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Species Interactions in Spruce–Fir Mixed Stands and Implications for Enrichment Planting in the Changbai Mountains, China

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*To identify the sapling species that can be planted in spruce–fir forest in the Changbai Mountains, China, we analyzed the associations among saplings and between saplings and adult trees of 4 tree species (spruce [*Picea koraiensis* Nakai], fir [*Abies nephrolepis* (Trautv.) Maxim.], Korean pine [*Pinus koraiensis* Sieb. et Zucc.], and lime [*Tilia amurensis* Rupr.]), and the spatial distribution of saplings under the adult trees. We observed positive associations between the saplings and adult trees of spruce, fir, Korean pine, and lime. In addition, the numbers of saplings of spruce, fir, Korean pine, and lime with distance from adult trees exhibited a positively skewed distribution. We conclude that saplings of any one or several of these 4 species can be planted in the mixed forests and the optimum distance between saplings and adults trees of the coniferous species is 2–3 m, whereas the corresponding optimal distance from the broadleaved lime is 4–5 m. Our results provide new insights into the development of reforestation techniques in spruce–fir forests in the Changbai Mountains.*

Keywords: *Interspecific association; enrichment planting; spatial distribution patterns; spruce–fir forest.*

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Introduction

Spruce–fir forest is one of the major forest types in the Changbai Mountains in northeastern China; it is generally considered to be the climax vegetation in the region. Since the 1970s, this forest type has suffered from intensive selective cutting aimed at timber extraction and hence it has become greatly degraded (Tang et al 2011). The current stand volume of degraded spruce–fir forest is 160 m^3 ha^{-1}, whereas for primary spruce–fir forest in this region the stand volume is reported to be around 350–400 m^3 ha^{-1} (Gong 2009). Therefore, restoration of the degraded secondary forest is urgently needed, especially in the context of climate change and biodiversity conservation (Girma et al 2010; Liu et al 2011).

Given previous intensive felling of the valuable climax tree species, such as *Abies nephrolepis* (Trautv.) Maxim., *Picea koraiensis* Nakai, *Pinus koraiensis* Sieb. et Zucc., and *Tilia amurensis* Rupr., fewer mature trees remain for natural regeneration (Dai et al 2003). Furthermore, following long-term anthropogenic disturbance the forest landscape is fragmented, which hinders seed dispersal of climax tree species from nearby primary forest. Enrichment planting for climax tree species—that is, a technique for promoting artificial regeneration of forests in which seedlings of preferred timber trees are planted in the understory of existing logged-over forests and then given preferential treatment to encourage their growth (Lamprecht 1989)—is therefore essential to facilitate the restoration process, and hence accelerate positive succession.

For sound enrichment planting, species selection and the species/individual spatial distribution for both saplings and adult trees, especially the spatial arrangement in primary forest, need to be identified in advance, in order to guide the restoration process (Zhang et al 2010). Indeed, selection of species can be easily determined by analyzing the importance value of the species in the overstory of remnant old-growth forest. Assessment of the species/individual spatial arrangement can be obtained through analyzing interspecific associations and spatial patterns of main tree species.

Interspecific association, which is one of the most important quantitative and structural characteristics of communities, indicates the spatial distribution relationship and functional dependency between different species (Peng et al 1999; Zhang et al 2003; Lin et al 2005). Many studies have explored the interspecific association of adult trees (eg Yu 2002; Hao et al 2007; Han et al 2009; Liu et al 2009a; Li et al 2011). However, less

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consideration has been given to the associations among saplings and between saplings and adult trees.

Spatial pattern is defined as the horizontal and vertical distribution of individuals, which is determined by a combination of historical and environmental factors (Janzen 1970; Newbery et al 1986; Kenkel 1988; Houle 1994; Camarero et al 2000; Takahashi et al 2001; Li et al 2008). Similarly, numerous studies have investigated the spatial patterns of either adult trees or saplings (Hou and Han 1997; Wang et al 2003; Li et al 2008; Liu et al 2008; Shu et al 2008; Han et al 2009). In contrast, the distribution of saplings in a circular pattern under adult trees is poorly explored.

We conducted the present study in an old-growth spruce–fir forest with the objectives of (1) identification of the species composition of dominant trees for selecting appropriate species in enrichment planting, (2) clarification of the interspecific association and spatial pattern of the main species in order to determine the species/individual arrangement, and (3) offering of detailed recommendations for enrichment planting for restoration of degraded spruce–fir forest.

Material and methods

Study site

The study area was located in the Jingouling Experimental Forest enterprise (43°22′N, 130°10′E) in the Xueling division of Laoye Ling Mountain in the Changbai Mountains, China. The altitude range of the area is 300–1200 m and the slopes mostly vary between 5° and 25°. The average annual temperature is about 3.9°C and the annual precipitation is 600–700 mm, with most rain falling in July. Frosts occur from mid-September to the end of May, with an average growing season of about 120 days. A gray–brown podzolic soil is present on the low and intermediate mountains in the area and is derived from the parent basalt rock. The study area was mainly covered with degraded secondary forest dominated by *A. nephrolepis* (Trautv.) Maxim. and *P. koraiensis* Nakai, in association with other tree species including *Pin. koraiensis* Sieb. et Zucc., *T. amurensis* Rupr., *Betula costata* Trautv., *Acer mono* Maxim., *Betula platyphylla* Sukaczev, and *Ulmus pumila* L. Primary forests, which have been under strict protection and represent the climax vegetation, are also found in this area, although their extent is limited.

