0.32
N input from litter ($\text{Mg ha}^{-1} \text{y}^{-1}$) (n.s.)	0.127 \pm 0.03	0.151 \pm 0.02	0.153 \pm 0.02	0.118 \pm 0.01
Fine root biomass (Mg ha^{-1})	1.19 \pm 0.29 b	1.20 \pm 0.06 b	1.83 \pm 0.40 b	2.84 \pm 0.43 a
Dead fine root production ($\text{Mg ha}^{-1} \text{y}^{-1}$) (n.s.)	0.679 \pm 0.13	1.045 \pm 0.26	1.084 \pm 0.19	1.103 \pm 0.19
Fine root production ($\text{Mg ha}^{-1} \text{y}^{-1}$)	1.408 \pm 0.21 bc	1.721 \pm 0.21 ab	2.110 \pm 0.41 ab	2.712 \pm 0.41 a
Mass remaining after 1-year of decomposition (fine root) (%)	41.65 \pm 6.00 bc	27.36 \pm 4.11 c	52.59 \pm 3.39 ab	60.45 \pm 3.39 a
Fine root decomposition rate k (y^{-1})	0.94 \pm 0.17 ab	1.38 \pm 0.15 a	0.66 \pm 0.06 bc	0.51 \pm 0.06 c
C input from fine root production ($\text{Mg ha}^{-1} \text{y}^{-1}$)	0.629 \pm 0.09 b	0.787 \pm 0.09 b	1.001 \pm 0.21 ab	1.285 \pm 0.21 a
N input from fine root production ($\text{Mg ha}^{-1} \text{y}^{-1}$) (n.s.)	0.016 \pm 0.004	0.023 \pm 0.003	0.023 \pm 0.01	0.030 \pm 0.01
C input from litter & fine root production ($\text{Mg ha}^{-1} \text{y}^{-1}$) (n.s.)	3.474 \pm 0.40	4.023 \pm 0.22	4.417 \pm 0.26	4.024 \pm 0.26
N input from litter & fine root production ($\text{Mg ha}^{-1} \text{y}^{-1}$) (n.s.)	0.143 \pm 0.03	0.173 \pm 0.02	0.176 \pm 0.01	0.147 \pm 0.01
Litter standing crop (Mg ha^{-1})	2.83 \pm 0.59 b	3.41 \pm 0.31 b	4.07 \pm 0.68 ab	5.43 \pm 0.79 a

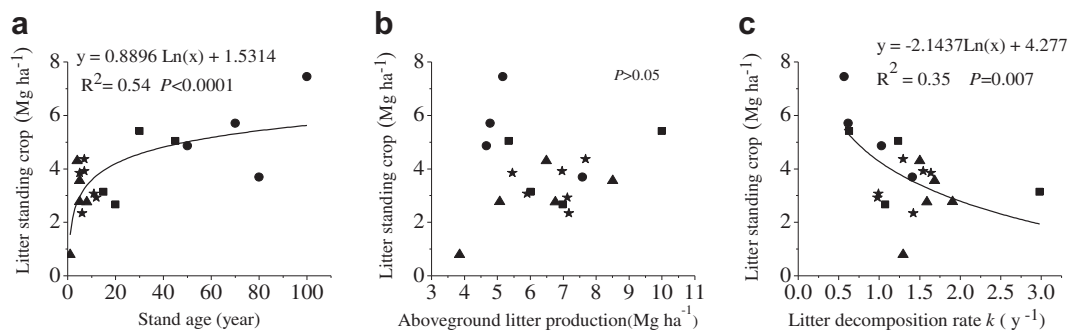


Fig. 2. Relationships between litter standing crop and stand age (a), aboveground litter production (b), and litter decomposition rate (c). (Each symbol represents the average of repetitions from each of the 19 different stands. Triangle: Grassland; Star: Shrub-grass land; Square: Young secondary forest; Circle: Mature secondary forest. Hereafter).

forest were significantly higher than in grassland and shrub-grass land (Table 4). Although the mean value of the soil TN storage demonstrated an increasing trend during vegetation succession (Table 4), the differences among grassland, shrub-grass land, young secondary forest, and mature secondary forest were not statistically significant (Table 4). However, the concentration of soil TN increased significantly with stand age ($R^2 = 0.31$, $P = 0.014$) (data not shown). Regression analyses showed that the soil TN concentration was the main factor in explaining the variation of soil net N mineralization rate ($R^2 = 0.36$, $P = 0.007$) (Fig. 6).

4. Discussions

4.1. Changes in litter and fine root production following agricultural abandonment

It is generally observed that annual litter production increases with stand age during vegetation succession (Waring and Schlesinger, 1985; Zhang et al., 1999; Yan et al., 2009; Menezes et al., 2010), and litter production may reach a maximum near canopy closure (Uselman et al., 2007). However, most litter studies focused on the forest stage during forest restoration (Yankelevich et al., 2006; Ostertag et al., 2008; Yang et al., 2010), little

attention has been paid to the early successional stages dominated by grass or shrub (Ostertag et al., 2008). In addition, litter production in forest stands refers only to litter from trees in a lot of previous studies (Uselman et al., 2007; Yan et al., 2009). Our results revealed an insignificant changes in total aboveground litter production among the successional stages of grassland, shrub-grass land, young secondary forest, and mature secondary forest, although their differences in vegetation composition and structure were remarkable (Zhang et al., 2010). The increase of woody plant litter and decrease of grass litter during vegetation succession had led to little changes in total litter production in different succession stages (Table 2; Fig. 1). Following agricultural abandonment, grass could establish rapidly in the former croplands, and produce a great quantity of aboveground litter because of the relatively good soil conditions (e.g., soil seed bank, soil fertility) inherited from croplands (Zhang et al., 2010). As the establishment and colonization of woody plants along with vegetation succession, the sources of dominant litter could be gradually replaced by woody plants (Fig. 1). Thus, our results imply a much smaller role of vegetation type in the annual total aboveground litter production than previously assumed.

