





Spatial patterns and storage composition of woody debris in a natural secondary forest dominated by *Pinus tabulaeformis* on Loess Plateau, China

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Abstract: Woody debris (WD) is an important part of natural *Pinus tabulaeformis* mixed stands, and it affects the forest ecosystem stability and development. The WD spatial patterns are especially important structural characteristics that can provide insights into forest dynamics. In this paper, the WD storage, WD spatial patterns and WD associations among the main species were examined in the natural secondary forest on Loess Plateau in northwest China. Data were collected in a 1 ha (100 m × 100 m) permanent plot, and all the trees with a diameter at breast height of more than 3 cm were measured and stem-mapped. Ripley's K functions from the spatial-point-pattern-analysis method were used to analyze the spatial distribution and associations. The results showed that: (1) The total storage of WD was 10.73 t/ha, fallen wood was the main source of WD, and the majority diameters were greater than 20 cm, and in intermediate levels of decay; (2) The overall spatial pattern was closely related to the spatial scale, which exhibited an aggregated pattern on a small scale, and a random pattern on a large scale. The spatial patterns of coarse woody debris also gradually transitioned from an aggregated pattern in fine scales

to a random pattern in broader spatial scales, which matched the overall spatial pattern. The spatial intensity was gradually decreased with the increasing diameters, and increased with the decomposition classes; (3) The WD of *Pinus tabulaeformis* species was negatively associated with *Betula platyphylla* and *Populus davidiana* on a small scale but positively associated with these species on a large scale. The spatial pattern and interspecies relations were the results of long-term interactions between the natural secondary forest community and the surrounding natural environment. These findings would provide a scientific basis for the sustainable management and protection of natural secondary forest ecosystems on Loess Plateau.

Keywords: Spatial pattern; Spatial association; Storage; Woody debris; Natural secondary forest; Loess Plateau.

Introduction

Woody debris (WD) is one of the most important components of forest ecosystems, which is defined as standing and fallen dead trees that

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cannot be captured by littertraps (Harmon and Franklin 1986). Natural science workers have focused extensively on WD mainly in the US and Canada, with certain studies conducted in European Countries, Brazil, Argentina, New Zealand and Malaysia (Chen and Harmon 1992). These researchers fully emphasized the positive influence of the reasonable management of WD on the protection of biodiversity. Currently, research subjects concerning WD in China include storage, composition, distribution, spatial heterogeneity, nutrient storage, nutrient pool and decomposition at research sites located mainly in the Changbai Mountains, Lesser Khingan Mountains, Qinling Mountains, Wuyi Mountains, Dinghu Mountains and Ailao Mountains (Chen and Xu 1991; Zhang et al. 2015; Yan et al. 2005; Song and Tang 2005). However, most of China's findings are in the initial stage of understanding, and most of the researches are limited to a relatively small spatial scale and have thus far failed to address the function.

The important ecological function of WD depends not only on its quantity but also the spatial distribution of the population (Ulyshen et al. 2004). The formation of WD occurs at different stages of tree individual development (from sapling to postmaturity) (Clark et al. 2002). A multiple-scale quantitative analysis of the spatial distribution and the influencing factors may help to improve the understanding of such ecological processes, including the causes of mortality in forest trees, the changing community dynamics, and the energy cycle of forest ecosystem. However, the spatial distribution pattern of WD remains poorly known in many forest types, which maybe partly because the area of most plots is relatively small.

In most cases, the dynamic pattern change for standing trees is often used to deduce the occurrence and structural features to indirectly determine the regeneration and succession. In addition, WD is often ignored that can be directly studied to reveal the environmental characteristics of the population, through which possible error arising from indirect deduction can be prevented. In previous studies, the spatial distribution of observed WD almost fully reflected the spatial pattern of the arborous layer of standing trees (von Oheimb et al. 2007; Storry et al. 2006). Currently, the study of the spatial distribution pattern of WD

in China is still in the early stages and is not yet system or integral. Compared to foreign countries, the study of WD in China has not included long-term location experiments, and most studies are limited to a small spatial scale, which tends to ignore the influence of rare or occasional phenomena. In particular, there are only a few reports on the quantitative analysis based on different compositions and different diameter class structures of WD.

The total amount of storage, the tree species composition and the decay stage distribution are fundamental characteristics of WD that have been previously assessed in different forests (Yuan et al. 2014; Hood et al. 2004). However, other important aspects, such as the size class distribution and spatial pattern, have seldom been examined in the temperate deciduous forests of China. In particular, forests dominated by *Pinus tabulaeformis*, which represent the most important forest communities in natural forest landscapes in the Loess Plateau, have gone under studied. The main reason for this shortcoming may be the small number of virgin and natural secondary forests in this region. The purpose of this paper is to analyze the quantity, quality, and spatial patterns of WD in a natural secondary forest dominated by *Pinus tabulaeformis* on Loess Plateau. A detailed understanding of the distribution and structure of WD is essential when formulating guidelines for forest management and provides a scientific basis for accelerating the secondary succession and sustainable development of natural secondary forest ecosystems.

1 Materials and Methods

1.1 Study area

The Loess Plateau is located in northwest China and is one of China's four large plateaus. This plateau is one of the birthplaces of the ancient civilization in China, and features the most concentrated distribution and largest areas of Loess on earth. Most importantly, the Loess Plateau shows some of the most serious areas for soil erosion and possesses one of the most vulnerable ecological environments in China (Tian et al. 2016). The study area was located in the

southeastern Loess Plateau, in northern Shaanxi Province. Detailed surveys were conducted in the Huanglong Mountains. The entire forest zone shows extreme irregularity, a complicated geological structure, and a fractured landform, with typical geographical structures of the Loess Plateau. The altitude ranges from 800m to 2500m, the annual average temperature is 10 °C, the frost-free lasts 175 days, the annual precipitation is 611.8 mm (mostly between July and September), and the annual evaporation capacity is 856.5 mm, and the general climate belongs to the warm temperate zone. The abrupt and broken topography mainly consists of granite and gneiss. The mean slope is 35° and the mean soil depth is 50 cm. The soil is classified as mountain brown earth.

The vegetation on Loess Plateau consists of North China flora, with more than 580 plant species and 46 arbor species in 29 genera and 22 families, and the stands age was about 60. The main arbor species include *Pinus tabulaeformis*, *Betula platyphylla*, *Populus davidiana*, *Quercus*

wutaishansea, *Acer ginnala*, *Pyrus betulaefoli*, *Toxicodendron verniciflu-um*, *Rataegi cuneatae*, *Populus simonii*, *Prunus davidiana*, *Juglans cathayensis* and *Betula albosinensis*.