Field measurements

In July 2010, sixty-eight 10 × 10-m regeneration plots with 10-m buffer zones were systematically established in primary forest. In each plot, the coordinates (*x* and *y*), diameter at breast height (DBH), height (*h*), and the crown width of adult trees (DBH ≥ 5 cm) were measured. Similarly, for each sapling ($h \geq 30$ cm and DBH ≤ 5 cm) we measured the coordinates (*x* and *y*), ground diameter, *h*, and crown width. We also surveyed all adult trees and saplings in the buffer zones by recording the species and coordinates (*x* and *y*).

Data analysis

Importance value: The importance value is a comprehensive quantitative indicator used to characterize the status and role of each species in the community. The larger the importance value of a tree species, the greater the dominance of the species in the plot. The importance value, relative dominance, abundance, and frequency of each species were calculated as follows:

$$\begin{aligned}&\text{Importance value of the tree layer (IV)} =\\&(\text{Relative abundance}) + (\text{Relative frequency}) +\\&(\text{Relative dominance})/3\end{aligned} \tag{1}$$

$$\begin{aligned}&\text{Relative dominance} =\\&(\text{Total basal area of the species}/\\&\text{Total basal area of all species}) \times 100\end{aligned} \tag{2}$$

$$\begin{aligned}&\text{Relative abundance} =\\&(\text{Number of individuals of the species}/\\&\text{Total number of individuals}) \times 100\end{aligned} \tag{3}$$

$$\begin{aligned}&\text{Relative frequency} =\\&(\text{Frequency of the species}/\\&\text{Sum of frequencies of all species}) \times 100\end{aligned} \tag{4}$$

Interspecific association analysis: Interspecific associations comprise positive association, negative association, and no association (Li and Shi 1994). Positive association means that 2 species are likely to be found in the same location and negative association means that species A is less likely to occur in the same community as species B. We used χ^2 statistics based on a 2 × 2 contingency table to examine interspecific associations (Zhang 2004). The formula is as follows:

$$\chi^2 = \frac{n[|ad - bc| - n/2]^2}{(a+b)(c+d)(a+c)(b+d)} \tag{5}$$

where n is the total number of quadrats, a is the number of quadrats with both A and B present, b indicates the number of quadrats with A only, c indicates the number of quadrats with B only, and d indicates the number of quadrats without A and B. When $\chi^2 < 3.841$, there is no interspecific association; when $3.841 \leq \chi^2 < 6.635$, there are certain associations between species; and when $\chi^2 \geq 6.635$, there are significant associations between species.

When $ad > bc$, the interspecific association is positive, and when $ad < bc$, the interspecific association is negative.

Nearest neighbor analysis: Average distances between saplings and adults of different tree species: given saplings of species A and adult trees of species B, the number of saplings of A is N, and the distance from a random sapling of species A to the nearest adult tree of species B is D_i. We calculated the average distance between saplings of species A and nearest adult trees of species B with the following formula:

$$\overline{D}=\frac{1}{N}\sum_{i=1}^{N}D_i \tag{6}$$

We used the formula to determine the degree of dependence of saplings of species A on adult trees of species B. Assuming that a sapling and a nearest adult tree constitute a sample unit, when the sample number exceeds 50 the average distance shows an approximately normal distribution.

$$\frac{(\overline{d}-\overline{D})}{\sigma/\sqrt{n}}\frac{approximately}{n\geq 50}\mathrm{N}(0,1) \tag{7}$$

Thus, we can obtain the formula:

$$P\left\{\left|\overline{d}-\overline{D}\right|\leq U_{\alpha}\cdot S/\sqrt{n-1}\right\}=1-\alpha \tag{8}$$

where is the average distance between the saplings of species A and the nearest adult tree of species B, S is the standard variance of the sample distance, and is the expected value of , with the confidence interval $[\overline{d}-U_{\alpha}\cdot S/\sqrt{n-1},\ \overline{d}+U_{\alpha}\cdot S/\sqrt{n-1}]$.

Distribution of the number of saplings with the distance between saplings and adult trees: The distribution area of saplings of species A around the nearest adult tree of species B was divided into annular zones (many concentric circles were drawn with the adult tree of species B at the center and the radius equal to a (a = 1, 2, 3, 4…); the region between 2 adjacent circles was an annular zone), and the number of saplings of species A in each annular zone was counted. The distance, for which the ratio of number of saplings of species A to all saplings is maximal, is the optimal distance for replanting saplings of species A under adult trees of species B.

