







Structure and regeneration dynamics of three forest types at different succession stages of spruce – fir mixed forest in Changbai Mountain, northeastern China


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
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Abstract: Analyzing and understanding the structure and growth dynamics of forests at different stages is helpful to promote forest succession, restoration and management. Three spots representing three succession stages of spruce-fir mixed forest (SF: polar-birch secondary forest, MF: spruce-fir mixed forest and PF: spruce-fir near primary forest) were established. Structure, growth dynamics during two growth seasons for dominant tree species, regeneration were examined, and a univariate *O*-ring function statistic was used to analyze the spatial patterns of main regeneration tree species. Results showed that, (1) composition of tree species, periodic annual increment (PAI) of the diameter at breast height (DBH), basal area for overstory trees and of ground diameter (DGH) for saplings, were significantly different with the succession; (2) the

current species composition and regeneration dynamics of SF suggested a development towards spruce-fir mixed forests. Pioneer species like *Betula platyphylla* will gradually disappear while climax species, such as *Abies nephrolepis*, *Pinus koraiensis*, *Picea koraiensis* and *Tilia amurensis* will dominate forest stands; (3) Despite the highest volume occurring in PF, and saplings in it grew better than in the others, this forest type is unstable because of its unsustainable structure of DBH class and insufficient regeneration; and (4) MF had the most reasonable distribution of DBH class for adult trees (DBH > 5.0 cm) and DGH class for saplings (H ≥ 30 cm and DBH ≤ 5 cm), as well as an optimal volume increment. Limiting canopy opening size can lessen the physiological stress and promote the growth and competitive status of regeneration. Management implications for increasing the gaps and thus creating better growth conditions for understory saplings and facilitating forest succession were discussed.

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Introduction

The Changbai Mountains are the tallest mountain range in Northeastern China. There is a distinct vertical distribution of four forest types along the elevational gradient, presenting a condensed picture of the array of temperate and boreal forests found across Northeastern China (Shao et al. 1996; Hao et al. 2007; Lina et al. 2011). Spruce-fir mixed forest is one of the major forest types and is generally considered to be one of the climax forest communities in the region (Zhao et al. 2012).

However, due to historical issues and the need for economic growth, the past century witnessed excessive logging and neglected cultivation derived a series of problems that almost exhausted exploitable forest resource in the region. This phenomenon was not improved until 1998, when China launched the Natural Forest Conversion Program and established the Changbai Mountain Natural Reserve (CMNR), shifting the primary purpose of forest management from wood production to ecological sustainability, taking ecological restoration and protection as key foci of management (Bai et al. 2011; Yu et al. 2011). Unfortunately, long-term excessive logging had already resulted in large amounts of logged primary forests replaced mainly by post-cut forests and secondary birch-aspen forests. At present, only some “islands” of the near primary forest stands can be found in reserves (Shao et al. 1994). Thus, in order to preserve habitats of biodiversity and decrease ecological disasters, it now becomes urgent to restore the widely distributed secondary and post-cut forests to the climax levels and protect the isolated primary forests (Chen et al. 2003; Murphy et al. 2010).

The composition and dynamics of regeneration is of primary importance in maintaining the natural composition of tree species. Successful regeneration is essential to the sustainable management of uneven-aged stands (Matthews 1989). Moreover, the two-dimensional spatial pattern of individual trees in a stand is fundamental in ecological theory (Condit et al.

2000), can affect growth rates, competition levels, and understory development (Duncan and Stewart 1991). The horizontal structure of a community can also reveal information on the stand history, population dynamics and the relationship of intraspecific and interspecific competition (Haase 1996). In recent decades, many researchers focus on the composition and distribution of vegetation of different forest types among the Changbai Mountains (Chen et al. 1963; Zhao et al. 2004; Yu et al. 2013). However, the stand structure of forests at different succession stages in spruce-fir mixed forest is rarely reported, especially with respect to saplings.

Accordingly, we examined the structure, growth dynamics, and the spatial pattern for overstory trees and understory saplings in three forest communities at different succession stages (SF: polar-birch secondary forest, MF: spruce-fir mixed forest, and PF: spruce-fir near primary forest) in the Changbai Mountains, to provide evidence for forest succession, restoration and management. Therefore, the goals of this study were: (1) to determine whether SF or MF are in positive succession or not, (2) which succession stage is the most beneficial for forest management, and (3) if PF is the optimal forest types or not?

1 Methods

1.1 Study area

The study was conducted in the Jingouling Experimental Forest Farm (43°17'N - 43°25'N, 130°5'E - 130°20'E) (Lei et al. 2007), Jilin Province, China, which is in the Xueling division of Laoye Ling Mountain in the Changbai Mountains (Figure 1). The concession consists of 16,286 hectares of forest, including 13,347 ha of natural stands and 2577 ha of plantations. The altitude ranges from 300 - 1200 m and slopes from 0°-35°. The average annual temperature is 4°C, ranging from -32°C (January) to 22°C (July), the average rainfall is between 600-700 mm. A dark brown forest soil is present in the area and is derived from the parent basalt rock (Forest 1988). The dominant tree species include *A. nephrolepis*, *Pinus koraiensis*, *Picea koraiensis*, *T. amurensis*, *B. platyphylla*, *Acer mono* and *Betula costata*. There

are limited areas with primary forests, which have been under strict protection and represent the climax vegetation.

1.2 Experimental design and data collection

Three forest stands experiencing similar environmental characteristics, such as soil, site conditions and climate environment, were selected in this region (Table 1). In polar-birch secondary forest (SF) and spruce-fir mixed forest (MF), two 1-ha (100 m × 100 m) plots were established in 2011 and 2012, respectively. We recorded the slope, elevation, and humus thickness at each plot. In each plot, the following measurements were made: tree species, the coordinates (X and Y), diameter at breast height measured at 1.30 m above ground, measured using a diameter tape (DBH), height (H), and the crown width of adult trees (DBH > 5.0 cm). Then the 1-ha plot was divided into 25 subplots of 400 m² with a grid of 20 m to ensure an accurate

and efficient sampling of stem coordinates (X, Y) (Bolte et al. 2014), with 9 central grids (0.36 ha area) for saplings (H ≥ 30 cm and DBH ≤ 5 cm). Each sapling was investigated by recording the species name, coordinates (X, Y), DGH (ground diameter), height and crown width. Furthermore, we calculated shrub cover and canopy closure in five 5 m × 5 m quadrants located at the center and four corners of each subplots. For SF, we carried out the repeat survey in 2013 for trees and 2015 for saplings. For MF, we carried out the repeat survey in 2014 for trees and saplings.