1.2 Data collection

In August 2014, a single permanent plot was established with an area of 1 ha (100 m×100 m) in natural secondary forest dominated by *Pinus tabulaeformis*, which had an average elevation of 1338 m and an average gradient of 30°, (the coordinate of its center is 35°46'58.7" N, 109°46' 3.3" E). Location of Honglong Mountains and sample plot were shown in Figure 1. The sample plot was divided into 25 blocks of 20 m × 20 m with high-precision TOPCON, and each piece of WD was identified to the species level and categorized as dead standing trees, fallen trees, stump roots, boughs and branchlets (Figure 2). The standard wood debris (diameter (*d*) ≥2.5 cm at the widest point) was classified according to the

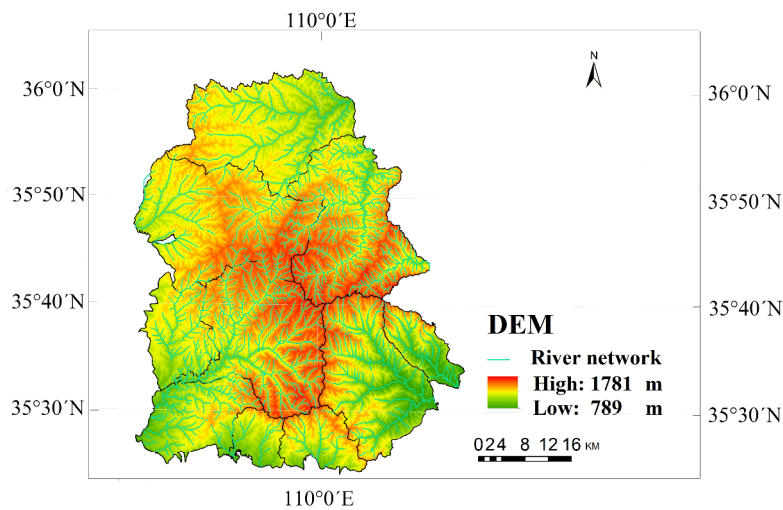


Figure 1 Location of the Huanglong Mountains and permanent plot.

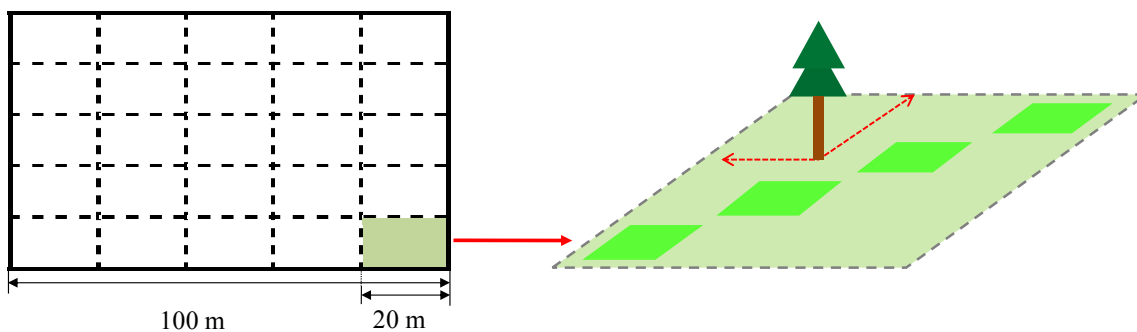


Figure 2 The setting of the sample and the method of investigation.

measurements used by the USDA Forest Service and Long Term Ecological Research (LTER), in which WD was classified according to diameter size as coarse woody debris (CWD), defined by $d \geq 10$ cm) and fine woody debris (FWD), defined by d of $2.5 \text{ cm} \leq d < 10 \text{ cm}$). For each WD inventoried, the following criteria were recorded in the field: species, length, type, diameter, and decomposition class, which ranged from 1 to 5 according to discrepancies in internal and external tissue characteristics (Sollins 1987) (Table 1).

1.3 Sampling and biomass measurement

Five samples were chosen from each decomposition class of each tree species. The WD of *Pinus tabulaeformis* had complete decomposition classes, but *Betula platyphylla* and *Populus davidiana* did not have class V, a total of 115 WD samples were collected to quantify the WD characteristics. In the early decomposition stages, the WD was cut into many disks (5 cm thick) using a saw, whereas in the advanced decomposition classes, the WD samples were most fragile. These samples were removed with aluminum plates with a known capacity and then the collected samples were sealed in plastic bags and transported to the laboratory. The sample volume (V_{sample}) was determined gravimetrically with water displacement, and subsequently dried to a constant weight at 70°C. The sample density (ρ_{sample}) was estimated as the ratio of dry mass to V_{sample} .

Prior to calculating the WD biomass, the volume of WD was regarded as V_{CWD} , which could

be considered a cylinder. Subsequently, Smalian's formula was used to produce a volume estimate through the length and cross-sectional areas at the basal and distal ends of the cylinder. The acquired volume should be the maximum estimates because the result of this formula tends to be slightly overestimated because the log or stump tapers as a frustum of a cone (Baker et al. 2007). Finally, the product of ρ_{sample} and V_{WD} was computed as the WD biomass (t/ha).

1.4 Statistical analysis

1.4.1 Importance value

The importance value is a comprehensive quantitative indicator used to characterize the status and role of each species in the community. A species with a larger importance value is considered to have greater dominance in the plot. The importance value was calculated from the equation (Feroz et al. 2008):

$$IV = \frac{\frac{n_i}{\sum_{i=1}^S n_i} * 100 + \frac{a_i}{\sum_{i=1}^S a_i} * 100 + \frac{f_i}{\sum_{i=1}^S f_i} * 100}{3} \quad (1)$$

where n_i is the number of individuals of the i th species, a_i is the basal area at the height of $H/10$ of trees belonging to the i th species, f_i is the number of quadrats in which the i th species appeared, and S is the total number of species.