In agreement with some previous studies (Makkonen and Helmisaari, 2001; Hertel et al., 2006; Uselman et al., 2007; Yang

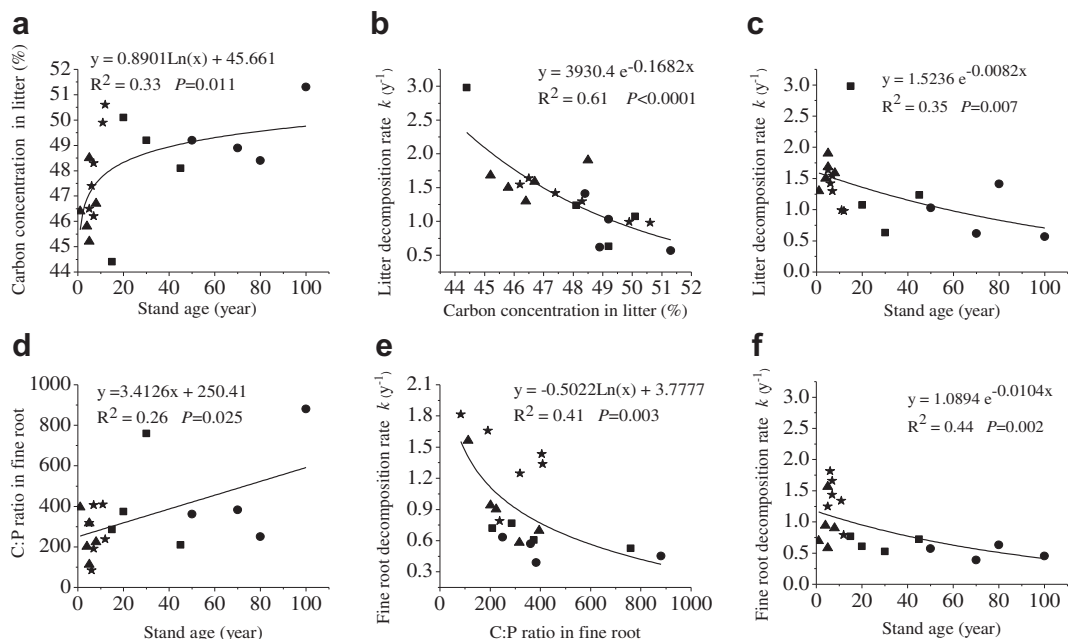


Fig. 3. Relationships among stand age, litter decomposition rate and litter carbon concentration (a, b, c). Relationships among stand age, fine root decomposition rate and C:P ratio in fine root (d, e, f).

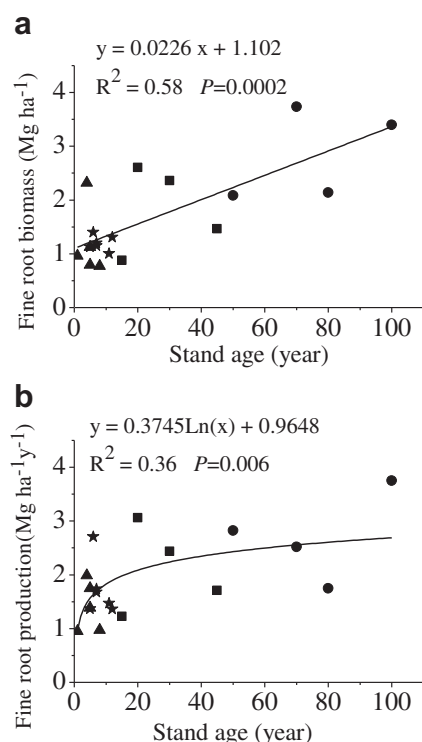


Fig. 4. Relationships between fine root biomass (a), fine root production (b) and stand age.

et al., 2010), the fine root production and biomass increased significantly with stand age in our study (Fig. 4). The transformation of vegetation abundance and composition during succession and the differences in physiology between successional species may be the reasons for the increasing fine root biomass and production (Uselman et al., 2007; Yang et al., 2010). Yet, a few studies demonstrated that differences in fine root production among different successional stages were not statistically significant, and fine root biomass had no significant relationship with stand age (Vanninen and Mäkelä, 1999) or showed a 'U-shaped' trend through succession (Yan et al., 2009). The discrepancy among different case studies may be attributed to the different environmental conditions and vegetation succession pathways.

4.2. Changes in litter and fine root quality and decomposition rate following agricultural abandonment

Changes in litter and fine root quality could be attributed to the replacement of species during the succession following agricultural abandonment (Table 1, Fig. 1). Some previous studies have shown that, fast growing and poorly defended grasses which are common in the initial years after cropland abandonment, tend to produce litter with a high decomposability, whereas slower-growing and better defended species in the latter successional stages produce poor-quality litter with low decomposition rates (Cortez et al., 2007; Marín-Spiotta et al., 2008; Castro et al., 2010). In our study both litter and fine root C concentration increased significantly with stand age, suggesting that litter quality associated with decomposability decline as woody species replace herbaceous species (Fig. 1). In addition, the higher fine root lignin concentration in forests together with the higher litter tannin concentration suggested that more recalcitrant compounds were produced in forests than in grassland and shrub-grass land. However, litter lignin concentration showed no significant differences among successional stages (Table 3), this may due to the fact that the litter material of grasses in our decomposition experiment included both leaves and stems, while for woody plants only leaf litter were used. The non-leaf components (i.e., twigs, bark, etc.) of woody plants could contain more lignin than leaf litter (O'Connell, 1987).

