

# Spatial Distributions and Spatial Associations of Dominant Tree Species in Korean Pine Broadleaved Old-Growth Forests in Changbai Mountains

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Zhang, Ch., Zhao, X., Liu, X. and von Gadow, K. 2010. Spatial Distributions and Spatial Associations of Dominant Tree Species in Korean Pine Broadleaved Old-Growth Forests in Changbai Mountains. *Baltic Forestry*, 16 (1): 66-75.

## Abstract

Pair correlation function  $g(r)$  was used to study the spatial patterns of five dominant species (*Pinus koraiensis*, *Quercus mongolica*, *Tilia amurensis*, *Fraxinus mandshurica*, *Acer mono*) in Korean pine and broadleaved multi-species forests in the Changbai Mountain areas. The spatial distribution at different growth stages (from saplings to small diameter trees and big trees) were studied, as well as the spatial associations of different species at different growth stages. Structural characteristics and distribution of canopy gaps, spatial relationships between canopy gaps and tree species with a height of less than 11.2 m were also explored by studying the canopy horizontal projection. *Pinus koraiensis* and *Quercus mongolica* were distributed randomly and *Acer mono* was in a clumped pattern at some studied scales ( $r=1-11$  m, 13-16 m, 20 m, 33 m and 43 m scales). *Fraxinus mandshurica* (at smaller scales  $r=5$  m) and *Tilia amurensis* ( $r=1-2$  m, 9-11 m and 16-18 m) occurred in a clumped distribution. Among 10 species pairs which consisted of five dominant tree species, there were three species pairs (*Pinus koraiensis* and *Tilia amurensis*, *Pinus koraiensis* and *Acer mono*, *Acer mono* and *Fraxinus mandshurica*) which showed mutual attraction at several scales. Three species pairs (*Pinus koraiensis* and *Fraxinus mandshurica*, *Tilia amurensis* and *Fraxinus mandshurica*, *Quercus mongolica* and *Acer mono*) showed spatial exclusion. *Quercus mongolica* and *Fraxinus mandshurica* appeared exclusions at  $r=21$  m scale and attractions at  $r=46$  m scale. The canopy gaps mainly occurred as a random distribution within the plot, with the exception of a regular distribution at the distances of  $r=6$  to 11 m.

**Key words:** Spatial distribution; spatial relationship; forest canopy gap; pair correlation function; Changbai Mountains

## Introduction

The micro-habitat surrounding individual trees depends on the spatial structure of a forest community, as well as on tree growth, mortality, seed production and the natural process of forest regeneration (Barot et al. 1999). Environmental heterogeneity, natural or human disturbance, intraspecific and interspecific competition, life history strategy, tree mortality, growth of seedlings and depressed trees, all these factors may contribute to the change of the spatial pattern in a forest community (Heegaard 2000, Heegaard and Hangelbroek 1999, Rozas 2003, Takahashi et al. 2001).

The spatial structure of a forest community can be defined as the spatial configuration pattern of individual plants which compose the community, including horizontal and vertical structural attributes. The

horizontal structure of a community reflects the stand history, population dynamics and the relationships of intraspecific and interspecific competition (Haase 1995). The vertical distribution of tree crown dimensions is an important stand attribute, and an important structural characteristic, which affects the horizontal distribution of sunlight in a forest community, which greatly influences tree growth and understory community structure (Latham et al. 1998). Forest gaps after canopy disturbance are closely related with species regeneration, growth and tree survival in a stand (Zhao et al. 2005). Gaps are causing a change of ecological condition and gap areas obviously generate a different ecological environment (Zhang et al. 2006). Different tree species have different strategies of occupying and utilizing the gaps, thus causing different regeneration patterns inside and outside the gap areas (Yu et al. 2001).

Various papers have been published which focus on the spatial distribution of tree species in Korean pine mixed woods in the Changbai Mountain area (Sun and Zhao 1997, Hou and Han 1997), on canopy patch characteristics (Guo 2002), and on the relationship between the disturbance status of forest gaps and the tree regeneration (Yu et al. 2001, Zang et al. 1998). What remains to be unknown are important ecological aspects, such as the spatial distribution of dominant tree species, and the pattern dynamics at different growth stages, as well as the spatial relationships between saplings and canopy gaps.

Thus, the main objectives of this paper are: (1) to analyse the spatial distribution of dominant tree species; (2) to investigate the spatial relationships between different dominant tree species; (3) to evaluate the spatial relationships between different growth stages; and (4) to assess the spatial relationships between forest gaps and tree species under canopy.

## Material and methods

### Study area

This research was carried out in a virgin Korean pine and broadleaved deciduous forest in the Changbai Mountains. The study area is located near the border of China and the Democratic People's Republic of Korea (DPRK). The elevation is 784m above sea level, and the geographic coordinates are N 42°20.211', E 128°05.705'. The nearest meteorological station, which belongs to the forest ecosystem research station of the Chinese Academy of Science in the Changbai Mountain areas, is less than 500 m away. The climate in the study area has been classified as a continental mountain climate which is affected by the monsoon, the annual average temperature is 3.3°C, the highest monthly average temperature is 20.5°C, measured in August, the lowest monthly average temperature is -16.5°C, measured in January. The extreme highest and lowest temperatures are 32.3°C and -37.6°C, respectively. The annual mean precipitation is 671.9 mm, the relative humidity is 66%. The precipitation is relatively uneven during the year. A relatively wet season occurs from June to August, and a relatively dry season begins in September and ends in May of the following year. The soil is a brown forest soil with a rootable depth of 20~100 cm. The topography is flat and slightly undulating.