1.4.2 Spatial point process analysis

The K -function is defined as the expected number of points occurring within distance t of a randomly chosen point and normalized by the

Table 1 Classification system of decomposition classes

Class	Leaf	Branch	Bark	Woody structure and integrity	Root intrusion	Indirect means
I	Existing	With branchlets and complete boughs	Complete and firm	Firm and intact	Absent	Fresh wood, 1~2 years after death
II	Absent	With some branchlets and complete boughs	Basically complete and partially loose	Firm, with some sapwood starting decomposition, with intact heartwood	Absent	Starting decomposition, and a blade can pierce for several mms
III	Absent	Without branchlets, and with some boughs	Partially existing, and loose	Relatively firm, with decomposed sapwood and intact heartwood	Sapwood area	A blade can pierce
IV	Absent	Absent	A little and loose	Partially firm, prone to cracking, with heartwood starting decomposition	Intrusion into partial heartwood	A blade can pierce for 2~5 cm
V	Absent	Absent	Absent	Loose, and easily turning into power	Penetration through the whole	Wood can be penetrated through randomly

intensity λ of the point pattern (Getis and Franklin 1987; Ripley 1977). $K(t)$ is the cumulative distribution function up to a given radius t . The $L(t)$ function is a transformation of Ripley's K-function (Besag 1977), which can linearize the $K(t)$ function, stabilize the variables, and makes the assumption close to 0 under a random distribution:

$$K(t) = A \sum_{i=1}^n \sum_{j=1}^n \frac{\delta_{ij}(t)}{n^2}; i \neq j \quad (2)$$

$$L(t) = \sqrt{\frac{K(t)}{\pi}} - t \quad (3)$$

where A is the area of sample plot, t is the scale of the distance, n is the stem number of the analyzed trees, and δ_{ij} is reciprocal to the proportion of the perimeter of a circle centered on event i and passing through event j , and lying within the plot. The value of $\delta_{ij}(t)$ is equal to 1 for a circle wholly contained within the plot area and greater than 1 when the edge correction is required (Koukoulas and Blackburn 2005). The maximum value (t) for rectangular plots is restricted to half of the short sides of a rectangle (Moeur 1993).

Under the null model of complete spatial randomness (CSR), the value of $L(t)$ is 0, whereas values of $L(t) < 0$ indicate a regular distribution and $L(t) > 0$ indicate an aggregated distribution at scale t . A Monte-Carlo simulation was conducted to test the statistical significance of $L(t)$ deviations from zero under the null hypothesis of CSR (Hou et al. 2004). Confidence intervals (99%) were generated using the high and low $L(t)$ values obtained from 1,000 random permutation simulations.

1.4.3 Inter-species spatial relation analysis

An analysis of the relationship between two species is actually the point pattern analysis of the two species, which is also called a multivariate point pattern analysis. The analysis of the Ripley's $\hat{K}_{12}(t)$ index was made by its transformation in $\hat{L}_{12}(t)$ (Hou et al. 2004; Greig-Smith 1964):

$$\hat{K}_{12}(t) = \frac{A}{n_1 n_2} \sum_{i=1}^{n_1} \sum_{j=1}^{n_2} w_{ij}^{-1} I_r(u_{ij}) \quad (4)$$

$$\hat{L}_{12}(t) = \sqrt{\hat{K}_{12}(t) / \pi} - t \quad (5)$$

where n_1 and n_2 are the numbers of the two classes of points per tree, and w_{ij} is the probability the plant can be observed. A value of $\hat{L}_{12}(t) =$

0 indicates that the two groups are spatially independent in t scale, values of $\hat{L}_{12}(t) > 0$ indicate a positive association and values of $\hat{L}_{12}(t) < 0$ indicate a negative association. To test the statistical significance of $\hat{L}_{12}(t)$ deviations from zero, the random labeling hypothesis was tested to analyze the relationships among species and the different growth stages.

All of the calculations and simulations were computed using the ADE-4 package (Thioulouse et al. 1997) at the ADE-4 website.

2 Results

2.1 Stand structure

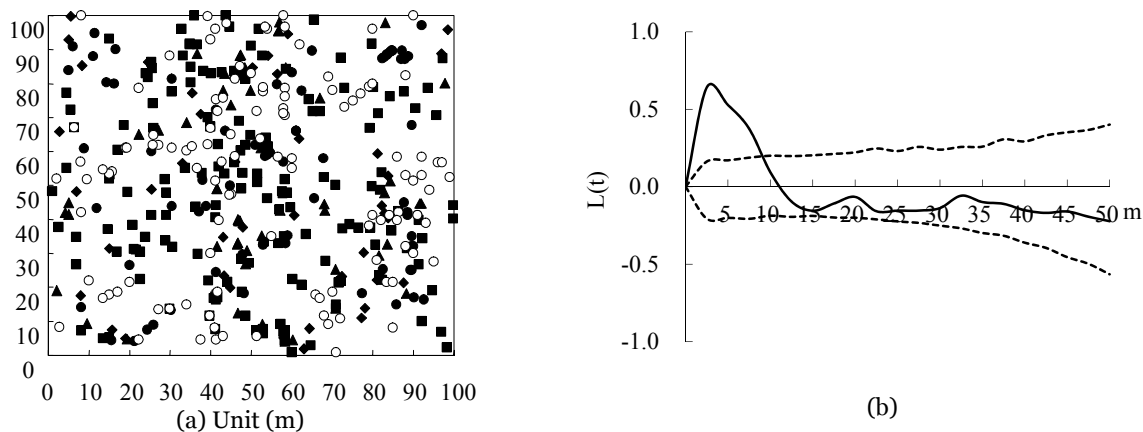
The total density of the canopy stage (DBH ≥ 3 cm) was 1024 trees/ha and consisted of 21 arbor species, and the basal area was 21.56 m²/ha. The density of *Pinus tabulaeformis* was comparatively higher among the canopy stage species (Table 2), the proportion of this species per hectare of basal area was 81.00%, and its importance value was 61.12%; thus, this species was considered the dominant species within the whole forest canopy and the top zonal tree species. *Quercus wutaishansea*, *Acer ginnala*, *Populus davidianas* and *Betula platyphylla*es showed high basal area. *Betula platyphylla* showed a comparatively lower density, but the average DBH was the second largest due to its thickness. During secondary succession, *Pinus tabulaeformis*, a shade-tolerant zonal top tree species, gradually became the dominant species.