Our results indicated litter decomposition rates decreased significantly and litter C concentration increased with stand age. It seems that the initial litter C concentration was the main factor in explaining the variation of decomposition rates (Fig. 3). Fine root decomposition rates also decreased and the C:P ratio in fine root increased with stand age, while the initial C:P ratio in fine root was the main factor in explaining the variation of decomposition rates. Thus, we inferred that the increasing C concentration in litter, and the increasing C:P ratio in fine root during succession, potentially drove the decreases in litter and fine root decomposition rate respectively.

The changing patterns and influencing factors of litter and fine root decomposition in relation to vegetation succession found in our study did not agree with some previous studies. For example, Ostertag et al. (2008) found that leaf litter decomposition rate did not change significantly with forest age, and fine root decomposition rate was faster in 60-year-old forest than 10-year-old and 30-year-old forest, and they concluded that site conditions were more

Table 3

Chemical properties (mean \pm SE) of litter and fine root material used in decomposition experiment (Different letters behind data indicated statistically significant differences among successional stages. **n.s.**, means no significant difference, $P > 0.05$).

	Grassland	Shrub-grass land	Young secondary forest	Mature secondary forest
Litter C (%)	46.5 \pm 0.6 b	48.2 \pm 0.7 ab	48.0 \pm 1.3 ab	49.5 \pm 0.6 a
Litter N (%) (n.s.)	2.02 \pm 0.21	2.23 \pm 0.18	2.18 \pm 0.06	2.15 \pm 0.12
Litter P (%)	0.31 \pm 0.05 a	0.22 \pm 0.04 ab	0.20 \pm 0.07 ab	0.15 \pm 0.02 b
Litter Lignin (%) (n.s.)	22.6 \pm 1.8	23.5 \pm 4.2	29.2 \pm 6.4	27.5 \pm 3.9
Litter tannin (%)	0.44 \pm 0.12 b	1.20 \pm 0.67 b	5.69 \pm 1.35 a	3.12 \pm 0.92 a
Litter C:N ratio (n.s.)	23.9 \pm 2.4	22.3 \pm 2.0	22.1 \pm 1.1	23.2 \pm 1.0
Litter N:P ratio	7.0 \pm 1.0 b	11.8 \pm 2.0 ab	13.3 \pm 2.6 a	14.9 \pm 2.4 a
Litter C:P ratio	166.8 \pm 28.4 b	248.9 \pm 37.5 ab	297.7 \pm 64.2 a	337.4 \pm 40.7 a
Litter lignin:N ratio (n.s.)	11.8 \pm 1.9	10.7 \pm 1.8	13.7 \pm 3.3	12.8 \pm 1.7
Fine root C (%)	44.7 \pm 0.4 b	45.9 \pm 0.4 ab	47.8 \pm 1.2 a	47.1 \pm 0.6 a
Fine root N (%) (n.s.)	1.06 \pm 0.16	1.34 \pm 0.10	1.23 \pm 0.25	1.07 \pm 0.17
Fine root P (%) (n.s.)	0.21 \pm 0.05	0.22 \pm 0.07	0.15 \pm 0.03	0.12 \pm 0.03
Fine root lignin (%)	24.8 \pm 4.6 c	24.4 \pm 2.6 b	40.6 \pm 5.7 a	33.8 \pm 2.9 ab
Fine root tannin (%) (n.s.)	1.26 \pm 0.68	2.01 \pm 0.81	1.68 \pm 0.62	1.51 \pm 0.51
Fine root C:N ratio (n.s.)	45.3 \pm 5.4	35.2 \pm 2.6	44.2 \pm 9.4	47.1 \pm 6.5
Fine root N:P ratio (n.s.)	5.5 \pm 0.8	8.1 \pm 1.7	9.0 \pm 1.2	10.6 \pm 3.3
Fine root C:P ratio	213.5 \pm 41.8 b	274.5 \pm 52.2 ab	407.0 \pm 122.3 ab	541.6 \pm 140.4 a
Fine root lignin:N ratio (n.s.)	25.8 \pm 6.6	18.6 \pm 2.3	40.4 \pm 13.6	35.1 \pm 7.5