The Korean pine – broadleaved forest is the climax vegetation type in the western regions of Changbai Mountains. The tree species include *Pinus koraiensis*, *Quercus mongolica*, *Tilia amurensis*, *Fraxinus mandshurica*, *Acer mono*, *Ulmus japonica*, *Tilia mandshurica*, *Acer barbinerve*, *Acer pseudo-siebold-*

*ianum*, *Acer trgmentosum*, *Acer mandshurica*, *Acer ukurunduense*, *Acer triflorum*, *Maackia amurensis*, *Phellodendron amurense*, *Betula costata*, *Populus ussuriensis* etc. *Pinus koraiensis*, *Quercus mongolica*, *Tilia mandshurica*, *Fraxinus mandshurica* and *Acer mono* are the dominant species in the community.

### Field measurement

A permanent research plot with an area of 100m×100m was established in the typical Korean pine and broadleaved forests in July 2005. The main plot was subdivided into 400 subplots, each covering an area of 5m×5m. The spatial coordinates, tree species, breast height diameter (dbh), tree height (h), crown width and height to the base of the live crown of all trees with dbh greater than 1cm were recorded. In order to study the spatial distribution and spatial relationships of the population at different growth stages, it is assumed that the dbh of a tree is related to its development stage. The trees were thus classified for convenience as saplings (h>2m, 1cm≤dbh<4cm), small diameter trees (4cm≤dbh<10cm) and big trees (dbh≥10cm) according to their dbh and height.

### Statistical analysis

The vertical strata of the community were divided based on a specific assumption related to a competition cut-off point among tree crowns. The height of the competition cut-off point ( $HCCP_k$ ) of the kth vertical stratum is calculated using the following equation:

$$HCCP_k = Cc * CL_k + HBLC_k \quad (1)$$

where Cc is the competition coefficient (here, we defined Cc=0.4, this value is based on field observations, assuming that the potential to stay in an advantageous position for the acquisition of light is greatest in the top 60% of the tree crown);  $CL_k$  is the crown length and  $HBLC_k$  is the height to the base of the live crown of the tallest tree in the kth stratum.

All trees were sorted in a descending order by height and crown length. The heights of the competition cut-off points ( $HCCP_k$ ) were calculated starting from the tallest tree with the longest crown length; all trees with a height larger than or equal to the  $HCCP_k$  of the tallest tree were grouped into the tallest stratum. The second stratum was formed in the same way, starting with the tallest tree which did not reach stratum 1. When a tree height is less than the  $HCCP_k$ , the  $HCCP_k$  was recalculated based on the tallest remaining tree with the longest crown length, until all trees were grouped or reach some pre-defined minimum limitation for strata definition (Latham et al. 1998). In this study, the trees were grouped into four vertical strata using  $HCCP_1, \dots, HCCP_4$ , as follows: the first stratum with tree heights

ranging from 26.1m to 37.1m, mainly consists of *Pinus koraiensis*, *Quercus mongolica*, *Tilia amurensis* and *Fraxinus mandshurica*. The second stratum with tree heights between 17.3 m and 26 m, includes *Pinus koraiensis*, *Tilia amurensis*, *Acer mono* and *Quercus mongolica*. The third stratum with tree height from 11.2 m to 17.2 m, includes *Acer mono*, *Tilia amurensis*, *Acer mandshurica*, *Acer pseudo-sieboldianum* and *Acer trgmentosum* as main tree species. Stratum four with tree height less than 11.2m, includes *Acer trigmentosum*, *Acer mono*, *Acer pseudo-sieboldianum*, *Acer barbinerve* and *Acer mandshurica* as main tree species. According to the classification results of the vertical strata, trees with a height of more than 11.2m were defined to belong to the overstory in this research.

All individual crowns of the overstory trees (with a height >11.2m) were regarded as oval shape and projected on the horizontal plane. Gaps with areas between 4 and 1000m<sup>2</sup> were defined as a canopy opening. Canopy openings were identified on the horizontal projection using MapInfo 7.5 and their perimeters, areas and coordinates of the centre of gravity were calculated. The canopy gaps, which extend over the plot boundary, were integrated by measuring the location and crown width of edge trees outside the plot. Two overlapping canopy gaps were regarded as two individual canopy gaps when the length of the overlap was less than 0.5m. Taking the coordinate of the center of gravity of a canopy gap as its location coordinates (Patton 1975).