2.2 Overall spatial distribution pattern

The coordinates of all the WD in the 1 ha permanent plot were shown in Figure 3a, which showed an aggregated pattern on a scale <11 m and showed a significantly random pattern on a scale >11 m, which revealed a maximum pattern intensity of 0.63 on a scale of 4 m (Figure 3b). The scale of 11 m was the boundary scale at which the spatial distribution transitioned from the aggregated pattern to the random pattern, which corresponded to the lowered value of $L_{12}(t)$ from its position above the top envelope curve to the position between the top and bottom envelope

Table 2 Basic structure characteristics of alive species

Family Name	Trees/ha		Breast-height basal area/ha		Average DBH (cm)	Important value (%)
	Number	%	Area (m ²)	%		
<i>Pinus tabuliformis</i>	557	51.38	17.42	81.00	20.0	61.12
<i>Quercus wutaishansea</i>	199	18.36	1.39	6.47	9.4	14.37
<i>Acer ginnala</i>	125	11.53	1.00	4.64	10.1	9.22
<i>Populus davidiana</i>	66	6.09	0.49	2.28	9.7	4.82
<i>Betula platyphylla</i>	29	2.68	0.41	1.93	13.5	2.55
<i>Swida macrophylla</i>	24	2.21	0.17	0.79	9.5	1.73
<i>Crataegi cuneatae</i>	18	0.65	0.06	0.54	6.5	1.20
<i>Ulmus macrocarpa Hance</i>	11	1.66	0.06	0.28	8.2	0.77
<i>Populus simonii</i>	8	1.01	0.09	0.27	12.0	0.63
<i>Toxicodendron vernicifluum</i>	7	0.74	0.12	0.42	14.5	0.61
<i>Pyrus betulifolia</i>	5	0.46	0.11	0.49	16.4	0.47
<i>Viburnum mongolicum</i>	5	0.46	0.06	0.28	12.5	0.40
<i>Betula albo-sinensis</i>	5	0.46	0.01	0.04	4.7	0.32
<i>Cornus officinalis Sieb</i>	4	0.37	0.03	0.14	9.9	0.29
<i>Abelia biflora</i>	4	0.37	0.01	0.03	4.6	0.26
<i>Platycladus orientalis</i>	3	0.28	0.02	0.02	9.1	0.21
<i>Koelreuteria paniculata</i>	3	0.28	0.01	0.09	7.4	0.20
<i>Viburnum dilatatum Thunb</i>	3	0.28	0.00	0.06	3.8	0.19
<i>Syringa oblata</i>	2	0.18	0.02	0.10	11.6	0.16
<i>Bothrocaryum controversum</i>	1	0.18	0.05	0.02	26.4	0.15
<i>Carya cathayensis</i>	2	0.09	0.00	0.08	4.7	0.13
<i>Prunus davidiana</i>	1	0.09	0.02	0.00	15.1	0.09
<i>Cornus walteri</i>	1	0.09	0.01	0.03	10.3	0.07
<i>Quercus aliena</i>	1	0.09	0.00	0.01	3.0	0.06



◆ Fallen tree; ▲ Dead standing tree; ■ Tree stump; ● Bough; ○ Fine woody debris.

Figure 3 Scatter diagram of distribution (a) and $L(t)$ values (b) for the whole woody species. The solid line shows actual $L(t)$ value, and dotted line correspond to 99% confidence intervals generated from 1,000 Monte Carlo simulations under the null hypothesis of complete spatial randomness. If $L(t)$ within confidence intervals, then the spatial pattern at distance t is entirely random; if $L(t)$ is above the upper confidence interval and below the lower confidence interval, then the spatial patterns indicate aggregated pattern and regular pattern, respectively ($p < 0.01$).

curves.

2.3 Spatial distribution of different compositions

The storage composition of WD directly affects the nutrient biomass and productivity. There were significant differences in different WD types (Table 3).

The CWD biomass was 10.31 t/ha and consisted of 96.09% of the total biomass; in contrast, the amount of FWD was 0.42 t/ha and consisted of only 3.91% of the total biomass. Fallen trees were the most common CWD component in this forest, with a biomass of 5.99 t/ha and accounting for 55.82% of the CWD; Dead standing trees

Table 3 The storage of woody debris in different composition

Composition	Storage (t/ha)	%	
CWD	Dead standing tree	2.34	21.81
	Fallen tree	5.99	55.82
	Tree stump	1.18	11.00
	Bough	0.80	7.46
	Total	10.31	96.09
FWD	0.42	0.93	
Total	10.73	100	

Notes: CWD is coarse woody debris (diameter ≥ 10 cm) and FWD is fine woody debris (2.5 cm ≤ diameter < 10 cm).

accounted for the second largest biomass, which accounted for 21.81% of the CWD. On Loess Plateau, fallen trees mainly resulted from aging and tree death, which occurred due to disease and insect pests in natural competition; moreover, large numbers of dead standing trees were blown down by strong winds.

The spatial distribution of the WD was analyzed according to composition (Figure 4). The fine woody debris showed a significantly aggregated pattern on a scale < 30 m, a random

pattern on scales ranging from 30 m to 40 m, and a regular pattern on a scale >40 m. The distribution patterns of all composition types except for FWD were in gradual transition from an aggregated pattern to a random pattern. For fallen trees with spatial distribution on Loess Plateau, the spatial scale of 20 m was the boundary scale at which the WD transitioned from an aggregated pattern to a random pattern. The decomposition scales of the stump roots and boughs of the dead standing trees ranged in scale from 25 m to 30 m.

2.4 Spatial distribution of different diameter class structures

The WD storage in the large-diameter class ($d > 20$ cm) was the majority in this forest, comprising 83.04%. In particular, the diameter class between 30 cm and 40 cm was the most dominant diameter class, which accounted for 8.91 t/ha and 43.52% of the total biomass, which was mainly due to the natural pruning density of the standing trees (Figure 5). Therefore, due to