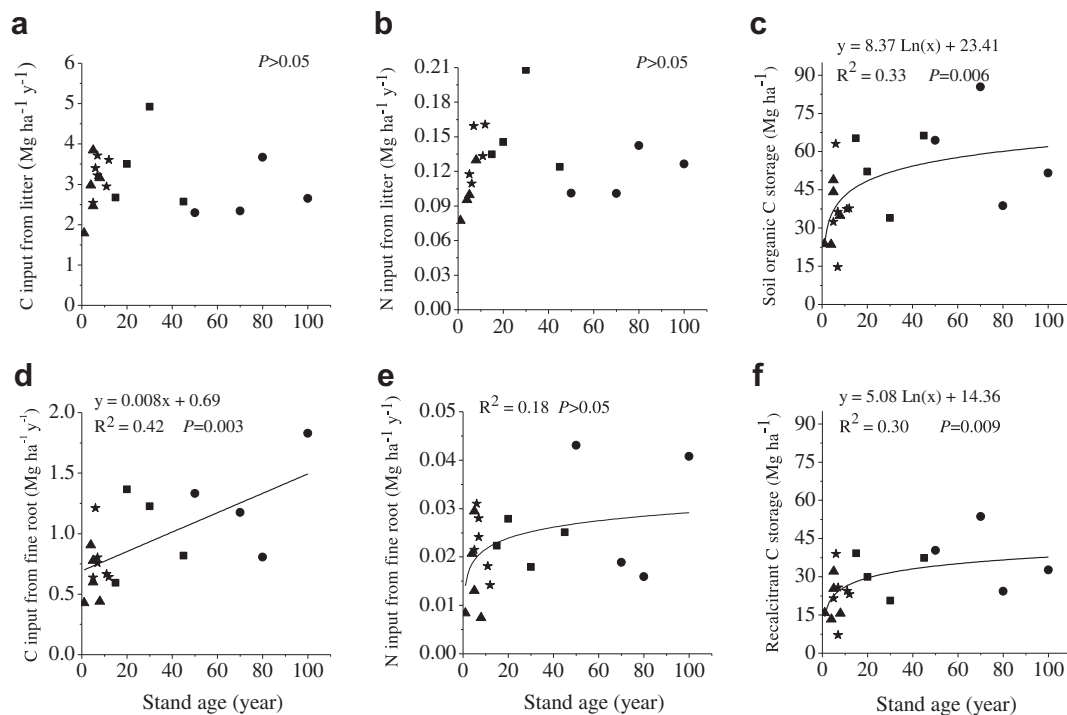


Fig. 5. Relationships between annual litter C/N input (a, b), fine root C/N input (d, e), SOC storage (c), RC storage (f) and stand age.

important controls than litter quality in their studied secondary forest stands. Mayer (2008) found that litter decomposition was fastest in old-growth forests (about 75 years old) compared to other successional stages (old-fields and transition forests), and they ascribed the higher decomposition rate in old-growth forest to the denser canopy cover and thicker litter layer which could lead to a cooler and wetter conditions in summer, sequentially shift the abundance/structure of microbial decomposers or influence grazing behavior of the macro-detritivore community (Mayer, 2008). In contrast to Mayer (2008), Xuluc-Tolosa et al. (2003) found that leaf litter decomposition was slightly faster in early successional phases of secondary vegetation than in old secondary forest (>50 years old). Cortez et al. (2007) and Kazakou et al. (2006; 2009) also found that litters produced by early successional communities tend to decompose more rapidly than those produced by vegetation from later stages (Kazakou et al., 2009). Thus, the changing patterns and influencing factors of litter and fine root decomposition during vegetation development were diverse and complex. The discrepancies among different case studies may be

attributed to the complex vegetation development trends, responses and interactions of biotic or abiotic factors associated with vegetation succession.

Litter decomposition could be affected by many factors, such as litter quality (e.g., N concentration, lignin concentration, C:N ratio, N:P ratio, lignin:N ratio, leaf dry matter content, holocellulose concentration, etc.), environmental variables (e.g., climate, vegetation, soil fertility, etc.), and decomposer (Aerts, 1997; Silver and Miya, 2001; Xuluc-Tolosa et al., 2003; Cortez et al., 2007; Mayer, 2008; Zhou et al., 2008; Kazakou et al., 2009; Castro et al., 2010). Litter lignin concentration, C:N ratio, and lignin:N ratio are frequently used as predictors of decomposition rate (Aerts, 1997; Zhou et al., 2008) but with exceptions. For instance, Castro et al. (2010) found that the three litter parameters (i.e., litter lignin concentration, C:N ratio, and lignin:N ratio) were not significantly related to litter decomposition rate in a Montado system. Hoorens et al. (2003) found that, for the woodland/old field species, only the initial litter C and P concentrations were significantly correlated with litter decomposition rate, and the species with a higher initial

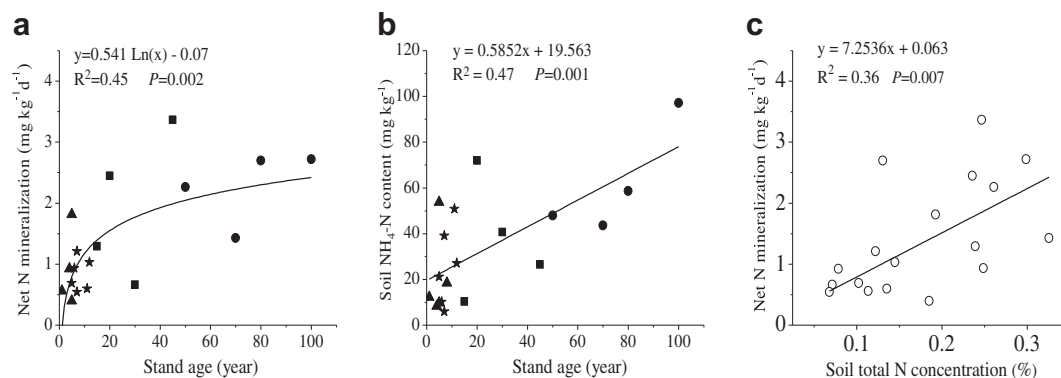


Fig. 6. Relationships between soil net N mineralization rate and stand age (a), soil $\text{NH}_4\text{-N}$ concentration and stand age (b), soil net N mineralization rate and soil TN concentration (c).

Table 4

Soil properties (mean \pm SE) under different successional stages (Different letters behind data indicated statistically significant differences among successional stages. **n.s.**, means no significant difference, $P > 0.05$).