In spruce-fir near primary forest (PF), a 0.20 ha (40 m × 50 m) plot was established in 1986. Subsequent, tree species, DBH, and height for the adult trees (DBH > 5.0 cm), were measured every 2 - 3 years from 1986 to 2014. In 2012, the plot was expanded to 0.25 ha (50 m × 50 m) for saplings. Then the 0.25-ha plot was divided into four 25-by-25 m subplots, and all saplings in the subplots were investigated in the same manner with as described above. We carried out the repeat survey in 2014 for trees and saplings.

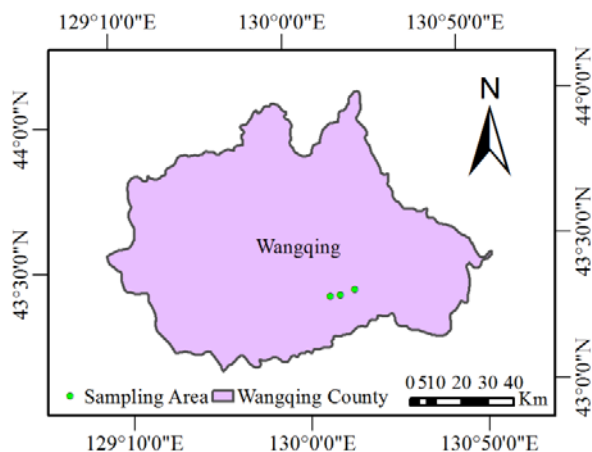


Figure 1 Location of study area and sampling sites. The study area is in the Jingouling Experimental Forest Farm, Wangqing County, Yanji City, Jilin Province, China.

Table 1 Basic information for three forest communities in Changbai Mountains at first time of survey (SF in 2011, MF and PF in 2012)

Forest types	Slope	Size (ha)	Elevation (m)	Humus thickness (cm)	Shrub cover	Canopy closure
SF	6°	1	680	7	45%	0.8
MF	6°	1	650	13	60%	0.7
PF	9°	0.25	700	15	50%	0.6

Note: SF: Polar-birch secondary forest; MF: Spruce-fir mixed forest; PF: Spruce-fir near primary forest. The same below.

1.3 Data analysis

1.3.1 Importance Value (IV)

The importance value (IV) is a comprehensive quantitative indicator used to characterize the status and role of each species in the community. A larger the importance value of a tree species means the greater dominance of the species in the plot. The importance value, relative dominance, abundance, and frequency of each species were calculated as follows (Zhang et al. 2014) :

$$IV(\text{adult trees}) = [(\text{Relative abundance}) + (\text{Relative dominance})] / 2 \tag{1}$$

$$IV(\text{saplings}) = [(\text{Relative abundance}) + (\text{Relative dominance}) + (\text{Relative frequency})] / 3 \tag{2}$$

$$\text{Relative dominance (adult trees)} = \frac{\text{Total basal area of the species}}{\text{Total basal area of all species}} \times 100 \tag{3}$$

$$\text{Relative dominance (saplings)} = \frac{\text{Total crown area of the species}}{\text{Total crown area of all species}} \times 100 \tag{4}$$

$$\text{Relative abundance} = \frac{\text{Number of individuals of the species}}{\text{Total number of individuals}} \times 100 \tag{5}$$

$$\text{Relative frequency} = \frac{\text{Frequency of the species}}{\text{Sum of frequencies of all species}} \times 100 \tag{6}$$

1.3.2 DGH class for saplings

For each plot, stem density, mean DBH, basal area for overstory adult trees and quantities, mean DGH, heights, and crown area for understory saplings were calculated for each individual species. Similar to the DBH classes for adult trees, the saplings are sorted by their DGH and split into eight classes; roman numerals are used to identify the eight classes, i.e., I: 0.3 cm ≤ DGH < 1.0 cm; II: 1.0 cm ≤ DGH < 2.0 cm; III: 2.0 cm ≤ DGH < 3.0 cm; IV: 3.0 cm ≤ DGH < 4.0 cm; V: 4.0 cm ≤ DGH < 5.0 cm; VI: 5.0 cm ≤ DGH < 6.0 cm; VII: 6.0 cm ≤ DGH < 7.0 cm; and VIII: 7.0 cm ≤ DGH.

1.3.3 Growth at individual and forest stand levels

The periodic annual increment (PAI) values for individuals (adult trees and saplings) and stands in each plot were calculated by Pressler's formula (Philip 1994) for the measurement period based on the values of living individuals that were recorded at the time of the study's establishment:

$$P_n = \frac{y_a - y_{a-n}}{y_a + y_{a-n}} \frac{200}{n} \quad (7)$$

where P_n is PAI, n is the number of years between inventories, y_a is the measure (DBH, basal area and volume for adult trees; DGH, height and crown area for saplings) in inventory a , and y_{a-n} is the measure in inventory $a-n$.

1.3.4 Analysis of spatial patterns

Ripley's K or L function is widely used in analyzing forest spatial structure and is a function that weighs the number of individuals in a circle of radius r around a central arbitrary point (Fajardo et al. 2006), and can provide information for a range of distances:

$$K(d) = \frac{A}{n^2} \sum_{i=1}^n \sum_{j=1}^n \delta(d_{ij}), i \neq j \quad (8)$$

$$L(d) = \sqrt{\frac{K(d)}{\pi}} - d \quad (9)$$

where A represents the plot area, n is the number of trees on the plot, d is a distance used as a radius of a circle around each tree, and trees are counted within this circle, $\delta(d_{ij})$ indicates a function representing 1 if $d_{ij} \leq d$ and 0 if $d_{ij} > d$, and d_{ij} is the distance between the i th and j th trees.