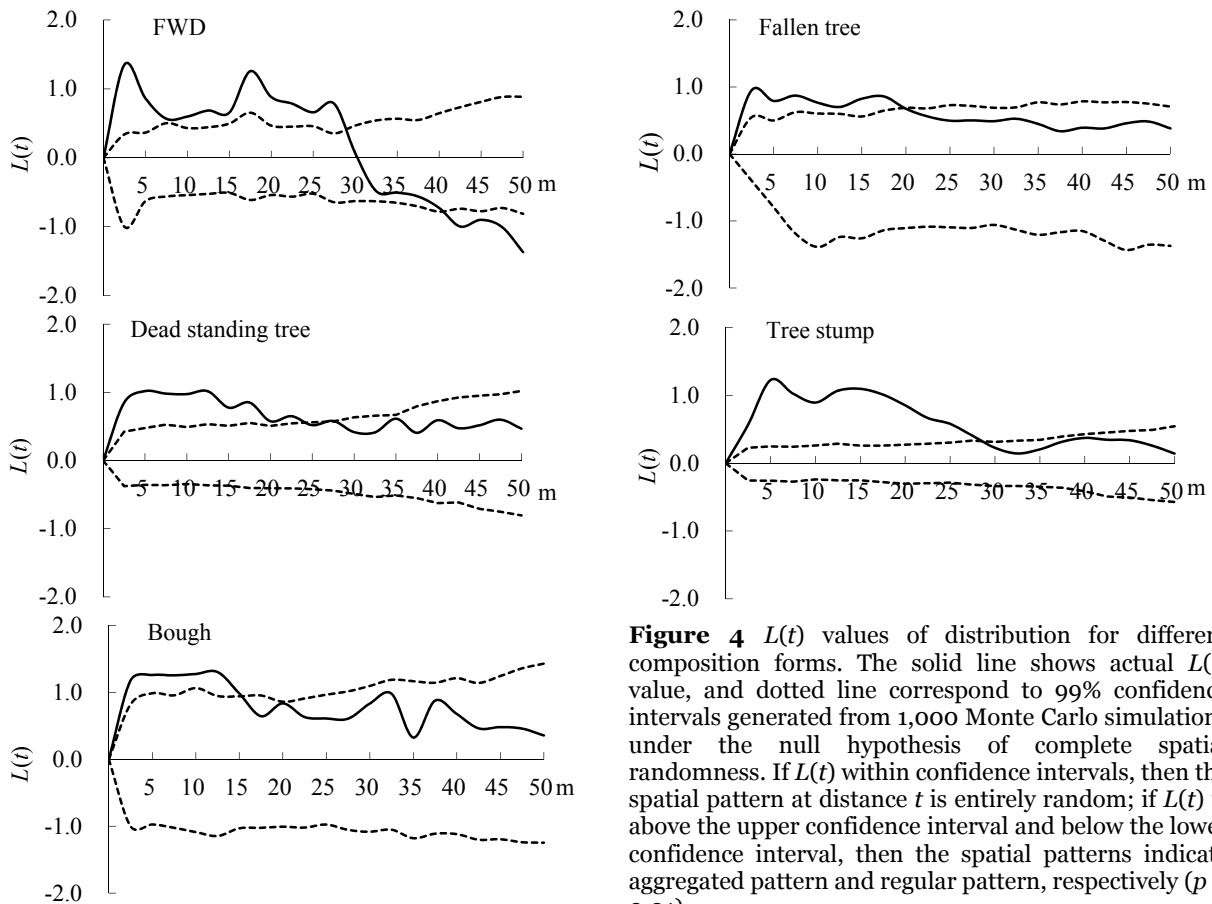


Figure 4 $L(t)$ values of distribution for different composition forms. The solid line shows actual $L(t)$ value, and dotted line correspond to 99% confidence intervals generated from 1,000 Monte Carlo simulations under the null hypothesis of complete spatial randomness. If $L(t)$ within confidence intervals, then the spatial pattern at distance t is entirely random; if $L(t)$ is above the upper confidence interval and below the lower confidence interval, then the spatial patterns indicate aggregated pattern and regular pattern, respectively ($p < 0.01$).

protection, natural succession, and development, the WD with diameter ranging from 20 cm to 40 cm formed a main portion of the forest.

The spatial distribution of the WD was analyzed according to the diameter class structure (Figure 6). The diameter class I ($2.5 \leq d < 10$ cm), i.e., FWD transitioned from the aggregated pattern

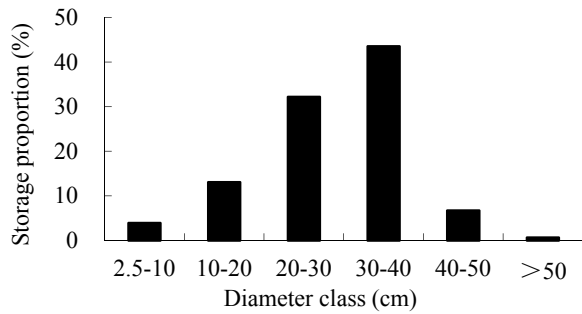
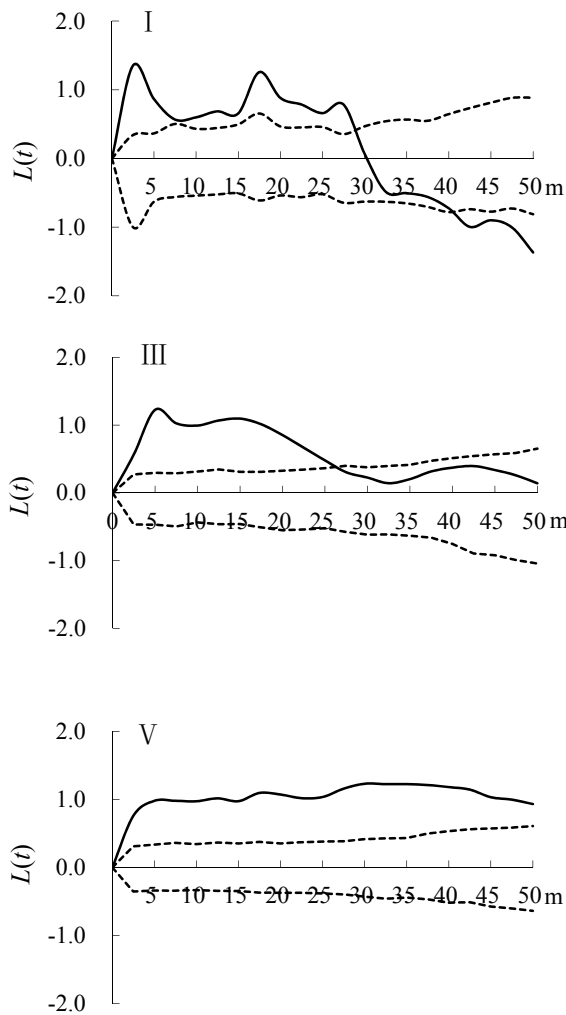