Results

Importance value of different tree species

Among the tree species studied, the importance value of fir (*A. nephrolepis*) was largest (27.98) and that of yew (*Taxus cuspidata* Sieb. et Zucc.) was smallest (0.27) (Table 1). On the basis of cluster analysis of the importance value (Figure 1), these species were divided into 3 groups: (1) *A. nephrolepis*, which had the highest importance value; (2) spruce (*P. koraiensis*), Korean pine (*Pin. koraiensis*) and lime (*T. amurensis*), for which the importance values were markedly higher than those of the remaining species; and (3) birch (*B. costata*), maple (*A. mono*), white birch (*B. platyphylla*), elm (*U. pumila*), larch (*Larix gmelinii* Rupr.), Cathay poplar (*Populus cathayana* Rehd.), Manchurian ash (*Fraxinus mandshurica* Rupr.), yew, and mixed hardwood species (because the importance value of these species were markedly smaller than those of the first 2 groups, these species were classified as a single group). The first 2 groups, for which the total importance values were close to 70, were the dominant species in the mixed stands. As reflected in their lower importance value (<30), the third group was composed of nondominant species.

Interspecific associations

Interspecific associations between saplings: The χ^2 test showed that among all species pairs, 40 pairs exhibited a positive association and 15 pairs showed a negative association. A statistically significant association was found between spruce × Korean pine and fir × Korean pine. The χ^2 test also indicated that the positively associated pairs with an association coefficient of >0.7 were fir × Korean pine, fir × lime, and fir × birch (Figure 2).

Associations between adult trees and saplings: The association between adult trees and saplings was analyzed for the 4 species with the highest importance value. The χ^2 test showed that 11 species pairs were positively associated and 5 species pairs were negatively associated. Statistically significant positive associations were observed for (saplings × adult trees) fir × fir and lime × fir. The χ^2 analysis also indicated that 5 pairs (saplings × adult trees), which comprised fir × lime, spruce × spruce, spruce × lime, Korean pine × Korean pine, and lime × lime, showed weakly negative associations (Figure 3).

Nearest distance from adult trees to saplings for 4 dominant species

Average distance between adult trees and saplings: The saplings of 4 dominant species (fir, spruce, Korean pine, and lime) were located closest to fir adult trees, followed by Korean pine and spruce, and were located furthest from lime adult trees (Tables 2–5).

Distribution of number of saplings with distance between saplings and adult trees: We analyzed the distribution of the saplings of the 4 dominant species on the basis of the distance between the saplings and adult trees. All skewness values were greater than 0. Therefore, the distribution was positively skewed (Tables 2–5; Figure 4). Thus, the sapling number first increased with the distance from the sapling to the adult tree, and then decreased beyond a certain

TABLE 1 Importance value and relative abundance, dominance, and frequency of all coniferous and broadleaved tree species in the spruce–fir mixed stands.

Species	Scientific name	Relative abundance	Relative dominance	Relative frequency	Importance value
Fir	*A. nephrolepis* (Trautv.) Maxim.	29.63	35.4	18.9	27.98
Spruce	*P. koraiensis* Nakai	15.74	22.83	16.49	18.35
Korean pine	*Pin. koraiensis* Sieb. et Zucc.	11.42	16.46	13.06	13.64
Lime	*T. amurensis* Rupr.	11.11	6.96	11.68	9.92
Birch	*B. costata* Trautv.	6.94	3.77	9.28	6.66
Maple	*A. mono* Maxim.	7.41	4.07	7.9	6.46
Mixed hardwood		5.71	2.2	8.59	5.5
White birch	*B. platyphylla* Sukaczev	4.48	3.29	4.81	4.19
Elm	*U. pumila* L.	3.24	1.52	3.78	2.85
Larch	*L. gmelinii* Rupr.	2.93	2.47	2.75	2.72
Cathay poplar	*P. cathayana* Rehd.	0.62	0.26	1.37	0.75
Manchurian ash	*F. mandshurica* Rupr.	0.62	0.48	1.03	0.71
Yew	*T. cuspidata* Sieb. et Zucc.	0.15	0.3	0.34	0.27

critical distance. The number of saplings of the 4 species reached maximum values at a distance of 2–3 m from an adult tree for fir, spruce, and Korean pine, and of 4–5 m for lime. The saplings of each species were mainly distributed in the range of 1–5 m from an adult tree for fir, 1–6 m for Korean pine and spruce, and 1–7 m for lime.

Discussion

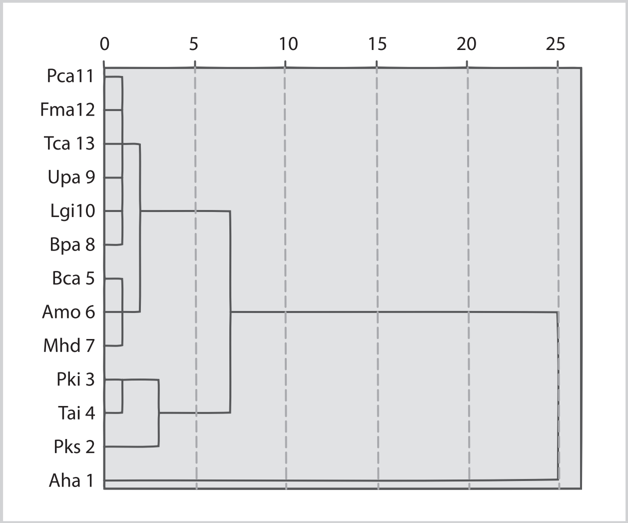
Interspecific associations

Interspecific associations between saplings of different tree species: Three major factors might cause the formation of interspecific associations (Yang et al 2007). The first factor is the competition type of the species, which can be classified as positive competition or negative competition. Two species are negatively associated if they are competitive with each other and positively associated if they are mutually promotive (Miller 1994; Wootton 1994; Callaway 1995; Hamback et al 2000; Rousset and Lepart 2000; Callaway et al 2002; Palmer et al 2003; Moeller 2004; Graff et al 2007; Brooker et al 2008). Second, one species creates suitable conditions for another species, and thus results in a positive association. For example, pioneer trees can create a regeneration environment suitable for certain shade-tolerant species that have difficulty regenerating in intense light conditions. Third, interaction between 2 species via physical or chemical factors may result in positive or negative associations (Guo et al 1997).