However, Ripley's K or L function provides the information for a range of distances. Thus, as the radius increases, small-scale information is included in the larger distances. This accumulation confounds the effects between large and small scales (Schurr et al. 2004; Wiegand and Moloney 2004; Perry et al. 2006). Thus, in order to overcome this disadvantage, as recommended by Wiegand and Moloney (Wiegand and Moloney 2004), the O -ring statistics based on Ripley's K or L function was used to analyze the spatial distribution patterns of tree positions. The O -ring statistics characterizes patterns by the frequency of points co-occurring at a given distance; thus, it can analyze the spatial patterns resulting from ecological processes easily and intuitively (Schurr et al. 2004; Wiegand and Moloney 2004). The O -ring statistics also includes univariate and bivariate statistics (Getzin et al. 2006). In this study, the univariate O -ring statistic was used to analyze the spatial patterns of the adult trees and saplings in the three plots. Complete spatial randomness (CSR) models were used to compute the confidence intervals (Getzin et al. 2006). We computed 99% confidence bands for $O(r)$ by running 499 simulations at intervals of 1 m from 1 -50 m.

Programita software was used for the spatial point pattern analysis (Wiegand and Moloney 2004). The existence of significant differences in mean DGH, mean height, mean crown area, increment and PAI for each species among the three forest types was separately tested using one-way analysis of variance (ANOVA, LSD t -test, $p < 0.05$) in SPSS 18.0 (Meng et al. 2011).

2 Results

2.1 Stand characteristics

2.1.1 Structure and composition of adult trees

A total of 19 tree species were recorded in all spots, while only nine of them occurred in primary forest areas. In the first survey (2011 for SF, 2012 for MF and PF), the total density and basal area for adult trees (>5 cm DBH) were 1794 stems ha⁻¹ and 20.99 m² ha⁻¹ in the SF plot, 1323 stems ha⁻¹ and 31.49 m² ha⁻¹ in the MF plot, and 450 stems ha⁻¹ and 37.76 m² ha⁻¹ in the SF plot, respectively.

Simultaneously, the density of trees for each species varied among the three plots (Table 2). *B. platyphylla* ranked as the most dominant in SF, with the highest values of for the number of individuals (669 stems ha⁻¹) and basal area (11.35 m² ha⁻¹), followed by *Pinus koraiensis*. However, with the process of forest succession, pioneer species, such as *B. platyphylla* and *Populus davidiana*, will disappear from the forest gradually (Table 2). *A. nephrolepis* and *Picea koraiensis* dominated in the MF areas with 38.67 and 15.64 of IV, respectively, while *T. amurensis* occupied 38.23 of IV in PF, followed by *Picea koraiensis* with 15.36IV. *Pinus koraiensis* showed the highest IV in SF while showing the worst in MF.

2.1.2 Structure and composition of saplings

The tree species and numbers of saplings ($H \geq 30$ cm and $DBH \leq 5$ cm) were so deficient with respect to adult trees. Only nine species of saplings occurred in the three forest types. In the first

survey, the density of naturally regenerated saplings in MF amounted to 2528 stems ha⁻¹, compared to 392 stems ha⁻¹ in SF and 572 stems ha⁻¹ in PF (Table 2), indicating that MF had the most sufficient saplings. In SF, 78% of saplings were *Pinus koraiensis*, while *A. nephrolepis* and *Acer* accounted for 43% and 44% of saplings in MF, respectively (Table 2). In PF, *Picea koraiensis* was the dominant saplings species, with 208 stems ha⁻¹, occupying 43% of the total saplings, followed by *A. nephrolepis* (143 stems ha⁻¹, with 23.10 of IV).

However, the status in SF was significantly better than in the others. The mean DGH in SF was 4.28 ± 0.15 cm, more than two times than in MF; while the mean height (3.24 ± 0.13 m) and mean canopy (2.56 ± 0.20 m²) in SF was two times and three times higher than in the others (mean DGH, mean height and mean canopy were 1.80 ± 0.04 cm, 1.48 ± 0.04 m and 0.63 ± 0.03 m², respectively, in MF, while they were 2.46 ± 0.15 cm, 2.04 ± 0.10 m and 0.89 ± 0.12 m², respectively, in PF),

Table 2 Characteristics of study forest stands in first survey (SF in 2011, MF and PF in 2012). Mean values ± standard error. MDB: mean DBH; BA: basal area of living trees; MDGB: mean DGH; MH: mean height; MC: mean crown area.

Species	Adult Trees				Saplings					
	Density	MDB (cm)	BA(m ² ha ⁻¹)	IV	Density	MDGB (cm)	MH (m)	MC (m ²)	IV	
Polar-birch secondary forest	BP	669±37	13.89±0.25	11.35±0.67	45.68	-	-	-	-	-
	TA	74±19	8.11±0.74	0.77±0.29	3.90	33±11	3.58±0.71a	2.89±0.55a	2.97±0.95ab	10.24
	PK1	400±27	9.05±0.52	2.95±0.44	18.18	189±26	4.75±0.17a	3.43±0.15a	2.85±0.26a	47.70
	AN	91±42	11.18±1.07	1.26±0.59	5.54	19±7	3.13±0.65a	2.00±0.37a	0.99±0.35a	5.03
	AM	30±9	9.72±2.08	0.33±0.20	1.62	69±36	4.29±0.41a	4.11±0.32a	2.94±0.60a	17.73
	PK2	22±4	9.94±0.92	0.19±0.05	1.07	64±25	3.41±0.32a	1.95±0.18a	1.72±0.46a	14.12
	Total	1794±79	10.99±0.13	20.99±0.95	100	392±64	4.28±0.15a	3.24±0.13a	2.56±0.20a	100
Spruce-fir mixed forest	BP	56±17	16.99±1.10	1.54±0.50	4.56	-	-	-	-	-
	TA	121±17	11.74±0.75	1.67±0.32	7.22	144±42	2.87±0.20a	2.47±0.17a	1.54±0.24b	11.56
	PK1	94±16	22.07±1.68	4.43±0.72	10.59	64±20	2.46±0.44b	1.60±0.26c	0.52±0.21b	4.89
	AN	470±40	16.22±0.46	13.04±1.26	38.47	1097±242	1.99±0.07b	1.33±0.05a	0.66±0.05a	38.66
	AM	27±8	14.45±1.99	0.48±0.14	1.78	1114±190	1.48±0.05b	1.55±0.06b	0.53±0.04b	36.19
	PK2	153±22	20.56±1.12	6.24±0.89	15.64	100±26	1.31±0.18c	0.83±0.11b	0.31±0.07b	7.57
	Total	1323±62	14.86±0.25	31.49±1.40	100	2528±248	1.80±0.04c	1.48±0.04b	0.63±0.03b	100
Spruce-fir near primary forest	TA	95±59	37.76±22.06	20.9±19.92	38.23	32±13	4.10±0.79a	2.66±0.40a	3.33±1.16a	11.70
	PK1	70±24	27.03±5.85	4.25±1.47	13.41	64±38	4.23±0.47a	2.59±0.33b	1.37±0.33b	15.52
	AN	60±60	29.31±3.78	4.79±4.79	13.01	148±24	2.56±0.24a	1.48±0.17a	0.64±0.14a	23.10
	AM	30±30	33.10±2.32	2.65±2.65	6.84	76±47	1.18±0.12b	1.08±0.16c	0.18±0.07b	10.88
	PK2	115±17	12.82±2.56	1.95±0.80	15.36	208±32	2.08±0.26b	0.92±0.12b	0.38±0.07b	27.58
	Total	450±25	26.34±2.05	37.76±20.02	100	572±90	2.46±0.15b	2.04±0.10b	0.89±0.12b	100