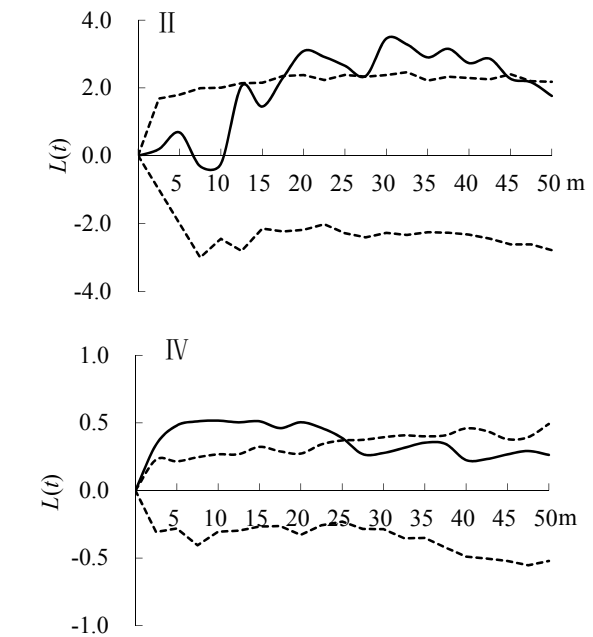
Figure 5 The storage proportion of woody debris in different diameter class.



to a random pattern and finally to a regular pattern, and its intensity decreased gradually with the expansion of the spatial scale range. For diameter class II to IV ($10 \leq d < 40$ cm), the intensity also decreased gradually with the increase of the diameter class. The spatial distribution of the diameter classes II, III and IV transitioned from aggregated patterns to random patterns, but for diameter class V ($40 \leq d < 50$ cm), the spatial distribution showed a significantly aggregated distribution on a scale < 50 m, which was mainly due to the small amount of woody debris in the diameter class V.

2.5 Spatial distribution of different decomposition classes

The decomposition class of WD reflects the characteristics of the nutrient cycle in the stand. In



I: $2.5 < d < 10$ cm; II: $10 < d < 20$ cm; III: $20 < d < 30$ cm; IV: $30 < d < 40$ cm; V: $40 < d < 50$ cm

Figure 6 $L(t)$ values of distribution for different diameter class structure. The solid line shows actual $L(t)$ value, and dotted line correspond to 99% confidence intervals generated from 1,000 Monte Carlo simulations under the null hypothesis of complete spatial randomness. If $L(t)$ within confidence intervals, then the spatial pattern at distance t is entirely random; if $L(t)$ is above the upper confidence interval and below the lower confidence interval, then the spatial patterns indicate aggregated pattern and regular pattern, respectively ($p < 0.01$).

general, the decomposition class of WD is positively correlated with the decomposition time. The biomass of the decomposition classes showed a wide range of variation (Figure 7). For *Pinus tabulaeformis*, the greatest proportion of WD biomass (including all decomposition classes) was class II (40.68%) and the smallest proportion was class V (2.50%). The greatest proportion of *Betula platyphylla* and *Populus davidiana* were class III (46.15% and 46.60% respectively), and there was no distribution in class V, due to the distribution of the top tree species and pioneer tree species among the standing trees on Loess Plateau.

The spatial distribution of WD was analyzed according to decomposition classes (Figure 8). The spatial intensity and scale of the WD increased with the decomposition classes. The spatial distribution of decomposition class showed an aggregated pattern on a scale < 10 m, a random pattern from 10 m to 35 m, and finally a regular pattern on a

scale > 35 m. The WD in decomposition class II at the 25 m scale transitioned from an aggregated pattern to a random pattern, whereas, this transition occurred in the WD in decomposition class III at the 40 m scale. The decomposition class

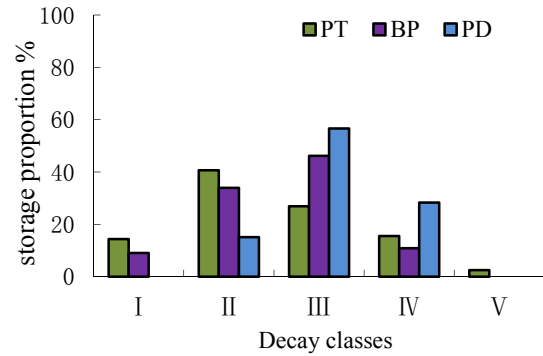
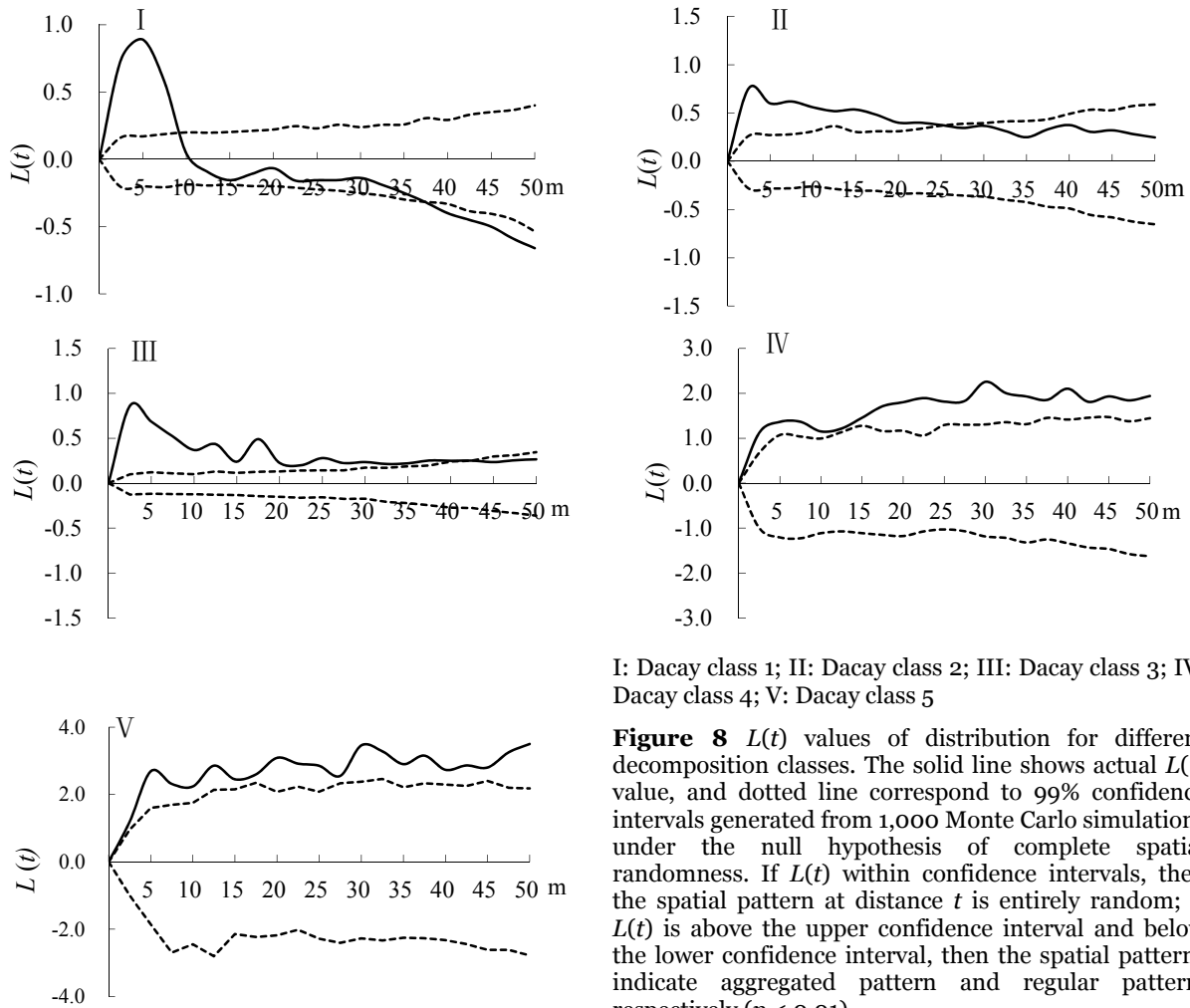