Our results showed that the associations between spruce saplings × Korean pine saplings, and between fir saplings × Korean pine saplings, were significantly positive (Figure 2). This might be because the saplings of spruce, Korean pine, and fir have similar ecological preferences and thus can share similar habitats. For example, the saplings have strong shade tolerance and can survive under a canopy in weak light, which might result in coexistence patterns among the species. Although the coexistence might induce competition and increase mortality, overall a positive interspecific association can be formed (Richard and Corine 2011).

Associations between adult trees and saplings: Significant positive associations between saplings and adult trees were observed for the species pairs fir × fir and lime × fir. The reason might be that saplings of fir and lime require a shady environment for regeneration, which is provided by adult trees of fir and Korean pine. In

FIGURE 1 Dendrogram from cluster analysis of the importance value of all overstory tree species in uneven-aged spruce–fir stands. The horizontal axis represents the relative distance between individuals and groups, for which the maximum value is 25. The dendrogram was generated with average-linkage clustering between groups. 1 Aha, *A. nephrolepis* (Trautv.) Maxim.; 3 Pki, *Pin. koraiensis* Sieb. et Zucc.; 2 Pks, *P. koraiensis* Nakai; 4 Tai, *T. amurensis* Rupr.; 5 Bca, *B. costata* Trautv.; 6 Amo, *A. mono* Maxim.; 7 Mhd, Mixed hardwood; 8 Bpa, *B. platyphylla* Sukaczev; 9 Upa, *U. pumila* L.; 10 Lgi, *L. gmelinii* Rupr.; 11 Pca, *P. cathayana* Rehd.; 12 Fma, *F. mandshurica* Rupr.; 13 Tca, *T. cuspidata* Sieb. et Zucc.



contrast, most of the other species pairs showed nonsignificant positive associations; however, to some extent this result might indicate that adult trees of most species create suitable conditions for saplings (Figure 3).

A significant negative association was observed for a few species pairs (Korean pine adults and saplings; spruce adults and saplings). The negative association might be attributable to human interference and environmental effects. For example, previously Korean pinecones were harvested because of their high economic value, and this led to a lack of saplings, which resulted in a negative association (Liu et al 2004). Consistent with our findings, a negative association between spruce adults and saplings was reported by Prokonev and Zhai (1964) and Chen et al (2005). This phenomenon could be explained by the Janzen-Connell theory, which states that soil pathogens and predators near spruce adult trees could induce high mortality of spruce saplings (Gilbert 2002).

Spatial distributions of saplings of the 4 dominant species around adult trees

Average distances between adult trees and saplings: The ranking of the average distance between saplings and adult trees of the 4 dominant species showed that saplings of the 4 species are most likely to regenerate under the canopy of fir adult trees and are least likely to

FIGURE 2 Half-matrix diagram of χ^2 associations among saplings of all species in uneven-aged spruce–fir stands.