Note: 1. Initials for the species names in column 2: BP-*Betula platyphylla*; TA-*Tilia amurensis*; PK1-*Pinus koraiensis*; AN-*Abies nephrolepis*; AM-*Acer mono*; PK2-*Picea koraiensis*. 2. The letters a, b and c indicate the level of significance between forest types using LSD's mean separation. Means with the same letter are not significantly different while means with different letters are significantly different; representing the results of differences in MGB, MH and MC among three forest types tested by one-way analysis of variance (ANOVA). Significance level was 0.05.

respectively. *T. amurensis* had the largest DGH and crown area in PF, and the largest height in MF.

2.2 Distribution of individuals with DBH class and DGH class

2.2.1 Distribution of adult trees in diameter class

Although the DBH class distribution for all trees shows a roughly inverse-J curve in both SF and MF (Figure 2 A & B), there was a significant difference in volume distributions among study stands: overall, trees were present in all DBH-classes up to 56 cm in the MF plot, while the SF plot had fewer trees in the larger diameter classes (>32 cm DBH), and PF exhibited irregularly distribution (Figure 2C). Trees with a smaller DBH class (8 cm ≤ DBH ≤ 22 cm) contributed 78% of the volume in SF, while the volume of trees with a medium DBH class (20 cm ≤ DBH ≤ 42 cm) accounted for 74% of the total volume in MF (Figure 2E). In contrast, there were 30 *T. amurensis* with DBH greater than 58 cm in PF.

2.2.2 Distribution of saplings in DGH

classes

The distribution of saplings in DGH classes in the first survey is illustrated in Figure 3. DGH class distribution of all saplings species assumed the shape of an inverse-J curve in MF, as did distribution of saplings, overall, in PF. DGH between 1.0 cm and 2.0 cm showed the highest percentage in MF and PF, occupying 38.2 % and 36.4 % of all saplings, respectively. *T. amurensis*, *A. nephrolepis*, *A. mono* and overall saplings in MF (Figure 3 A, C, D & F) showed a peak in stem numbers at DGH class II (from 1.0 cm to 2.0 cm of DGH) and declined sharply in larger-sized classes, while *Picea koraiensis* showed a gradual decrease in stem number. With regard to DGH of *Picea koraiensis* and overall saplings in SF (Figure 3 E & F), the strongest regeneration occurred in class IV (from 3.0 cm to 4.0 cm of DGH), and saplings between classes IV and VII (from 3.0 cm to 7.0 cm of DGH), accounted for 65% of all saplings.

2.3 Growth

2.3.1 Increment between two survey periods

PF lost the largest amount of overstory trees

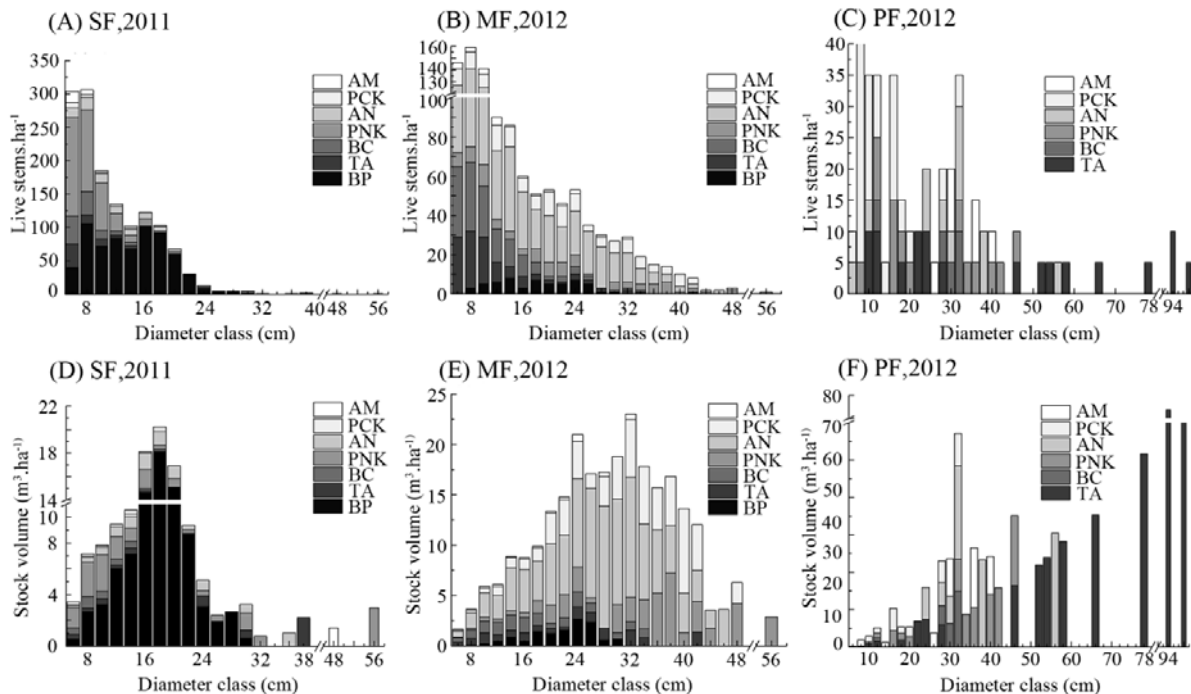


Figure 2 Density-diameter (A-C) and stock volume-diameter (D-F) distribution of live trees in first survey (SF in 2011, MF and PF in 2012.) on the three stands as converted per 1 ha. AM-*Acer mono*; PCK-*Picea koraiensis*; AN-*Abies nephrolepis*; PNK-*Pinus koraiensis*; BC-*Betula ostata*; TA-*Tilia amurensis*; BP-*Betula platyphylla*. SF: Polar-birch secondary forest; MF: Spruce-fir mixed forest; PF: Spruce-fir near primary forest.