Figure 7 The storage of woody debris in different decomposition classes (PT represents *Pinus tabulaeformis*; BP represents *Betula platyphylla*; PD represents *Populus davidiana*).



I: Dacay class 1; II: Dacay class 2; III: Dacay class 3; IV: Dacay class 4; V: Dacay class 5

Figure 8 $L(t)$ values of distribution for different decomposition classes. The solid line shows actual $L(t)$ value, and dotted line correspond to 99% confidence intervals generated from 1,000 Monte Carlo simulations under the null hypothesis of complete spatial randomness. If $L(t)$ within confidence intervals, then the spatial pattern at distance t is entirely random; if $L(t)$ is above the upper confidence interval and below the lower confidence interval, then the spatial patterns indicate aggregated pattern and regular pattern, respectively ($p < 0.01$).

V showed an aggregated pattern at all scales.

2.6 Spatial correlation between dominant species

The WD biomass significantly differed between the main tree species. As a dominant coniferous tree, *Pinus tabulaeformis* had the highest WD biomass, which reached 7.99 t/ha, and accounted for 74.46%, which was more than two times greater than that of the other tree species (Table 4). Furthermore, the broadleaf species *Betula platyphylla* ranked second in WD biomass (20.60%). Interestingly, although *Populus davidiana* was the most frequently associated broadleaf tree species, the WD biomass of this species amounted for less than 4% of the total.

Table 4 Storage and proportion of species composition

Species	Biomass (t/ha)	Proportion (%)
<i>Pinus tabulaeformis</i>	7.99	74.46
<i>Betula platyphyllaes</i>	2.21	20.60
<i>Populus davidiana</i>	0.53	4.94
Total	10.73	100

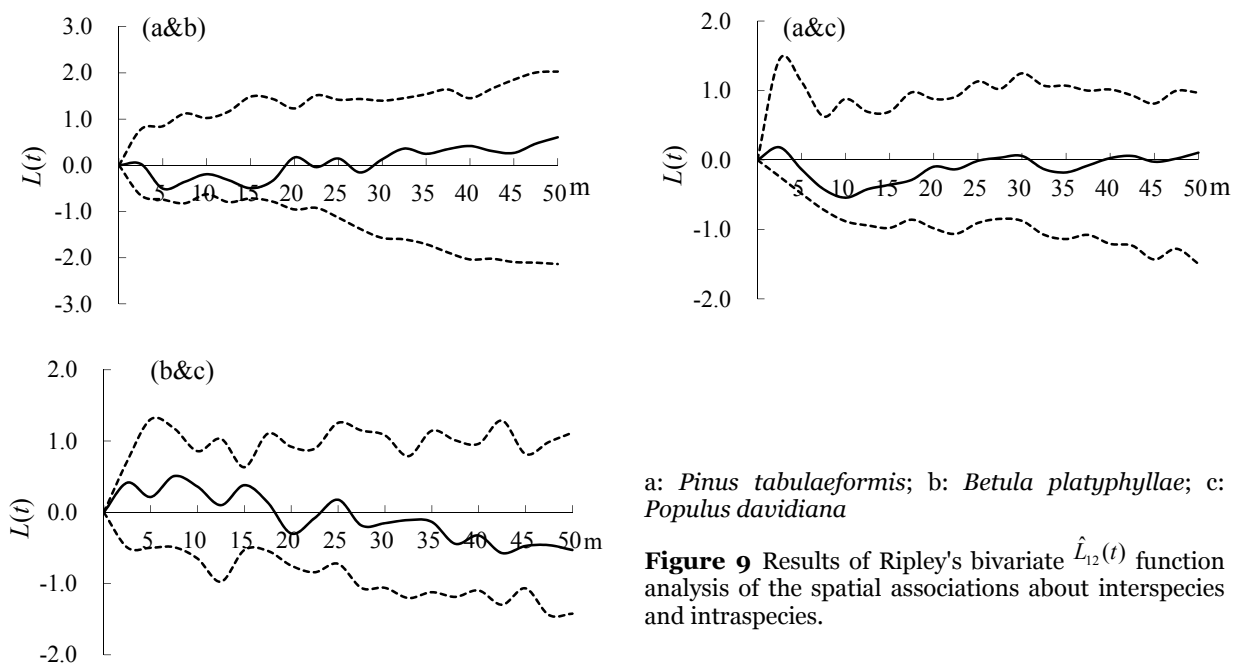
Pinus tabulaeformis was negatively associated with *Betula platyphylla* and *Populus davidiana* on small scale and positively associated with these two species on a large scale (Figure 9). The community was fairly stable as a top species and two pioneer species had reached mutualism, in which the three

species shared resources. The interspecies relationship between *Betula platyphylla* and *Populus davidiana* evolved from a positive association on small scale to a negative association on large scale and the values of $\hat{L}_{12}(t)$ fluctuated around 0, which showed mutual independence.