Ripley's *K*-function is one of the most popular functions of explorative spatial point pattern analysis (Ripley 1976, Dale 1999), it can be expressed as:

$$K(r) = A \sum_{j=1}^n \sum_{i=1}^n w_{ij} I_r(i, j) / n^2 \quad (2)$$

where  $i, j = 1, 2, \dots, i \neq j$ ;  $n$  is the total number of individuals in the plot;  $r$  is the distance category, usually referred to as the "scale";  $d_{ij}$  is the distance between individual  $i$  and individual  $j$ ,  $A$  is the area of the plot,  $w_{ij}$  is the edge correction, i.e. the ratio of the circle projection length in the plot to the circle perimeter, where  $i$  refers to the circle centre and  $d_{ij}$  to its radius. When  $d_{ij} \leq r$ , the value of  $I_r(i, j)$  is 1; otherwise the value of  $I_r(i, j)$  is 0.

Ripley's  $K_{12}$  function was used to determine the spatial relationships between two groups. The definition is:

$$K_{12}(r) = (n_1 n_2)^{-2} A \sum_{i=1}^n \sum_{j=1}^n w_{ij}^{-1} I_r(u_{ij}) \quad i \neq j \quad (3)$$

where  $n_1, n_2$  are the number of two-type groups. It is a counter-variable that is set at 1 if the distance  $u_{ij}$  between groups  $i$  and  $j$  is  $\leq r$ , otherwise  $I_r = 0$ .

In analogy to a probability density function, which is the derivative of a cumulative distribution function, there is a counterpart to the *K* function, namely pair correlation function  $g(r)$ , which takes into consideration pairs of neighbours separated by distance  $r$  (Stoyan and Stoyan 1994). The pair correlation function  $g(r)$  can be obtained after differentiation and normalization of *K*( $r$ )

$$g(r) = \frac{dK(r)}{dr} / (2\pi r) \quad (4)$$

Values of  $g(r)$  below 1 indicate repulsion, values above 1 indicate clustering for point pairs of such distance  $r$ . Bivariate  $g_{12}(r)$  statistic is the analogue of Ripley's  $k_{12}(r)$  when replacing the circles by rings with radius  $r$ , and  $g_{12}(r)$  gives the expected number of points of pattern 2 at distance  $r$  from an arbitrary point of pattern 1. It can be obtained as follows:

$$g_{12}(r) = \frac{dK_{12}(r)}{dr} / (2\pi r) \quad (5)$$

Values of  $g_{12}(r)$  above 1 indicate attraction between the two patterns within the rings area. Similarly, values of  $g_{12}(r)$  below 1 indicate repulsion between the two patterns within the rings. The calculation of the  $g$ -function involves a selection of the rings width. No enough points will fall into the different distance classes if the rings width is too small. On the other hand, the  $g_{12}(r)$  statistic will lose the advantage that it can isolate specific distance classes if the rings are too wide. In this paper, ring width ( $dr$ ) was defined as one meter.

As recommended by Patton (1975) and Wiegand and Moloney (2004), the *L*-function based on Ripley-*K* statistics was used to analyze spatial distribution patterns of canopy gaps and spatial interactions between canopy gaps and understorey trees (tree height less than 11.2m). The formula of *L*( $r$ ) and  $L_{12}(r)$  are as follows:

$$L(r) = \sqrt{K(r)/\pi} - r \quad (\text{Besag 1977}) \quad (6)$$

$$\text{and } L_{12}(r) = \sqrt{K_{12}(r)/\pi} - r \quad (\text{Diggle 1983; Haase 1995; Ripley 1976}) \quad (7)$$

Values of *L*( $r$ ) below 0 indicate repulsion, values above 0 indicate clustering for point pairs. Values of  $L_{12}(r) > 0$  indicate that there are on average more points of pattern 2 within distance  $r$  of points of pattern 1 as one would expect under independence, thus indicating attraction between the two patterns up to distance  $r$ . Similarly, values of  $L_{12}(r) < 0$  indicate repulsion between the two patterns up to distance  $r$ .

Ninety nine percent confidence intervals generated from 10,000 realisations of the Poisson process were calculated for  $g$ -function and *L*-function (Thioulose et al. 1997). For univariate analysis, when the

value is greater than, equal to or less than the 99% confidence intervals, the distribution was assumed to be clumped, random or regular, respectively. For bivariate analysis, when the value is greater than, equal to or less than the 99% confidence intervals, the relationships between the two analyzed types are significantly positive (attraction), spatially independent or significantly negative (repellence), respectively. The *g*-function and *L*-function were computed using *ade-4* software in the *ade-4* homepage (<http://pbil.univ-lyon1.fr/ADE-4-old/ADE-4.html>).

**Results**

Tree species density, dbh class distribution and canopy structure

Some density characteristics of 5 dominant tree species with a dbh ≥4cm are shown in Table 1. The dbh areas of *Pinus koraiensis* and *Quercus mongolica* showed the highest percentage among all the indi-

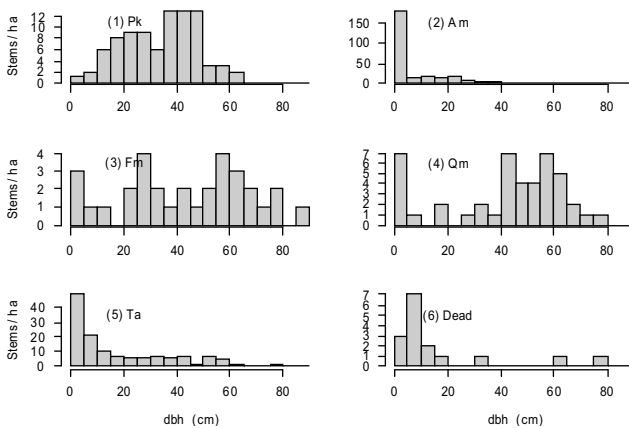
viduals, accounting for 25.4% and 21.7%, respectively. *Tilia amurensis* and *Fraxinus mandshurica* account for 19.8% and 15.8%, respectively. The dbh areas of *Acer mono* are only 6% of the total dbh areas, but the species occurs with 11.6% of stem numbers.