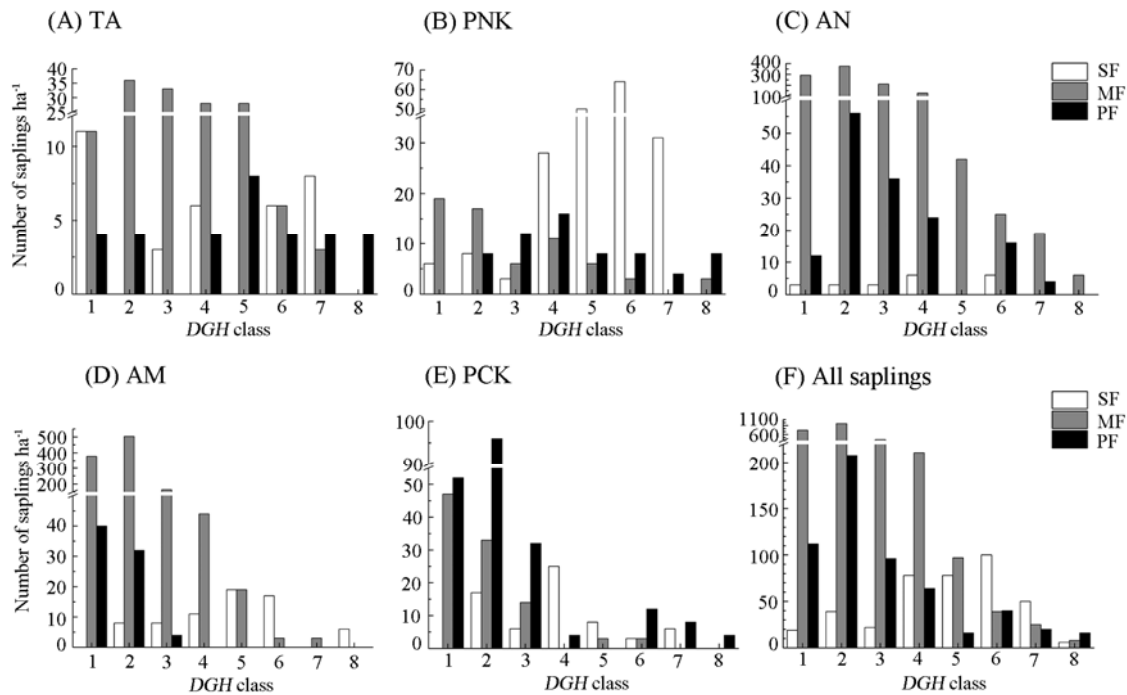


Figure 3 Density-DGH class distribution of saplings in first survey (SF in 2011, MF and PF in 2012) on the three stands as converted per 1 ha. TA-*Tilia amurensis*; PNK-*Pinus koraiensis*; AN-*Abies nephrolepis*; AM-*Acer mono*; PCK-*Picea koraiensis*. SF: Polar-birch secondary forest; MF: Spruce-fir mixed forest; PF: Spruce-fir near primary forest.

Table 3 Dead density and growth status of study forest stands during the interval. Dead density, basal area increment and volume increment of trees are values between two years, others are values per year.

Species	Adult trees				Saplings				
	Dead density	DBH increment (cm y ⁻¹)	Basal area increment (m ² ha ⁻¹)	Volume increment (m ³ ha ⁻¹)	Dead density	DGH increment (cm y ⁻¹)	Height increment (m ² ha ⁻¹ y ⁻¹)	Crown area increment (m ³ ha ⁻¹ y ⁻¹)	
Polar-birch secondary forest	BP	15±5	0.20±0.01	0.65±0.24	5.88±2.20	-	-	-	
	TA	0	0.19±0.02	0.04±0.06	0.33±0.52	14±8	0.16±0.04ab	0.22±0.05a	1.21±0.46a
	PK1	10±4	0.16±0.01	0.18±0.09	1.36±0.69	44±21	0.13±0.03ab	0.18±0.02a	0.53±0.06b
	AN	1±1	0.25±0.03	0.10±0.23	0.93±2.22	6±4	0.08±0.03b	0.14±0.07a	0.30±0.19a
	AM	0	0.18±0.02	0.02±0.03	0.11±0.23	19±14	0.09±0.02a	0.25±0.05a	0.85±0.24a
	PK2	0	0.33±0.05	0.03±0.04	0.23±0.41	11±6	0.13±0.02a	0.07±0.02a	0.22±0.04a
	Total	52±10	0.20±0.01c	1.40±0.05b	13.21±3.56b	108±32	0.12±0.01b	0.17±0.02a	0.56±0.07a
Spruce-fir mixed forest	BP	0	0.43±0.03	0.15±0.22	1.39±2.11	-	-	-	
	TA	6±3	0.23±0.02	0.12±0.12	1.05±1.17	39±11	0.12±0.03b	0.19±0.03a	0.60±0.12a
	PK1	4±2	0.20±0.02	0.15±0.13	1.76±1.49	14±8	0.06±0.02b	0.06±0.01b	0.17±0.04a
	AN	28±7	0.22±0.01	0.63±0.28	6.80±3.12	333±73	0.10±0.01b	0.09±0.01a	0.27±0.02a
	AM	1±1	0.23±0.07	0.03±0.05	0.21±0.36	244±61	0.08±0.01b	0.10±0.01b	0.31±0.03b
	PK2	6±3	0.26±0.02	0.27±0.24	3.00±2.78	28±9	0.09±0.02a	0.06±0.01a	0.17±0.03ab
	Total	69±14	0.23±0.01b	1.66±0.08a	15.33±4.52a	658±95	0.09±0.004c	0.10±0.004b	0.30±0.02b
Spruce-fir near primary forest	TA	0	0.37±0.08	0.38±0.60	4.05±6.58	8±5	0.37±0.18a	0.19±0.08a	0.67±0.29a
	PK1	4±4	0.47±0.09	0.28±0.12	3.41±1.59	12±8	0.24±0.08a	0.14±0.03ab	0.18±0.07a
	AN	12±8	0.29±0.05	0.12±0.24	1.44±2.87	40±14	0.20±0.04a	0.09±0.02a	0.22±0.09a
	AM	8±8	0.15±0.07	0.04±0.07	0.29±0.58	20±12	0.15±0.03ab	0.11±0.02b	0.08±0.03b
	PK2	32±32	0.22±0.04	0.07±0.05	0.59±0.50	32±11	0.14±0.03a	0.07±0.01a	0.11±0.03b
	Total	72±49	0.33±0.03a	1.06±0.41b	11.43±9.72b	132±18	0.18±0.02a	0.10±0.01b	0.23±0.05b