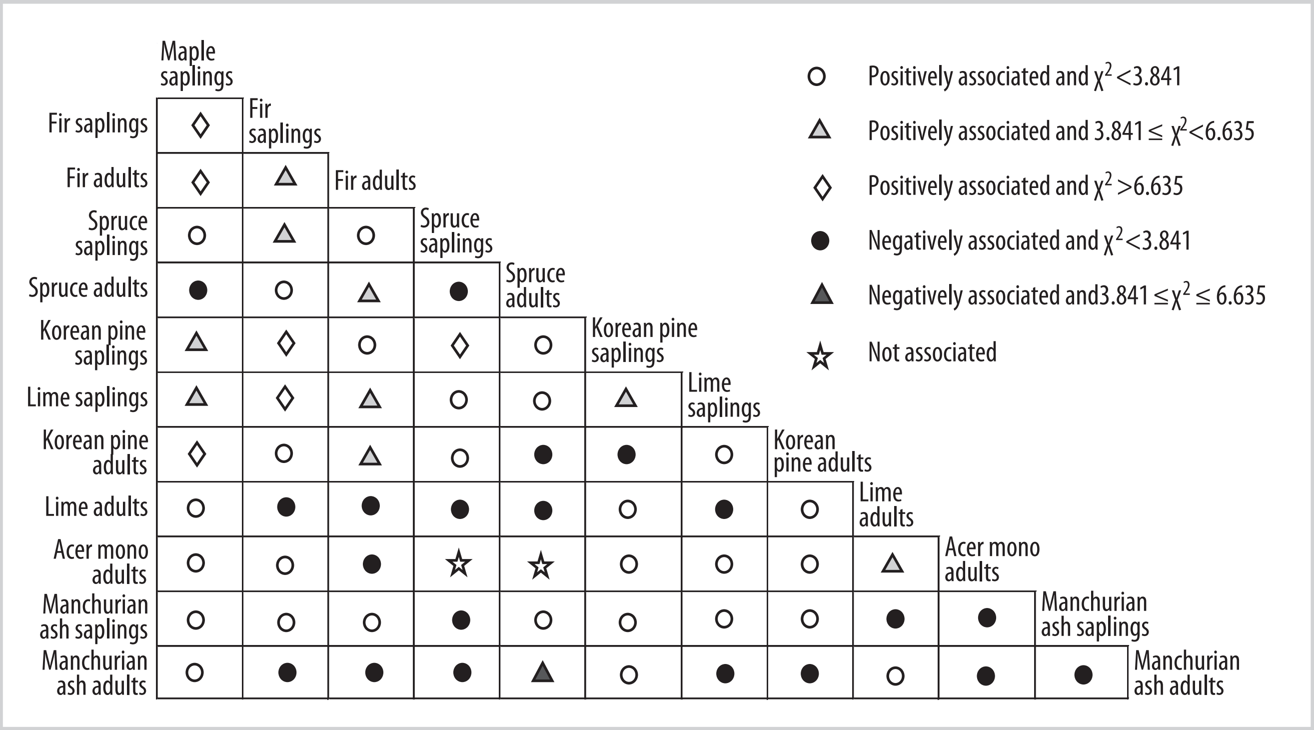
	Maple	Fir	Spruce	Korean pine	Lime	Elm	Manchurian ash	Birch	Oak	Yew
Fir	○									
Spruce	○	○								
Korean pine	○	▲	▲							
Lime	○	○	○	○						
Elm	○	○	●	○	○					
Manchurian ash	○	○	●	○	○	○				
Birch	●	○	○	○	○	○	●			
Oak	○	○	○	○	○	●	○	○		
Yew	○	○	○	●	●	○	●	●	○	
White birch	●	○	●	●	●	○	○	○	●	●

○ Positively associated and $\chi^2<3.841$

▲ Positively associated and $3.841 \le \chi^2<6.635$

● Negatively associated and $\chi^2 <3.841$

FIGURE 3 Half-matrix diagram of χ^2 associations between saplings and adult trees of 4 dominant species in uneven-aged spruce–fir stands.



	Maple saplings	Fir saplings	Fir adults	Spruce saplings	Spruce adults	Korean pine saplings	Lime saplings	Korean pine adults	Lime adults	Acer mono adults	Manchurian ash saplings
Fir saplings	◇										
Fir adults	◇	△									
Spruce saplings	○	△	○								
Spruce adults	●	○	△	●							
Korean pine saplings	△	◇	○	◇	○						
Lime saplings	△	◇	△	○	○	△					
Korean pine adults	◇	○	△	○	●	●	○				
Lime adults	○	●	●	●	●	○	●	○			
Acer mono adults	○	○	●	☆	☆	○	○	○	△		
Manchurian ash saplings	○	○	○	●	○	○	○	○	●	●	
Manchurian ash adults	○	●	●	●	▲	○	●	●	○	●	●

○ Positively associated and $\chi^2 < 3.841$

△ Positively associated and $3.841 \leq \chi^2 < 6.635$

◇ Positively associated and $\chi^2 > 6.635$

● Negatively associated and $\chi^2 < 3.841$

▲ Negatively associated and $3.841 \leq \chi^2 \leq 6.635$

☆ Not associated

establish under lime adult trees, which was consistent with their interspecific associations (Tables 2–5). In contrast, some results were not consistent with the interspecific association analysis. For example, nearest neighbor analysis indicated that fir and Korean pine saplings most favored growing under the canopy of fir adult trees, which is inconsistent with the results of the interspecific association analysis. This finding might be because of the difference in analytical approach of the 2 methods.

TABLE 2 Distances between saplings of the 4 dominant species and *A. nephrolepis* adult trees.[a)]

Statistics for distance	Saplings			
	Aha	Pki	Pks	Tai
Estimated mean (m)	3.54	3.19	3.02	3.39
Upper limit of the mean (m)	3.39	2.89	2.77	3.08
Lower limit of the mean (m)	3.68	3.48	3.27	3.70
Maximum (m)	10.00	9.09	8.56	9.94
Minimum (m)	0.10	0.29	0.14	0.24
Sample variance	1.925	1.849	1.718	2.004
Skewness	0.501	0.771	0.755	0.823
Kurtosis	−0.203	0.366	0.371	0.057
Sample number (stem)	681	147	182	162

[a)] Aha, *A. nephrolepis* (Trautv.) Maxim.; Pki, *Pin. koraiensis* Sieb. et Zucc.; Pks, *P. koraiensis* Nakai; Tai, *T. amurensis* Rupr.