The individuals of *Tilia amurensis* and *Acer mono* mainly appeared in the smaller dbh classes, and generally showed a reverse *J* shaped diameter distribution. *Pinus koraiensis* occurred in all dbh classes, but mainly with dbh's between 10 and 50cm. The densities for the individuals ≥1cm at dbh of *Quercus mongolica* and *Fraxinus mandshurica* were lower than other tree species, which were 45 stems/ha and 31 stems/ha, respectively.

The individuals of *Quercus mongolica* are mainly represented in the bigger dbh classes, while *Fraxinus mandshurica* occurred with a relatively regular distribution in all dbh classes, the difference of individual numbers were only 0-4 stems/ha in the different dbh classes (Figure 1).

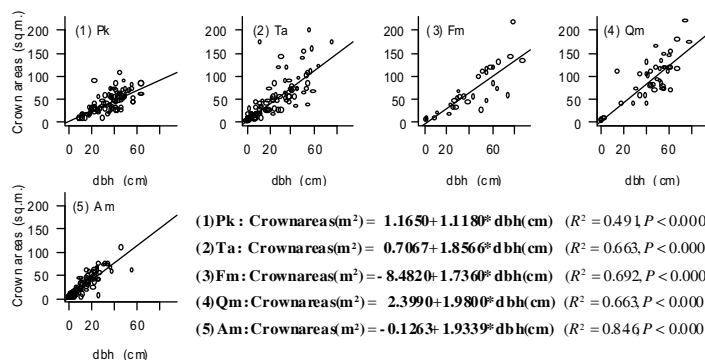
**Table 1** Species composition, density and maximum dbh of all live trees >4cm dbh of dominant tree species

Tree species	Species codes	Basal area (m <sup>2</sup> /ha)	Percent of total basal area (%)	Stems per ha	Percent of total stems per ha (%)	Maximum dbh (cm)
<i>Pinus koraiensis</i>	Pk	9.31	25.42	87	13.85	63.8
<i>Quercus mongolica</i>	Qm	7.96	21.74	40	6.37	79.0
<i>Tilia amurensis</i>	Ta	7.24	19.77	92	14.65	76.0
<i>Fraxinus mandshurica</i>	Fm	5.81	15.85	28	4.46	88.0
<i>Acer mono</i>	Am	2.21	6.02	73	11.62	55.4
Others		4.10	11.21	308	49.05	119.8
Totals		36.64	100	628	100	



The crown cover areas of individual trees were calculated using the known crown widths and the area formula of an assumed oval shape. The relationships between crown areas and dbh's for 5 dominant tree species are shown in Figure 2. The results indicate that the area ranges of *Pinus koraiensis*, *Quercus mongolica*, *Acer mono*, *Fraxinus mandshurica* and *Tilia amurensis* were 5.85-103.34m<sup>2</sup>, 1.21-215.93m<sup>2</sup>, 0.52-108.69m<sup>2</sup>,

**Figure 1** The dbh class distributions of dominant tree species and dead trees within the research plot. Pk: *Pinus koraiensis*; Qm: *Quercus mongolica*; Ta: *Tilia amurensis*; Fm: *Fraxinus mandshurica*; Am: *Acer mono*. Dead: Dead trees >4cm at dbh



(1)Pk :  $Crownarea(m^2) = 1.1650 + 1.1180 * dbh(cm)$  ( $R^2 = 0.491, P < 0.0001$ )  
 (2)Ta :  $Crownarea(m^2) = 0.7067 + 1.8566 * dbh(cm)$  ( $R^2 = 0.663, P < 0.0001$ )  
 (3)Fm :  $Crownarea(m^2) = -8.4820 + 1.7360 * dbh(cm)$  ( $R^2 = 0.692, P < 0.0001$ )  
 (4)Qm :  $Crownarea(m^2) = 2.3990 + 1.9800 * dbh(cm)$  ( $R^2 = 0.663, P < 0.0001$ )  
 (5)Am :  $Crownarea(m^2) = -0.1263 + 1.9339 * dbh(cm)$  ( $R^2 = 0.846, P < 0.0001$ )

**Figure 2.** Relationships between crown areas and dbh of 5 dormant tree species. Pk: *Pinus koraiensis*; Qm: *Quercus mongolica*; Ta: *Tilia amurensis*; Fm: *Fraxinus mandshurica*; Am: *Acer mono*