Note: 1. Initials for the species names in column 2: BP-*Betula platyphylla*; TA-*Tilia amurensis*; PK1-*Pinus koraiensis*; AN-*Abies nephrolepis*; AM-*Acer mono*; PK2-*Picea koraiensis*. 2. a, b, c represent the results of differences in increment among three forest types tested by one-way analysis of variance (ANOVA). Significance level was 0.05.

from 2012 to 2014, with a total of 72 ± 49 trees dying, occupying 16% of adult trees in 2012. However, the DBH increment in PF exceeded the others. The volume increment in MF was $15.33 \pm 4.52 \text{ m}^3 \text{ ha}^{-1}$ during those two years (Table 3), which was significantly higher than in SF ($13.21 \pm 3.56 \text{ m}^3 \text{ ha}^{-1}$ during those two years) and PF ($11.43 \pm 9.72 \text{ m}^3 \text{ ha}^{-1}$ during those two years). In the understory, the height increment and crown increment of saplings in SF were the highest, and *Pinus koraiensis* growth was better in this forest type. *T. amurensis* was the fastest-growing species in the three forest types.

2.3.2 Periodic annual increment

The periodic annual increment (PAI) of DBH for most species in SF was better than in PF or MF, except for *B. platyphylla*. The PAI of DBH for *Picea koraiensis* in SF was 3.42%, significantly better than all other species in all spots (Figure 4A). The PAI of DGH for saplings overall, in PM was the greatest, while it was the worst in SF. The PAI of sapling height was similar to that of DGH, except *T. amurensis*, which grew more rapidly in MF than in the others. The PAI of crown area, overall, was different from DGH or height, with the fastest

growth in MF (Figure 4).

2.3.3 Spatial distribution of saplings

The spatial distribution of tree stems clearly differed between forest layers and size classes among the three plots. However, there was nearly no change between the two surveys for each forest type (Figure 5). In the first survey, adult trees showed clumped distributions at scales < 3 m in SF and MF, while random distribution dominated the residual scales for all spots.

The positions of the investigated saplings exhibited clumped distributions at smaller scales in all spots, especially at short distances. Saplings in MF were above the confidence interval at smaller scales (1 - 9 m) which appeared as significantly clumped patterns, then appeared uniform patterns at larger scales, 13-22 m, 24 m, 30 m and 34 - 45 m (Figure 5E). Saplings in SF were significantly clumped at scales of 1-10 m, then dominated by regular distributions when scaled up (Figure 5D). Saplings in PF were clustered at smaller scales (1-6 m).

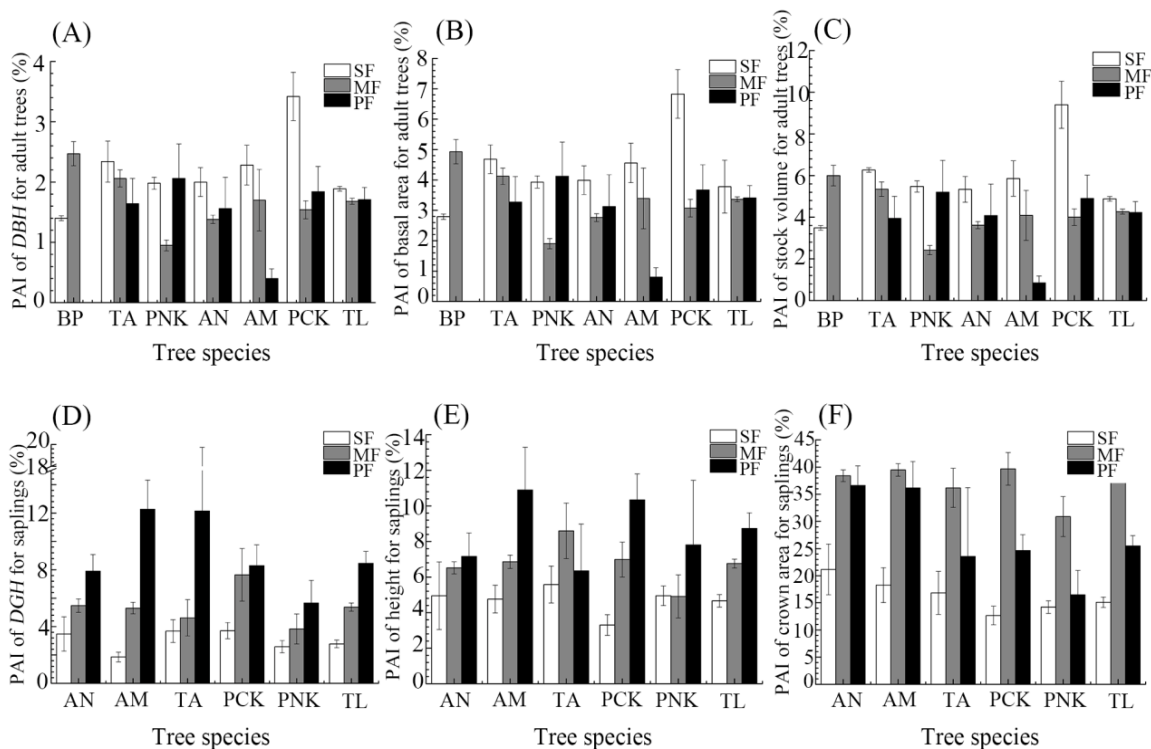


Figure 4 Annual PAI of dominant tree species for trees (A-D) and for saplings (D-F) on the three stands, error bar represents standard error. BP: *B. platyphylla*; TA: *T. amurensis*; PNK: *Pinus koraiensis*; AN: *A. nephrolepis*; AM: *Acer mono*; PCK: *Picea koraiensis*; TL: Total adult trees or saplings. SF: Polar-birch secondary forest; MF: Spruce-fir mixed forest; PF: Spruce-fir near primary forest.