	Grassland	Shrub-grass land	Young secondary forest	Mature secondary forest
Total C storage (Mg ha ⁻¹)	39.50 \pm 6.90 c	43.48 \pm 7.33 bc	62.41 \pm 2.15 ab	69.37 \pm 7.48 a
Organic C storage (Mg ha ⁻¹)	32.82 \pm 5.04 b	38.89 \pm 6.94 b	54.39 \pm 7.53 ab	64.15 \pm 11.37 a
Recalcitrant C storage (Mg ha ⁻¹)	19.05 \pm 3.30 b	24.73 \pm 4.50 b	31.74 \pm 4.22 ab	40.33 \pm 7.13 a
Total N storage (Mg ha ⁻¹) (n.s.)	2.81 \pm 0.42	3.14 \pm 0.54	3.93 \pm 0.84	4.49 \pm 0.66
Total P content (%) (n.s.)	0.056 \pm 0.02	0.049 \pm 0.01	0.079 \pm 0.03	0.048 \pm 0.01
Total K content (%) (n.s.)	1.15 \pm 0.25	0.90 \pm 0.19	0.93 \pm 0.18	0.84 \pm 0.22
NO ₃ -N + NH ₄ -N (mg kg ⁻¹)	43.26 \pm 11.86 b	51.14 \pm 10.44 ab	59.36 \pm 9.59 ab	84.23 \pm 13.37 a
Net N mineralization (mg kg ⁻¹ d ⁻¹)	0.65 \pm 0.37 b	0.83 \pm 0.11 b	1.94 \pm 0.60 ab	2.28 \pm 0.30 a

litter C concentration generally decomposed slower. In an influential review of global litter decomposition experiments, Aerts (1997) found that there was no good chemical predictor of decomposition rate in temperate region. Thus, the litter quality parameter as decomposition rate indicators seems to be multiple.

In our study, litter decomposition rate was negatively correlated with initial C concentration, lignin concentration, and lignin:P, while the litter C concentration was significantly positively correlated with lignin concentration. Stepwise regression analyses showed that initial litter C concentration was the main factor in explaining the variation in litter decomposition rates. That might result from that our litter materials include a wide range of species, i.e., from early successional grass to shrub, early successional trees, and latter successional trees (Table 1). In addition, we used the mixed litter materials which were weighed according to the proportion of each dominant litter species in corresponding stands (Table 1). We inferred that the increased litter C concentration might indicate an increased presence of structural polymers (e.g., lignin, cellulose, hemicellulose, etc.), and the litter C concentration may simply reflect an overall level of decomposability for our litter materials. However, further studies are needed to clarify the litter C fractions and its changes during vegetation succession.

4.3. C and N input from litter and fine root

The litter and fine root are the main input of C and N to soil and stand floor (Xuluc-Tolosa et al., 2003; Steinaker and Wilson, 2005; Uselman et al., 2007; Ostertag et al., 2008). Although vegetation community structure and composition changed remarkably during succession (Zhang et al., 2010), our results showed that there were no significant differences in total C and N inputs from litterfall among the grassland, shrub-grass land, young secondary forest, and mature secondary forest either (Table 2). Thus, vegetation type might have played a limited role in the annual total C and N inputs from litterfall. Similar results also have been reported by Montané et al. (2010), who found that the annual aboveground litter C net inputs were remarkably similar after shrub encroachment into mountain grasslands.

The litter standing crop increased significantly with stand age, and decreased significantly with increasing litter decomposition rate, but not correlated with litter production (Fig. 2). These results imply that the accumulation of litter standing crop during vegetation development could be attributed to the decreases in litter decomposition rate partly caused by changes in litter quality, rather than the increase in litter production.

The increasing soil C with stand age in our study may be explained partly by the increasing C input from fine root. However, the C and N contribution from fine root production was relatively small when compared to the aboveground litter (Table 2). The annual total C and N inputs from litter and fine root production (together) were surprisingly similar among grassland, shrub-grass land, young secondary forest, and mature secondary forest (Table 2), which could be due to the little differences in

aboveground litter production among the four successional stages. The increasing SOC and RC storage with vegetation succession can not be explained by the changes in annual C input from litterfall (Table 2, Table 4, Fig. 5). According to our results, the changes in litter and fine root quality and decomposition rate may be more important controls than total litter production for belowground C sequestration (Figs. 2 and 3). In agreement with our findings, Montané et al. (2010) have also demonstrated that the litter quality, not the quantity, drive the accumulation of SOC after shrub encroachment into mountain grasslands in the Alt Pirineu Natural Park of Pyrenees. Litter quality may control belowground C sequestration by influencing microbial composition and activity, chemical transformations during humification, synthesis of new compounds that are more resistant to decay, etc (Marín-Spiotta et al., 2008; Montané et al., 2010).

Although the mean value of the soil TN storage seems to show an increasing trend during vegetation succession (Table 4), the differences among the four successional stages (i.e., grassland, shrub-grass land, young secondary forest, and mature secondary forest) are not statistically significant. The insignificant differences might result from the large variability in soil TN storage (Table 4). The increase in soil TN concentration following agricultural abandonment may be attributed to increasing N fixation (Berendse, 1990; Knops and Tilman, 2000). The increasing soil TN concentration during vegetation succession has also been reported by some previous studies (Berendse, 1990; Knops and Tilman, 2000; Wang, 2002). The net N mineralization rate increased with the increasing SOC and total N concentration, while the SOC and TN concentration increased with stand age (Zhang et al., 2012). Thus, the increase in soil net N mineralization with stand age may be attributed to the increasing concentration of soil TN and SOC during succession. By providing organic substrates for the growth and activity of soil microorganism, e.g., nitrifiers and ammonifiers, the SOC and TN could be the most important factors related to the change in soil N mineralization during succession (Lamb, 1980; Vitousek et al., 1989; Berendse, 1990). Further, some previous studies also reported that the mineralization rate increased with an increasing amount of organic matter during secondary succession (Berendse, 1990).