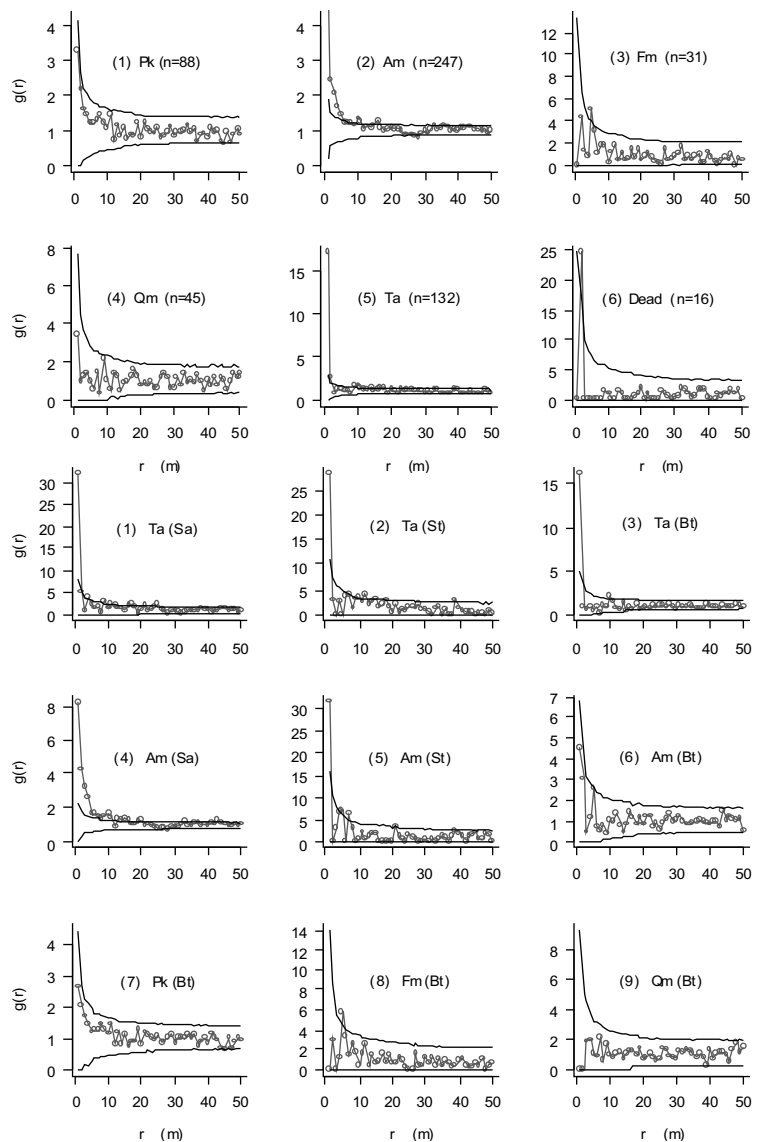
3.29-213.58m<sup>2</sup> and 0.38-198.45m<sup>2</sup>, respectively. The crown areas of 5 dominant tree species increased with increasing dbhs. The relationships between crown areas and dbhs may be expressed by the linear model Crown area (m<sup>2</sup>)  $\alpha + \beta * dbh$  (cm).

**Spatial distributions of dominant tree species**

Pair correlation function  $g(r)$  analysis for all individual trees indicated that *Pinus koraiensis* and *Quercus mongolica* appeared to be randomly distributed at all studied scales. *Fraxinus mandshurica* was clumped and significantly regular at scale  $r=5m$  and  $r=48m$  respectively. *Tilia amurensis* were above the confidence interval at smaller scales (i.e.,  $r=1-2m$ ,  $9-11m$  and  $16-18m$ ) which appeared significantly clumped patterns. *Acer mono* was clumped at 1-5m, 10-11m and 16m scales. Dead trees >4cm at dbh were distributed randomly at all scales except for  $r=1m$  within the plot (Figure 3).

The univariate analysis of  $g(r)$  at different growth stages indicated that the saplings of *Tilia amurensis* appeared significant clumped at the scales of 1m, 4m, 9m, 17m and 25m; the small diameter trees appeared clumped at  $r=1m, 7m, 12m, 15m, 18m$  and 39m scales and big trees clumped at scale  $r=10m$ . The saplings of *Acer mono* were significantly clumped at the scales of 1-11m, 13-16m, 20m, 33m and 43m, while the small diameter trees were clumped at scales  $r=1m, 5m$  and 7m, and big trees were randomly distributed at all studied scales. Due to the few saplings of *Pinus koraiensis*, *Fraxinus mandshurica* and *Quercus mongolica*, the spatial distributions of these species are only presented for big trees. The results show that big trees of *Fraxinus mandshurica* appeared significantly clumped at scale  $r=5m$ ; big trees of *Pinus koraiensis* and *Quercus mongolica* are randomly distributed at all studied scales (Figure 4).