TABLE 3 Distances between saplings of the 4 dominant species and Pki adult trees.[a)]

Statistics for distance	Saplings			
	Aha	Pki	Pks	Tai
Estimated mean (m)	4.69	4.70	5.03	3.54
Upper limit of the mean (m)	4.47	4.25	4.53	3.23
Lower limit of the mean (m)	4.92	5.15	5.54	3.85
Maximum (m)	13.75	11.11	12.99	10.16
Minimum (m)	0.14	0.32	0.38	0.22
Sample variance	2.672	2.540	2.965	1.935
Skewness	1.095	0.973	0.998	0.863
Kurtosis	1.043	0.602	1.541	0.12
Sample number (stem)	529	124	133	151

[a)] Aha, *A. nephrolepis* (Trautv.) Maxim.; Pki, *Pin. koraiensis* Sieb. et Zucc.; Pks, *P. koraiensis* Nakai; Tai, *T. amurensis* Rupr.

Distribution of saplings with the distance between saplings and adult trees: We observed that the number of saplings of all 4 dominant species increased with increment in the distance from a mature tree until a maximum value was reached, and then decreased steadily at greater distances (Figure 4). This finding can be illustrated to a certain extent by relying on the Janzen-Connell theory, namely: (1) the number of seedlings/seeds is negatively correlated with the distance between the seedlings/seeds and mature trees, and (2) high mortality is more likely to occur in the vicinity of the mature trees because of soil pathogens and predators near the mature trees. In accordance with (1), the number of spruce, fir, Korean pine, and lime seeds/seedlings decreases with distance from the mature tree, whereas for (2) the optimal distance at which the maximum number of saplings is reached occurs at a certain distance from mature trees rather than in their immediate vicinity (Figure 4). This is consistent with the conclusion of Schupp and Jordano (2011). Besides, the same results were also found between saplings and heterogenic adult trees, which might be explained as follows: (1) high mortality tends to occur near the adult trees due to soil pathogens and predators according to the Janzen-Connell theory; (2) the saplings of these 4 climax tree species could successfully survive under a shady environment; and (3) the crown in the upper layer inhibits the growth of shrubs and herbs, reduces their competitiveness with the saplings, and hence leads to the aggregation of most saplings under the canopy (Jin et al 2005).

The maximum number of saplings for coniferous species (fir, spruce, and Korean pine) was observed at a

TABLE 4 Distances between saplings of the 4 dominant species and Pks adult trees.[a)]

Statistics for distance	Saplings			
	Aha	Pki	Pks	Tai
Estimated mean (m)	4.83	4.41	5.03	4.29
Upper limit of the mean (m)	4.59	3.96	4.55	3.79
Lower limit of the mean (m)	5.07	4.86	5.50	4.79
Maximum (m)	14.39	13.64	13.69	13.86
Minimum (m)	0.34	0.24	0.59	0.36
Sample variance	3.048	2.838	3.043	3.056
Skewness	0.71	1.002	0.8041	0.762
Kurtosis	−0.088	0.44	0.131	0.646
Sample number (stem)	603	154	158	146

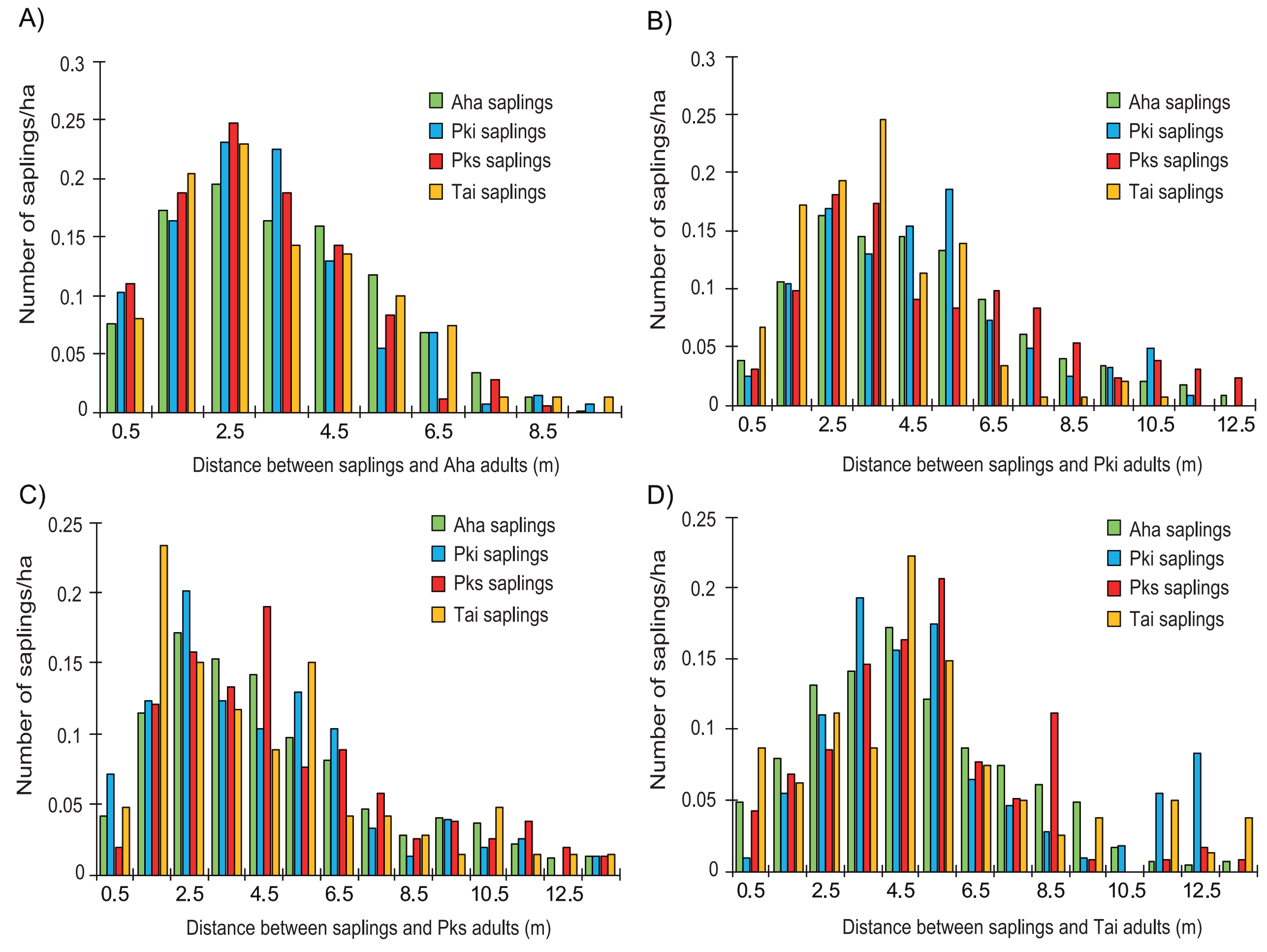
[a)] Aha, *A. nephrolepis* (Trautv.) Maxim.; Pki, *Pin. koraiensis* Sieb. et Zucc.; Pks, *P. koraiensis* Nakai; Tai, *T. amurensis* Rupr.