5. Conclusions

A novel contribution of our study comes from simultaneous measurements of litter and fine root production, quality, decomposition, C and N input in ecosystems along a secondary succession gradient following agricultural abandonment. Results showed little changes in aboveground total litter production and annual total C and N input even though there was increasing dominance of woody plants during vegetation succession. Meanwhile, the underground fine root production, fine root biomass, and C input from fine root increased significantly with stand age. The initial quality parameters, i.e., the litter C concentration and fine root C:P ratio, were the main factors in explaining the variation of decomposition rates of litter and fine root, respectively. The accumulation of litter standing

crop during vegetation development was attributed to the decreases in litter decomposition rate partly caused by changes in litter quality, rather than increases in production. Thus, during vegetation development following agricultural abandonment, changes in vegetation type had a much smaller role in the annual total litter production and the total litter C and N input than previously assumed, while the changes in quality and decomposition rate may be the more important factors influencing C accumulation in stand floor and soil.

Acknowledgements

This research was supported by the National Natural Science Foundation of China (31130010 and 31200340) and the Chinese Academy of Sciences (XDA05060500). We thank Mr. Xinzhi Liu and Mr. Zhongyin Xia for the assistance in field work. We are grateful for the comments and constructive suggestions from the editor and two anonymous reviewers.

References

- Aerts, R., 1997. Climate, leaf litter chemistry and leaf litter decomposition in terrestrial ecosystems: a triangular relationship. *Oikos* 79, 439–449.
- Berendse, F., 1990. Organic-matter accumulation and nitrogen mineralization during secondary succession in heathland ecosystems. *Journal of Ecology* 78, 413–427.
- Bontti, E.E., Decant, J.P., Munson, S.M., Gathany, M.A., Haddix, M.L., Owens, S., Burke, I.C., Parton, W.J., Przeszlowska, A., Harmon, M.E., 2009. Litter decomposition in grasslands of central North America (US Great Plains). *Global Change Biology* 15, 1356–1363.
- Bray, J.R., Gorham, E., 1964. Litter production in forests of the world. *Advances in Ecological Research* 2, 101–157.
- Castro, H., Fortunel, C., Freitas, H., 2010. Effects of land abandonment on plant litter decomposition in a Montado system: relation to litter chemistry and community functional parameters. *Plant and Soil* 333, 181–190.
- Chazdon, R.L., 2008. Beyond deforestation: restoring forests and ecosystem services on degraded lands. *Science* 320, 1458–1460.
- Cheng, X., Luo, Y., Chen, J., Lin, G., Chen, J., Li, B., 2006. Short-term C₄ plant *Spartina alterniflora* invasions change the soil carbon in C₃ plant-dominated tidal wetlands on a growing estuarine island. *Soil Biology & Biochemistry* 38, 3380–3386.
- Connin, S.L., Virginia, R.A., Chamberlain, C.P., 1997. Carbon isotopes reveal soil organic matter dynamics following arid land shrub expansion. *Oecologia* 110, 374–386.
- Cortez, J., Garnier, E., Pérez-Harguindeguy, N., Debussche, M., Gillon, D., 2007. Plant traits, litter quality and decomposition in a Mediterranean old-field succession. *Plant and Soil* 296, 19–34.
- Cramera, V.A., Hobbs, R.J., Standisha, R.J., 2008. What's new about old fields? Land abandonment and ecosystem assembly. *Trends in Ecology and Evolution* 23, 104–112.
- Cusack, D.F., Chou, W.W., Yang, W.H., Harmon, M.E., Silver, W.L., Team, T.L., 2009. Controls on long-term root and leaf litter decomposition in neotropical forests. *Global Change Biology* 15, 1339–1355.
- Davidson, E.A., Reis de Carvalho, C.J., Figueira, A.M., Ishida, F.Y., Ometto, J.H.B., Nardoto, G.B., Sabá, R.T., Hayashi, S.N., Leal, E.C., Vieira, I.C.G., Martinelli, L.A., 2007. Recuperation of nitrogen cycling in Amazonian forests following agricultural abandonment. *Nature* 447, 995–998.
- Gill, R.A., Burke, I.C., 1999. Ecosystem consequences of plant life form changes at three sites in the semiarid United States. *Oecologia* 121, 551–563.
- Guo, L.B., Gifford, R.M., 2002. Soil carbon stocks and land use change: a meta analysis. *Global Change Biology* 8, 345–360.
- Hagerman, A.E., 1987. Radial diffusion method for determining tannin in plant extracts. *Journal of Chemical Ecology* 13, 437–449.
- Hättenschwiler, S., Tiunov, A.V., Scheu, S., 2005. Biodiversity and litter decomposition in terrestrial ecosystems. *Annual Review of Ecology, Evolution and Systematics* 36, 191–218.
- Hättenschwiler, S., Gasser, P., 2005. Soil animals alter plant litter diversity effects on decomposition. *Proceedings of the National Academy of Sciences of the United States of America* 102, 1519–1524.
- Hertel, D., Hölscher, D., Köhler, L., Leuschner, C., 2006. Changes in fine root system size and structure during secondary succession in a Costa Rican montane oak forest. *Ecological Studies* 185, 283–297.
- Hibbard, K.A., Archer, S., Schimel, D.S., Valentine, D.W., 2001. Biogeochemical changes accompanying woody plant encroachment in a subtropical savanna. *Ecology* 82, 1999–2011.
- Hoorens, B., Aerts, R., Stroetenga, M., 2003. Does initial litter chemistry explain litter mixture effects on decomposition? *Oecologia* 137, 578–586.
- Huang, W., Siemann, E., Wheeler, G.S., Zou, J., Carrillo, J., Ding, J., 2010. Resource allocation to defence and growth are driven by different responses to generalist and specialist herbivory in an invasive plant. *Journal of Ecology* 98, 1157–1167.