**Figure 3.** Plot of  $g(r)$  against scale  $r$  showing the spatial distribution of dominant tree species. All live trees >1cm at dbh for each species and all dead trees >4cm were included in the analysis. Red line with circles indicates  $g(r)$  against scale  $r$ ; Thin lines correspond to 99% confidence intervals generated from 10,000 Monte Carlo simulations under the null hypothesis of complete spatial randomness. n values in brackets are the number of trees. Pk: *Pinus koraiensis*; Qm: *Quercus mongolica*; Ta: *Tilia amurensis*; Fm: *Fraxinus mandshurica*; Am: *Acer mono*



**Figure 4.** Spatial distribution for sapling (Sa:  $h > 2m, 1cm \leq dbh < 4cm$ ), small diameter tree (St:  $4cm \leq dbh < 10cm$ ) and big tree (Bt:  $dbh \geq 10cm$ ) of dominant tree species. Red lines with circles indicate  $g(r)$  against scale  $r$ ; Thin lines correspond to 99% confidence intervals generated from 10,000 Monte Carlo simulations under the null hypothesis of complete spatial randomness. Pk: *Pinus koraiensis*; Qm: *Quercus mongolica*; Ta: *Tilia amurensis*; Fm: *Fraxinus mandshurica*; Am: *Acer mono*

**Spatial relationships**

There are no significant relationships between different growth stages (saplings, small diameter trees and big trees) for *Fraxinus mandshurica*, *Pinus koraiensis* and *Quercus mongolica*. Mutual attraction between saplings and small diameter trees of *Tilia amurensis* occurs at scale  $r=16m$ , as well as saplings and big trees; small diameter trees and big trees appeared to be mutually attracted at scale  $r=1m$ . The saplings and small diameter trees of *Acer mono* showed an independent association, while mutual repulsion was observed between the saplings and big trees at the scale of 5m. No significant interactions were found between small diameter trees and big trees (Table 2).

A bivariate analysis of  $g_{12}(r)$  indicated that of the 10 species pairs which consisted of 5 dominant species, *Pinus koraiensis* and *Tilia amurensis*, *Pinus koraiensis* and *Acer mono*, *Acer mono* and *Fraxinus mandshurica* appeared to have significant mutual attractions. *Pinus koraiensis* and *Fraxinus mandshurica*, *Tilia amurensis* and *Fraxinus mandshurica*, *Quercus mongolica* and *Acer mono* showed spatially mutual exclusions. *Quercus mongolica* and *Fraxinus mandshurica* showed exclusions at a scale with  $r=21m$  and attractions at a scale with  $r=46m$  (Table 2). Live *Pinus koraiensis* showed repulsion with dead trees  $>4cm$  at dbh at a scale with  $r=38m$ , and *Quercus mon-*

*golica* was associated with dead trees  $>4cm$  at dbh at a scale with  $r=13m$ .

**Distribution of canopy gaps**

Canopy gaps in the Korean pine - broadleaved forests are mainly caused by natural mortality and wind-throw (Guo et al. 1998, Wu 1997, Yu et al. 2001). Forest gaps caused by tree mortality are usually medium to small sized, with gap areas ranging from 4 to 60m<sup>2</sup> 88.9% forest gap areas in the study plot are less than 100m<sup>2</sup>, the largest area of a canopy gap was 302.8 m<sup>2</sup>, and this area was about four times the size of the average canopy gap (Figure 5a). A univariate analysis of Ripley's  $L(r)$  indicated that canopy gaps appeared to be regularly distributed at scales  $r=6-11m$  and randomly distributed at other scales (Figure 5b). The structure analyses of canopy gaps are based on the canopy projection in this research, and the conclusion obtained in this way was the same as that based on the oval shape investigation method (Zhang et al. 2006).

A bivariate analysis of Ripley's  $L_{12}(r)$  between canopy gaps and 10 tree species under canopy indicated that the relationships appeared to be one of mutual exclusion between canopy gaps and *Acer mandshurica*, *Tilia amurensis* and *Ulmus japonica* at scales  $r=13-17m$ , 11m and 17m respectively. There were no significant spatial relationships between canopy

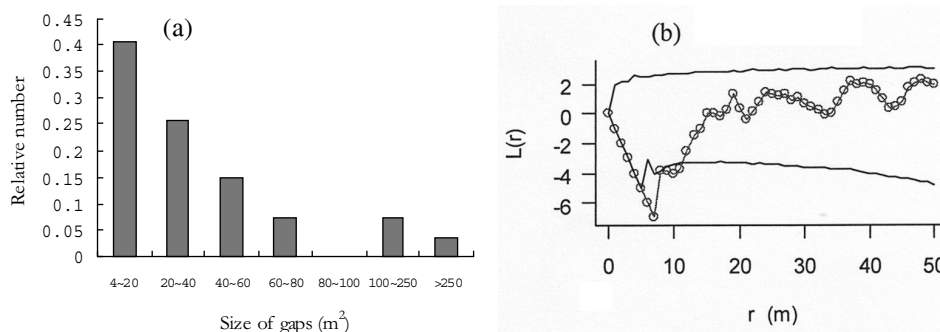
**Table 2.** Spatial association calculated by  $g_{12}(r)$ -function between different tree species, and between different growth stages