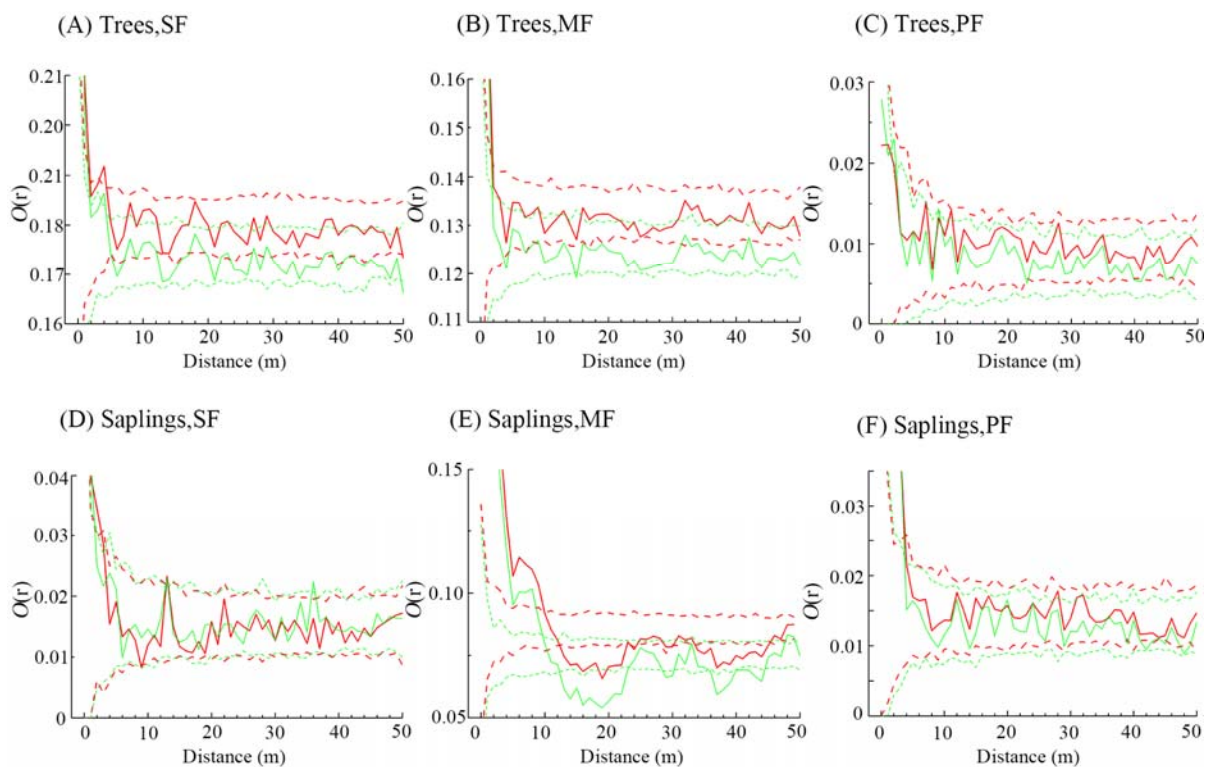


Figure 5 Spatial distribution for adult trees (A-C) and saplings (D-F) of three spots in interval. Red solid lines indicate the $O(r)$ values in first survey (SF in 2011, MF and PF in 2012), green solid lines in second survey (SF in 2013 for trees and 2015 for saplings, MF and PF in 2014). Dashed lines correspond to the 99% confidence intervals generated from 499 complete spatial randomness simulations (again red: first survey; green: second survey). When the solid line was above the upper envelope, inside both envelopes, or below the lower envelope, the pattern was assumed to be significantly aggregated, spatially random, or regular. SF: Polar-birch secondary forest; MF: Spruce-fir mixed forest; PF: Spruce-fir near primary forest.

3 Discussion

3.1 Species composition at different forest types

Structure and composition of forest communities are the basis for determining the direction of its succession (Hooper et al. 2005). Understanding the floristic characteristics and structure of different successional stages is important for facilitating forest restoration processes (Meng et al. 2011). Tree species composition, tree size diversity and understory regeneration quantity showed significant differences among the three forest types. Species richness of adult trees in SF and MF are larger than in PF. The comparatively high species richness in the SF and MF is due to the coexistence of light-demanding species (such as *B. platyphyllaa*, *Syringa amurensis*, and *Populus davidiana*) established early in the succession and shade-

tolerant species (such as *A. nephrolepis*, *Pinus koraiensis*, and *Picea koraiensis*) already established at the both successional stages (Connell 1978; Denslow et al. 1985). Similar results were reported by Grau (1997) who also found higher species richness in the earlier successional stages than the later ones. This could be interpreted that forest composition eventually tends to converge to a general ‘climax’ composition acting as a distant force (Pickett and McDonnell 1989).

Adams et al. (2010) considered that natural forest stand development would account for the increase in basal area over time, but with no certainty with respect to the increase in density. Basal area, which can be associated with woody volume and biomass accumulation, and the presence of very large trees was much lower in the secondary forests than in the primary forest (Grau et al. 1997). Results of this study showed the decrease in density of trees with the succession while increasing in basal area.