- Hui, D., Robert, B.J., 2009. Assessing interactive responses in litter decomposition in mixed species litter. *Plant and Soil* 314, 263–271.
- Jackson, R.B., Mooney, H.A., Schulze, E.D., 1997. A global budget for fine root biomass, surface area, and nutrient contents. *Proceedings of the National Academy of Sciences of the United States of America* 94, 7362–7366.
- Jha, P., Mohapatra, K.P., 2010. Leaf litterfall, fine root production and turnover in four major tree species of the semi-arid region of India. *Plant and Soil* 326, 481–491.
- Kazakou, E., Vile, D., Shipley, B., Gallet, C., Garnier, E., 2006. Covariations in litter decomposition, leaf traits and plant growth in species from a Mediterranean old-field succession. *Functional Ecology* 20, 21–30.
- Kazakou, E., Violle, C., Roumet, C., Pintor, C., Gimenez, O., Garnier, E., 2009. Litter quality and decomposability of species from a Mediterranean succession depend on leaf traits but not on nitrogen supply. *Annals of Botany* 104, 1151–1161.
- King, J.S., Albaugh, T.J., Allen, H.L., Buford, M., Strain, B.R., Dougherty, P., 2002. Below-ground carbon input to soil is controlled by nutrient availability and fine root dynamics in loblolly pine. *New Phytologist* 154, 389–398.
- Kirk, T.K., Obst, J.R., 1988. Lignin determination. *Methods in Enzymology* 161, 87–101.
- Klotzbücher, T., Kaiser, K., Guggenberger, G., Gatzek, C., Kalbitz, K., 2011. A new conceptual model for the fate of lignin in decomposing plant litter. *Ecology* 92, 1052–1062.
- Knops, J.M.H., Tilman, D., 2000. Dynamics of soil nitrogen and carbon accumulation for 61 years after agricultural abandonment. *Ecology* 81, 88–98.
- Lal, R., 2004. Soil carbon sequestration impacts on global climate change and food security. *Science* 304, 1623–1627.
- Lamb, D., 1980. Soil nitrogen mineralisation in a secondary rainforest succession. *Oecologia* 47, 257–263.
- Lu, R.K., 2000. Soil Agro-chemical Analyses. Agricultural Technical Press of China, Beijing (in Chinese).
- Makkonen, K., Helmisaari, H.S., 2001. Fine root biomass and production in Scots pine stands in relation to stand age. *Tree Physiology* 21, 193–198.
- Marin-Spiotta, E., Swanston, C.W., Torn, M.S., Silver, W.L., Burton, S.D., 2008. Chemical and mineral control of soil carbon turnover in abandoned tropical pastures. *Geoderma* 143, 49–62.
- Matamala, R., Gonzalez-Meler, M.A., Jastrow, J.D., Norby, R.J., Schlesinger, W.H., 2003. Impacts of fine root turnover on forest NPP and soil C sequestration potential. *Science* 302, 1385–1387.
- Matthews, E., 1997. Global litter production, pools, and turnover times: estimates from measurement data and regression models. *Journal of Geophysical Research* 102, 18771–18800.
- Mayer, P.M., 2008. Ecosystem and decomposer effects on litter dynamics along an old field to old-growth forest successional gradient. *Acta Oecologica* 33, 222–230.
- Meier, I.C., Leuschner, C., 2010. Variation of soil and biomass carbon pools in beech forests across a precipitation gradient. *Global Change Biology* 16, 1035–1045.
- Menezes, C.E.G., Pereira, M.G., Correia, M.E.F., dos Anjos, L.H.C., Paula, R.R., de Souza, M.E., 2010. Litter contribution and decomposition and root biomass production in forests at different successional stages in Pinheiral, RJ. *Ciência Florestal* 20, 439–452.
- McClagherty, C.A., Aber, J.D., Melillo, J.M., 1982. The role of fine roots in the organic matter and nitrogen budgets of two forested ecosystems. *Ecology* 63, 1481–1490.
- Montané, F., Romanyà, J., Rovira, P., Casals, P., 2010. Aboveground litter quality changes may drive soil organic carbon increase after shrub encroachment into mountain grasslands. *Plant Soil* 337, 151–165.
- O'Connell, A.M., 1987. Litter dynamics in Karri (*Eucalyptus diversicolor*) forests of South-Western Australia. *Journal of Ecology* 75, 781–796.
- Ohtsuka, T., Shizu, Y., Nishiwaki, A., Yashiro, Y., Koizumi, H., 2010. Carbon cycling and net ecosystem production at an early stage of secondary succession in an abandoned coppice forest. *Journal of Plant Research* 123, 393–401.
- Olson, J.S., 1963. Energy-storage and balance of producers and decomposers in ecological-systems. *Ecology* 44, 322–331.
- Ostertag, R., 2001. Effects of phosphorus and nitrogen availability in fine root dynamics in Hawaiian montane forests. *Ecology* 82, 485–499.
- Ostertag, R., Marin-Spiotta, E., Silver, W.L., Schulten, J., 2008. Litterfall and decomposition in relation to soil carbon pools along a secondary forest chronosequence in Puerto Rico. *Ecosystems* 11, 701–714.
- Ren, Y., Wang, M.L., Yue, M., Li, Z.J., 1998. Plant of Giant Panda's Habitat of Qinling Mountains. Shanxi Science and Technology Press, Xian (in Chinese).
- Rey-Benayas, J.M., Martins, A., Nicolau, J.M., Schulz, J.J., 2007. Abandonment of agricultural land: an overview of drivers and consequences. *CAB Reviews: Perspectives in Agriculture, Veterinary Science, Nutrition and Natural Resources* 2, 1–14.
- Roberts, M.J., Lubowski, R.N., 2007. Enduring impacts of land retirement policies: evidence from the Conservation Reserve Program. *Land Economics* 83, 516–538.
- Rovira, P., Vallejo, V.R., 2007. Labile, recalcitrant, and inert organic matter in Mediterranean forest soils. *Soil Biology & Biochemistry* 39, 202–215.
- Ruess, R.W., Hendrick, R.L., Burton, A.J., Pregitzer, K.S., Sveinbjornsson, B., Allen, M.F., Maurer, G.E., 2003. Coupling fine root dynamics with ecosystem