Associations	Scale r (m)																							
	1	2-3	4	5	6-12	13	14	15	16	17-20	21	22-32	33	34-37	38	39	40-42	43	44	45	46	47-48	49	50
Pk-Ta	+	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	+	o	o	o
Pk-Am	o	o	+	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o
Pk-Qm	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o
Pk-Fm	o	o	o	o	o	o	o	o	o	o	o	-	o	o	-	o	o	o	o	o	o	o	o	o
Ta-Am	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o
Ta-Qm	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o
Ta-Fm	o	o	o	o	o	o	-	-	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o
Am-Qm	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	-	o	o	o	o	o	o	o
Am-Fm	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	+	o
Qm-Fm	o	o	o	o	o	o	o	o	o	-	o	o	o	o	o	o	o	o	o	o	+	o	o	o
Pk-Dead	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	-	o	o	o	o	o	o	o	o
Qm-Dead	o	o	o	o	o	+	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o
Am-Dead	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o
Fm-Dead	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o
Ta-Dead	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o
Ta(Sa)-Ta(St)	o	o	o	o	o	o	o	+	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o
Ta(Sa)-Ta(Bt)	+	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o
Ta(St)-Ta(Bt)	+	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o
Am(Sa)-Am(St)	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o
Am(Sa)-Am(Bt)	o	o	o	-	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o
Am(St)-Am(Bt)	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o

+: Positive association; -: Negative association; o: Independent association. Pk: *Pinus koraiensis*; Qm: *Quercus mongolica*; Ta: *Tilia amurensis*; Fm: *Fraxinus mandshurica*; Am: *Acer mono*; Dead: Dead trees  $>4cm$  at dbh. Sa: sapling ( $h>2m$ ,  $1cm \leq dbh < 4cm$ ), St: small diameter tree ( $4cm \leq dbh < 10cm$ ); Bt: big tree ( $dbh \geq 10cm$ )

gaps and *Pinus koraiensis*, *Quercus mongolica*, *Tilia mandshurica*, *Acer trigmentosum*, *Acer mono*, *Acer pseudo-sieboldianum* and *Acer barbinerve*.

**Figure 5** (a). Size distribution of forest canopy gaps; and (b) spatial distribution pattern of forest canopy gaps in the research areas. Red line with circles indicates  $L(r)$  against scale  $r$ ; Thin lines correspond to 99% confidence intervals generated from 10,000 Monte Carlo simulations under the null hypothesis of complete spatial randomness



## Discussion

### Spatial distribution

The spatial distribution of tree species mainly depends on the propagation characteristics and the mode of seed dispersal (Hedenås et al. 2003, Laaka-Lindberg 2000). For example, the Korean pine mainly reproduces by seeds. The seed burial behaviour of animals (Chen and Guo 1992) and the shade-tolerance during the seedling/sapling stage (Kong et al. 2005, Yao et al. 1985) both appear to cause a random distribution of seedlings under the canopy (Figure 3(1)). The seed dispersal of *Fraxinus mandshurica* is mainly affected by gravity and most seeds are dispersed within the crown width range of mother trees (Han and Wang 2002). The limited dispersal ability of the seeds may be the main cause for the clumped pattern at small scale ( $r=5\text{m}$ ; Figure 3(3)). *Quercus mongolica* is a pioneer tree species (Swaine and Whitmore 1988) and shade-intolerance (Masaki et al. 1992). The individual trees at canopy level mainly grew from the seedlings and saplings which regenerated in the forest gaps after the canopy disturbance, the *Quercus mongolica* trees had low density and most individuals belong to big trees (Figure 1(4)). *Quercus mongolica* is a light demanding species with a random spatial pattern (Figure 3(4)). This leads to the conclusion that *Quercus mongolica* will be ousted from the canopy layer and displaced by other species in the future.

The spatial distribution dynamics of a tree species is a process which seems to form mainly high aggregation to random patterns. An example is the population development of *Tilia amurensis* and *Acer mono*. The range of distances with significant clumping is gradually decreasing from saplings to small diameter trees to big trees (Figure 4(1)-(6)). It appears that big

trees show a tendency to occur in a random distribution. Some results indicated that with increasing tree size, the spatial distribution of Korean pine tends to

change from slightly clumped to random (Hou and Han 1997). Due to the individual tree mortality, the clumped and random distributions of the population will not become more regular (Kent Dress 1980). Thus, the decreasing spatial aggregation during the population growth is probably mainly caused by density-induced self-thinning within the clumped patches. Also, the absence of small individuals of *Pinus koraiensis* and *Fraxinus mandshurica* (Figure 1(1)(3)) and the random spatial distribution (Figure 3(1)(3)), both indicated that the secure habitats which are good for seed germination and seedling recruitment become increasingly limited in time and space (Harper et al. 1961).

### Spatial relationships

The population structure reflects the population regeneration process (Takahashi et al. 2001) and the intraspecific and interspecific competition type (Béland et al. 2003). The size distribution of *Tilia amurensis* and *Acer mono* is of the reverse *J* shape type (Figure 1(2)(5)), and this implies that the environment under the canopy was suitable for seedling recruitment and survival of these two species. The saplings, small diameter trees and big trees of *Tilia amurensis* appeared as a clumped distribution pattern, and with the mutual attraction, this indicated that seedlings of *Tilia amurensis* are highly dependent on big trees in their vicinity. There is mutual attraction between saplings and big trees of *Tilia amurensis* at scale  $r=1\text{m}$ , but this relationship was not found in other tree species (Table 2). Saplings and big trees of *Acer mono* even showed mutual repulsion at scale  $r=5\text{m}$ , and this indicated that some existing mechanism restrict the survival and growth of seedlings and saplings of *Acer mono* around big trees of *Acer mono*. So what could be such a mechanism? Janzen (1970) and Connell et

al. (1984) hypothesize that the closer the seeds or seedlings are to their big parent trees, the higher will be the mortality caused by species-specific animal predation and pathogens. The same phenomenon of equal species repulsion has been observed in tropical forests. Although there are no related reports on the validation on the Janzen-Connell hypothesis in the Korean Pine - broadleaved forests, the Janzen-Connell hypothesis can provide a reasonable explanation on the phenomenon of "mosaic" or "reverse position" of saplings and big trees in this research.