TABLE 5 Distances between saplings of the 4 dominant species and Tai adult trees.[a)]

Statistics for distance	Saplings			
	Aha	Pki	Pks	Tai
Estimated mean (m)	5.00	5.72	5.13	5.21
Upper limit of the mean (m)	4.73	5.11	4.65	4.49
Lower limit of the mean (m)	5.26	6.32	5.62	5.94
Maximum (m)	14.39	14.30	14.12	14.20
Minimum (m)	0.25	0.35	0.42	0.26
Sample variance	2.764	3.254	2.663	3.397
Skewness	1.031	0.911	0.76	1.106
Kurtosis	1.139	0.65	−0.082	1.653
Sample number (stem)	416	110	117	82

[a)] Aha, *A. nephrolepis* (Trautv.) Maxim.; Pki, *Pin. koraiensis* Sieb. et Zucc.; Pks, *P. koraiensis* Nakai; Tai, *T. amurensis* Rupr.

FIGURE 4 Relationship between the ratio of the number of saplings to all saplings with the distance between adults and saplings of 4 dominant species. 1 Aha, *A. nephrolepis* (Trautv.) Maxim.; 2 Pki, *Pin. koraiensis* Sieb. et Zucc.; 3 Pks, *P. koraiensis* Nakai; 4 Tai, *T. amurensis* Rupr.



distance of 2–3 m, whereas for the broadleaved species lime the corresponding distance was 4–5 m (Figure 4). This is consistent with the crown widths of coniferous and broadleaved tree species. Therefore the larger the crown width was, the longer the optimal distance where maximum saplings occurred. Our results are slightly inconsistent with the conclusion of Jin et al (2005), who argued that the maximum number of saplings was mainly distributed in the range of 1.5–3.5 m from the nearest adult tree. The reason for the discrepancy is probably that Jin et al (2005) did not classify the adult tree species into coniferous and broadleaved species when analyzing the spatial distribution of saplings. In future it might be more advisable to conduct this kind of analysis with coniferous and broadleaved species separately.

Conclusions and recommendations

We conclude that: (1) saplings of any one or several species among Korean pine, spruce, fir, and lime are the best choice for enrichment planting in an uneven-aged spruce–fir forest stand; and (2) the optimum distance of saplings from an adult tree is 2–3 m from fir, Korean pine, and spruce adult trees and 4–5 m from lime adult trees. These results provide critical information for definition of the optimum spatial arrangement of saplings of different species for enrichment planting.

In contrast to natural regeneration, which is reliant on seed dispersal mediated by wind and animals, artificial regeneration by enrichment planting is an expensive method, but has an obvious advantage in terms of the flexibility of either species combinations or spatial arrangements. For example, seedlings or saplings of Korean pine, spruce, fir, and lime can be planted at the above-mentioned optimal distance from fir, Korean pine, spruce, and lime adult trees in accordance with the findings in this study. In addition, the number of seedlings and saplings planted can be precisely controlled in accordance with the species composition of the upper canopy, stem density, and site conditions. For example, a greater number of seedlings or saplings could be planted in forest with a low density of trees in the upper canopy and in high-quality sites.

Overall, the spatial distribution of saplings of different species from adult trees and the mechanisms responsible are complex. The potential mechanisms include the ecological preferences of tree species (Xu 2001), intraspecific and interspecific competition (He and Duncan 2000; Druckenbrod et al 2005), microenvironmental factors (Sugita and Tani 2001; Mori and Komiyama 2008), site condition, and chemical interactions between tree species (Silvera et al 2003; Wright et al 2005), and hence further exploration of the mechanisms responsible is needed in order to further refine enrichment planting techniques in such a context.