- carbon cycling in black spruce forests of interior Alaska. *Ecological Monographs* 73, 643–662.
- Schindler, M.H., Gessner, M.O., 2009. Functional leaf traits and biodiversity effects on litter decomposition in a stream. *Ecology* 90, 1641–1649.
- Silver, W.L., Miya, R.K., 2001. Global patterns in root decomposition: comparisons of climate and litter quality effects. *Oecologia* 129, 407–419.
- Silver, W.L., Thompson, A.W., McGroddy, M.E., Varner, R.K., Dias, J.D., Silva, H., Crill, P.M., Keller, M., 2005. Fine roots dynamics and trace gas fluxes in two lowland tropical forest soils. *Global Change Biology* 11, 290–306.
- Steinaker, D.F., Wilson, S.D., 2005. Belowground litter contributions to nitrogen cycling at a northern grassland-forest boundary. *Ecology* 86, 2825–2833.
- Swan, C.M., Gluth, M.A., Horne, C.L., 2009. Leaf litter species evenness influences nonadditive breakdown in a headwater stream. *Ecology* 90, 1650–1658.
- Trumbore, S.E., Gaudinski, J.B., 2003. The secret lives of roots. *Science* 302, 1344.
- Uselman, S.M., Qualls, R.G., Lilienfein, J., 2007. Fine root production across a primary successional ecosystem chronosequence at Mt. Shasta, California. *Ecosystems* 10, 703–717.
- Vanninen, P., Mäkelä, A., 1999. Fine-root biomass of Scots pine stands differing in age and soil fertility in southern Finland. *Tree Physiology* 19, 823–830.
- Vitousek, P.M., Matson, P.A., Van Cleve, K., 1989. Nitrogen availability and nitrification during succession primary, secondary, and old-field seres. *Plant and Soil* 115, 229–239.
- Wang, G.H., 2002. Plant traits and soil chemical variables during a secondary vegetation succession in abandoned fields on the Loess Plateau. *Acta Botanica Sinica* 44, 990–998.
- Waring, R.H., Schlesinger, W.H., 1985. *Forest Ecosystems: Concepts and Management*. Academic, San Diego (CA), p. 340.
- Xuluc-Tolosa, F.J., Vester, H.F.M., Ramírez-Marcial, N., Castellanos-Albores, J., Lawrence, D., 2003. Leaf litter decomposition of tree species in three successional phases of tropical dry secondary forest in Campeche, Mexico. *Forest Ecology and Management* 174, 401–412.
- Yan, E.R., Wang, X.H., Guo, M., Zhong, Q., Zhou, W., Li, Y.F., 2009. Temporal patterns of net soil N mineralization and nitrification through secondary succession in the subtropical forests of eastern China. *Plant and Soil* 320, 181–194.
- Yang, L.Y., Wu, S.T., Zhang, L.B., 2010. Fine root biomass dynamics and carbon storage along a successional gradient in Changbai Mountains, China. *Forestry* 83, 379–387.
- Yang, Y., Luo, Y., Finzi, A.C., 2011. Carbon and nitrogen dynamics during forest stand development: a global synthesis. *New Phytologist* 190, 977–989.
- Yankelevich, S.N., Fragoso, C., Newton, A.C., Russell, G., Heal, O.W., 2006. Spatial patchiness of litter, nutrients and macroinvertebrates during secondary succession in a Tropical Montane Cloud Forest in Mexico. *Plant and Soil* 286, 123–139.
- Zhang, K., 2011. Restoration of abandoned agricultural lands the Qinling Mountains: ecosystem structure and process. Ph. D. dissertation, Graduate University of the Chinese Academy of Sciences, P.R. China.
- Zhang, K., Cheng, X., Dang, H., Ye, C., Zhang, Q., 2012. Soil nitrogen and denitrification potential as affected by land-use and stand age following agricultural abandonment in a headwater catchment. *Soil Use and Management* (Article first published online).
- Zhang, K., Dang, H., Tan, S., Wang, Z., Zhang, Q., 2010. Vegetation community and soil characteristics of abandoned agricultural land and pine plantation in the Qinling Mountains, China. *Forest Ecology and Management* 259, 2036–2047.
- Zhang, Q., Song, Y., Wu, H., You, W., 1999. Dynamics of litter amount and its decomposition in different successional stage of evergreen broad-leaved forest in Tiantong, Zhejiang province. *Acta Phytocologica Sinica* 23, 250–255 (in Chinese).
- Zhou, G., Guan, L., Wei, X., Tang, X., Liu, S., Liu, J., Zhang, D., Yan, J., 2008. Factors influencing leaf litter decomposition: an intersite decomposition experiment across China. *Plant and Soil* 311, 61–72.