In addition, the dependence of tree regeneration on sufficient radiation and a canopy gap environment also suggests a negative relationship between juvenile individuals and big trees of the same species (Hamill and Wright 1986). Tanaka (1995) reports a positive relationship between the mortality rate after seed dispersal and the seed density for *Acer mono* var. *marmoratum* f. *dissectum*. The closer the seed is to the parent tree, the higher is the mortality of the seeds and seedlings which is caused by predation and other unknown factors. Guo (2002) has shown that the juvenile individuals of *Acer mono* are mainly distributed under the canopy of *Pinus koraiensis* and *Tilia amurensis* in the Korean Pine - broadleaved forests, and are seldom distributed under mature *Acer mono* trees. These results support the conclusion of mutual repulsion between juvenile individuals and big trees of *Acer mono* to some degree.

Most population structure and forest community models assume that canopy gaps are randomly distributed in space or that they are only related to tree age or tree growth (Busing and Clebsh 1987, Kienast and Kuhn 1989, Lorimer et al. 1988, van Daalen and Shugart 1989, Vanclay 1989). However, there is also some evidence that the canopy gaps in tropical forests appeared as a clumped distribution (Lawton and Putz 1988), and that the canopy gaps of boreal temperate Korean Pine broadleaved forests appeared as a regular distribution (Guo et al. 1998, Wu 1997, Zang 1998).

The results of this study showed that the spatial distribution of canopy gaps was random at all scales except at close range ( $r=6-11\text{m}$ ) where it was regular. Usually, the trees under canopy experience many disturbances. They may be able to reach the canopy layer, but the random distribution of the canopy gaps increased the effect of randomness on the vegetation establishment process under the canopy, and the small gap areas and randomly distributed forest gaps also increased the opportunities of interspecific random competition. This is a reasonable hypothesis, which will be investigated in a subsequent study.

## Acknowledgement

*This work was in part funded by National Natural Science Foundation of China (Project 30771716), and by the 11th five-year National Science and Technology plan of China (Project 2006BAD03A0804).*

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Received 26 September 2008

Accepted 15 March 2010

## ПРОСТРАНСТВЕННАЯ СТРУКТУРА И ВЗАИМОСВЯЗЬ ДОМИНИРУЮЩИХ ДРЕВЕСНЫХ ПОРОД В ГОРНЫХ ЛЕСАХ ЧАНГБЭЙ В КИТАЕ

Чуньюй Чжан, Сюхай Чжао, Сяодун Лю и Клаус фон Гадов

Резюме

С использованием корреляционной функции  $g(r)$  была изучена пространственная структура пяти преобладающих пород (*Pinus koraiensis*, *Quercus mongolica*, *Tilia amurensis*, *Fraxinus mandshurica*, *Acer mono*) в смешанных лесах горной местности Чангбэй в Северном Китае. Наряду с пространственными распределениями было изучено взаимовлияние деревьев на различных стадиях роста. Кроме того, на основании данных о горизонтальных проекциях крон были рассмотрены структурные характеристики и распределения разрывов в пологе древостоев, а также взаимосвязь между ними и древесными породами высотой до 11,2 м.

Установлено, что *Pinus koraiensis* и *Quercus mongolica* характеризуются случайным, а *Acer mono* групповым типом пространственного распределения при расстояниях между деревьями  $r=1-11$ , 13-16, 20, 33 and 43 м. Групповой тип распределения наблюдался также у *Fraxinus mandshurica* при расстоянии  $r=5$  м и *Tilia amurensis* при расстояниях  $r=1-2$ , 9-11 и 16-18 м.

Среди 10 пар, образованных пятью преобладающими древесными породами, у трех (*Pinus koraiensis* and *Tilia amurensis*, *Pinus koraiensis* and *Acer mono*, *Acer mono* and *Fraxinus mandshurica*), в ряде случаев наблюдалось благотворное взаимовлияние деревьев. Еще у трех пар пород (*Pinus koraiensis* and *Fraxinus mandshurica*, *Tilia amurensis* and *Fraxinus mandshurica*, *Quercus mongolica* and *Acer mono*) пространственный анализ позволил выявить неблагоприятное взаимное влияние. У *Quercus mongolica* и *Fraxinus mandshurica* наблюдалось как благотворное, так и неблагоприятное взаимовлияние при расстояниях между деревьями соответственно в 21 и 46 м.

Было установлено, что разрывы в пологе древостоев в пределах экспериментальной площади располагаются преимущественно случайным образом, за исключением равномерного их распределения при расстояниях  $r$  от 6 до 11 м.

**Ключевые слова:** пространственное размещение, взаимовлияние деревьев, полог насаждений, корреляционная функция, горы Чангбэй