3 Discussions

3.1 Storage composition

The WD distribution in the present secondary forest dominated by *Pinus tabulaeformis* was a result of comprehensive influences from the forest developmental stage, which were caused by past selective logging and more recent natural and anthropogenic interferences. However, the amount of WD was 10.31 t/ha, which were far below the lower limit of the global records (e.g., the global range in reserves of natural coniferous forests varies from 30 t/ha to 200 t/ha). Yuan et al. (2014) reported an equivalent amount (12.56 t/ha) of WD in a natural secondary forest of *Pinus tabulaeformis* nearby our study site, whereas He et al. (2011) showed a lower value (7.706 t/ha) in an adjacent natural forest of *Pinus tabulaeformis*. The accumulation of WD was expected to be dynamically mediated by the various factors controlling WD production and decomposition (Stevens 1997). These differences were mainly due



a: *Pinus tabulaeformis*; b: *Betula platyphyllae*; c: *Populus davidiana*

Figure 9 Results of Ripley's bivariate $\hat{L}_{12}(t)$ function analysis of the spatial associations about interspecies and intraspecies.

to two aspects: firstly, the climate, site quality, species composition, disturbance, and the degree greatly affected the death and decomposition rates of dead standing trees as well as the biomass of WD (Sollons 1982); and secondly, differences existed in the definition standards for the diameter class. Moreover, due to the lower WD storages in the study area, the natural secondary forest maybe subjected to long-term frequent human activities.

In terms of the WD composition in the present natural secondary forest on Loess Plateau, fallen trees, followed by dead standing trees, were a principal in put source of WD, this finding was consistent with suggestions from other reports (Keller et al. 2004; Delaney et al. 1998; Carmona et al. 2002). Generally, most of the WD in natural forests was derived from gradual accumulation after ecosystems suffered from severe disturbances (e.g., wind throw). However, a surge in WD biomass can also be suddenly created by serious windstorms. For instance, in 1986, a catastrophic tornado produced up to 1000 ha of logs in the Changbai Mountains (Chen and Harmon 1992). Thus, we believed that the substantial biomass in the *Pinus tabulaeformis* forest should primarily result from the most recent local pulses in mortality, which were driven by a combination of strong winds and steep topography. This explanation can be verified by the fact that these *Pinus tabulaeformis* forests (30–40 cm) were usually observed on mountain ridges, windward slopes and abrupt slopes. For the diameter class below 50 cm, the woody debris biomass proportion of fallen trees was greater than that of dead standing trees; whereas for a diameter class ≥ 50 cm, the WD biomass gap between fallen trees and dead standing trees was gradually narrowed.

3.2 Spatial pattern

The population structure and spatial distribution of a species were always the result from interactions between the biological characteristics and the environment (Hao et al. 2007), and the distribution regularities of WD deeply reflected natural succession and regeneration. The spatial patterns and affinities were analyzed for the coexistence of overall WD in the *Pinus tabulaeformis* forest (Figure 3), which was in transition from an aggregated pattern to a

random pattern and showed a similar distribution to the WD in a typical broadleaf *Korean pine* forest in the Lesser Khingan Mountains, Heilongjiang Province, China (Liu and Jin 2010). For a natural *Beech* forest, the spatial distribution structure of WD and standing tree species showed a random pattern in 8 ha of a sample plot, whereas the same species in a 14.3 m \times 14.3 m sample plot showed an aggregated pattern (Rademacher and Winter 2003). Similarly, according to a study on *Beech* in three sample plots, both standing trees and WD showed aggregated patterns (Müller-Using and Bartsch 2003), thus, the spatial scale was used as a variable factor to characterize the spatial distribution trend.

The diameter class structure was a factor that influenced the spatial pattern of WD (Parish et al. 1999; Edman and Jonsson 2001). For instance, the spatial distribution of woody debris for different diameter classes which showed aggregated patterns on a small-scale and random patterns on a big scale (Figure 6), which was consistent with the results by Rouvinen and Kouki (2002) in Eastern Finland, who showed that WD in the small diameter class had an aggregated pattern and large diameter class had a random pattern. The spatial structure of the branchlets on Loess Plateau transitioned from an aggregated pattern to a random pattern and then to a regular pattern, which was different from the composition of the other WD. The composition difference also existed in a temperate forest in Albania, in which broken boughs and stump roots among the WD showed an aggregated distribution, while other constituents showed a random distribution. In terms of the spatial distribution of tropical forests in Wald, Norway, only fallen trees were in an aggregated distribution, which indicated that the different constituents of WD differed in terms of spatial distribution (Meyer 1999).

3.3 Spatial relationship

A strong correlation between WD biomass and living tree biomass was previously reported by several studies (Siitonen et al. 2000; Pedlar et al. 2002). Notwithstanding, there had been no investigation on living tree biomass. Our results showed that *Pinus tabulaeformis* was the dominant tree species, consisting of $> 51\%$ of the total number of living trees (Table 2), thus, the dominant WD input was from *Pinus tabulaeformis*

(Table 4). The positive/negative association among species affected the succession progression. *Pinus tabulaeformis* was negatively associated with *Betula platyphylla* and *Populus davidiana* on the small scale, but positively associated with these species on the large scale (Figure 8). Generally, a negative interspecific relationship implied interspecific competition (Rejmanek and Lep 1996), but our results implied that *Pinus tabulaeformis* occupied the largest area and had a positive relationship with other two species. In particular, *Pinus tabulaeformis* had positive affinity with the other species, which indicated that *A. holophylla* was a dominant species at this study site. Contrary to the expectation of positive associations, *Betula platyphylla* and *Populus davidiana* did not show any significant associations. This may have been due to their low density at the study site and was thought to be a late successional species that occurred with shade tolerance and high reproductivity. In contrast, the low shade resistance of *Betula platyphylla* and *Populus davidiana* may preclude the formation of understories, which caused a thin-out. These two species were thought to be late succession species with shade tolerance and high reproductivity.

In addition to competition, the development structure was partially affected by the population history. Although the *Pinus tabulaeformis* forest on Loess Plateau had been scarcely affected by artificial disturbance since the implementation of the Natural Forest Protection Program, the stand structures and development had been affected by forest management measures. In the small scale range, virgin forests were capable of long-term continuous production of WD owing to their highly

differentiated age structures; however, due to the implementation of forestry measures and artificial interference, the ages of near-natural forests were relatively consistent. Furthermore, compared to virgin forests, the amounts and structures of WD with artificial interference were decreasing. Near-natural forests, such as *Pinus tabulaeformis* forests, required centuries of non-interference cycles for development to be close to the state of virgin forests. In particular, data from a more permanent plot was ideal for the analysis of the spatial structure of WD. Because there were few data for virgin *Pinus tabulaeformis* forests, research on the storage and structures of near-natural *Pinus tabulaeformis* forests were important references for future regional development and management program. Future researches will focus on succession progression based on the long-term monitoring of WD in dedicated permanent sample plots.

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