3.2 Non-spatial structure of forest types during succession

When compared to the spatial structure of the forest, the size structure of a species can reflect insight into the forest dynamics (Takahashi et al. 2001; Zhang et al. 2010). Although DBH classes distributions of all trees displayed an inverse-J shape in SF, the pioneer species will gradually disappear because of the absence of saplings and climax species (such as *A. nephrolepis*, *Pinus koraiensis*, *Picea koraiensis*, and *T. amurensis*), illustrating that the SF is in forward succession, spruce and fir in SF are poised strategically to replace *B. platyphylloa* as the dominant tree species in the study area. MF had a large number of saplings, and the DBH class distribution of either adult trees or saplings appears as an inverse-J shaped, suggesting the continuous population regeneration and favorable conditions for the establishment and survival of saplings.

In general, primary forest was considered as a better forest type than secondary forest or plantation forest, with the richest tree species or highest biodiversity (Kessler et al. 2005; Gunn et al. 2014), but our results seem to be different from previous studies: although the largest stock volume occurred in PF, but we do not consider that it can develop stably because of the irregular DBH class distribution, this forest type has reached the aging and renewal phases (a negative increase of living stock volume from its highest in 2008, then decreasing over the time). Zhang et al. (2015) also reported that community stability for spruce-fir mixed forest in the same study regions was better than for spruce-fir near primary forests, and the latter one was over mature with low productivity.

It is worth mentioning that the numbers of saplings in DGH class I was less than the later one, because of the absence of saplings with height less than 30 cm in our study.

3.3 Growth of trees and saplings

The PAI of DBH for most species in SF was better than in PF or MF, except for *B. platyphylloa*, which had no saplings occurring in understory, illustrating that this pioneer species will gradually disappear from the forest stand; its absence in PF proves this. At the same time, the PAI of DBH for

later-successional species in SF, such as *Picea koraiensis*, was significantly better than all other species in all spots, also indicating that the percent of climax species will gradually increase in the future decades.

Regeneration processes and their dynamics have a significant impact on the stability and functional efficiency of forest stands (Malik et al. 2014). Quantifying height growth has often been used as a proxy for aboveground primary growth (Ruel and Pineau 2002). The PAI of saplings' heights in PF was higher than in SF and MF, except for *T. amurensis*, showing that the decrease of overstory trees provides a better growth condition for the remaining saplings. The PAI of the crown area for saplings in MF was the highest, and we consider this is the result of competition with the limited-lighting understory. Saplings have to expand their lateral growth to receive more lighting received. Murphy et al. (2010) also reported that a species allocating more biomass to lateral growth had a greater capacity to capture light in light limiting environments.

High shade-tolerance and the ability to modify the growth form for survival in dense shade are key features for the long-term persistence of species in the understory (Antos et al. 2005). Generally, seedlings of shade-tolerant species benefit from the presence of a continuous or partial forest cover that stabilizes the microclimate by preventing extreme light, temperature, and humidity fluctuations (Dumais and Prévost 2007). This sheltered ecological niche is favorable, even essential, to the regeneration of many conifer species that naturally establish in the understory (Grayson et al. 2012), but the saplings need greater light conditions. Growth of DGH and height for saplings in PF were better than in SF or MF, and we think they may benefit from the "Bolaven", a typhoon that occurred in 2012, which caused massive damage to the overstory trees in PF (living stock volume in it declined from 513.61 m³ ha⁻¹ in 2008, to 377.86 m³ ha⁻¹ after the typhoon in 2012). The falling of large trees created canopy openings in the forest, and then changes of these environmental factors in PF facilitated the growth of DGH and height for saplings. Drobyshev et al. (2001) and Dumais et al. (2014) proposed that limiting the canopy opening size in partial harvests can lessen the physiological stress and promote the growth and competitive

status of advance red spruce regeneration, which we believe the typhoon played such a function on PF, much like the partial harvests. Moreover, *Pinus koraiensis*, a mid-tolerant species with a type of *K* growth strategy, needs strong sunlight for growth during sapling stage (Dai et al. 2011), suffering from a high mortality and low growth rate during the sapling stage in SF, since the closed canopy does not provide high light conditions. These results are consistent with previous studies (Li et al. 1990). Thus, the selective cutting of some canopy trees could enhance the growth of pine saplings (Shao et al. 1994).

3.4 Spatial structure of three forest types during the two surveys

The spatial structure for adult trees at all scales in PF and scales exceeding 3 m in SF and MF in our study, exhibited a random distribution, and similar results were reported by Szwagrzyk (1992) who considered that tree distributions in unmanaged forests shown a predominance of random patterns. We believe that self-thinning is the major processes causing this, although self-thinning was believed to produce regular patterns (Ford 1975).

Saplings had completely different spatial distribution pattern from adult trees, with a significantly clumped patterns at smaller scales, which we argued that the limited dispersal ability of seeds may be the main reason for the clumped pattern of saplings at smaller scales (Grubb 1977). Additionally, this result is not entirely unexpected if it assumes that regeneration of seedlings is clustered in the vicinity of parent trees (Zhang et al. 2014) and regeneration almost exclusively takes place in the shelter of the parent stand with limited canopy openings (Hofmeister et al. 2008). Clumped distributions of regeneration have also been reported in other managed stands (Fröhlich and Quednau 1995).

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There was no obviously difference of spatial structure during the survey period in our study, which may be due to the short two years interval. We need long-term observations to reveal the dynamics of the spatial structure.

4 Conclusion

In our study area, SF is being in positive succession forward to MF. MF has the highest number of saplings in it, and with reasonable DBH class for adult trees and DGH class for saplings. At the same time, PAI of DBH in MF was the better than the other ones. From the perspective of sustainable forest management, MF will maintain a stable structure and high timber productivity in the long-term. PF had the maximum amount of living standing wood volume during the survey period, but this forest type is unstable both in the terms of forest overstory structure itself and its ability to resist to environmental disturbances. In order to sustainably management and maximize the economic efficiency of forest products, we suggest measures, such as selective cutting, should be taken in SF and MF to result in limiting the open size, which can not only provide certain woody products, but also promote better growth conditions for the remaining saplings understory.

It is important to understand forest dynamics based on continued monitoring using permanent plots. However, our study was unable to show the significant difference of spatial structure, individual growth, and the impact of the disturbance among the three forest types due to the short interval. We should conduct more detailed, long-term, continued investigations in the future. At the same time, it is necessary for direct supporting data to understand the influence of wind on forest stand composition and structure in different forest types.

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