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REFERENCES

Brooker RW, Maestre FT, Callaway RM, Lortie CL, Cavieres LA, Kunstler G, Liancourt P, Tielbörger K, Travis JMJ, Anthelme F, Armas C, Coll L, Corcket E, Delzon S, Forey E, et al. 2008. Facilitation in plant communities: The past, the present, and the future. *Journal of Ecology* 96:18–34.

Callaway RM. 1995. Positive interactions among plants. *Botanical Review* 61: 306–349.

Callaway RM, Brooker RW, Choler P, Kikvidze Z, Lortie CJ, Michalet R, Paolini L, Pugnaire FI, Newingham B, Aschehoug ET, Armas C, Kikodze D, Cook BJ. 2002. Positive interactions among alpine plants increase with stress. *Nature* 417:844–848.

Camarero JJ, Gutiérrez E, Fortin MJ. 2000. Spatial pattern of subalpine forest-alpine grassland ecotones in the Spanish Central Pyrenees. *Forest Ecology and Management* 134:1–16.

Chen DM, Pan DC, Liu CL. 2005. Analysis on micro-habitat variables affecting natural regeneration and survival of saplings in *Picea schrenkiana* stand [in Chinese]. *Journal of Xinjiang Agricultural University* 28(3):35–39.

Dai LM, Shao GF, Chen G, Liu XS, Li Y. 2003. Forest cutting and regeneration methodology on Changbai Mountain [in Chinese]. *Journal of Forestry Research* 14(1):56–60.

Druckenbrod DL, Shugart HH, Davies I. 2005. Spatial pattern and process in forest stands within the Virginia piedmont. *Journal of Vegetation Science* 16(1): 37–48.

Gilbert GS. 2002. Evolutionary ecology of plant diseases in natural ecosystems. *Annual Review of Phytopathology* 40:13–43.

Girma A, Mosandl R, El Kateb H, Masresha F. 2010. Restoration of degraded secondary forest with native species: A case study in the highland of Ethiopia. *Scandinavian Journal of Forest Research* 25(Suppl 8):86–91.

Gong ZW. 2009. *Dynamics of Forest Succession and Restoration Strategies for Degraded Spruce-fir Forest in Changbai Mountain* [PhD dissertation]. Beijing, China: Beijing Forestry University.

Graff P, Aguiar MR, Chaneton E. 2007. Shifts in positive and negative plant interactions along a grazing intensity gradient. *Ecology* 88:188–199.

Guo ZH, Zhuo ZD, Chen J, Wu MF. 1997. Interspecific association of trees in mixed evergreen and deciduous broadleaved forest in Lushan Mountain [in Chinese]. *Acta Phytoecologica Sinica* 21:424–43.

Hamback PA, Agren J, Ericson L. 2000. Associational resistance: insect damage to purple loosestrife reduced in thickets of sweet gale. *Ecology* 81: 1784–1794.

Han WH, Li XK, Ye D, Xiang W, Song T, Cao H. 2009a. Interspecific association and correlation between dominant woody plant species in an evergreen and deciduous broad-leaved mixed forest of karst area, Northwest Guangxi [in Chinese]. *Journal of Mountain Science* 27(6):719–726.

Han YZ, Chen ZF, Chang J, Wang YQ. 2009b. The pattern of natural regeneration in plantation of Manchurian ash [in Chinese]. *Journal of Shanxi Agricultural University* 20:335–338.

Hao ZQ, Zhang J, Song B, Ye J, Li BH. 2007. Vertical structure and spatial associations of dominant tree species in an old-growth temperate forest [in Chinese]. *Forest Ecology and Management* 252:1–11.

He F, Duncan RP. 2000. Density-dependent effects on tree survival in an old-growth Douglas fir forest. *Journal of Ecology* 88:676–688.

http://dx.doi.org/10.1659/MRD-JOURNAL-D-11-00125.1

Hou XY, Han JX. 1997. Simulation analysis of spatial patterns of main species in the Korean pine broadleaved forest in Changbai Mountain. *Acta Phytoecologica Sinica* 21(3):242–249.

Houle G. 1994. Spatiotemporal patterns in the components of regeneration of four sympatric tree species, *Acer rubrum, A. saccharum, Betula alleghaniensis* and *Fagus grandifolia*. *Journal of Ecology* 82:39–53.

Janzen DH. 1970. Herbivores and the number of tree species in tropical forests. *American Naturalist* 104:501–528.

Jin YH, Li DQ, Jiang HX, Zhou L. 2005. Quantitative dynamics on natural regeneration of secondary forest during the restoration period in Changbai Mountain area [in Chinese]. *Journal of Nanjing Forestry University* 29:65–68.

Kenkel NC. 1988. Pattern of self-thinning in jack pine: Testing the random mortality hypothesis. *Ecology* 69:1017–1024.

Lamprecht H. 1989. *Silviculture in the tropics*. Rossdorf, Germany: TZ-Verlagsgesellschaft.

Li L, Wei SG, Huang ZL, Ye WH, Cao HL. 2008. Spatial patterns and interspecific associations of three canopy species at different life stages in a subtropical forest, China [in Chinese]. *Journal of Integrative Plant Biology* 50(9):1140–1150.

Li LH, Shi SB. 1994. Preliminary study on interspecific association and combined population patterns of stipa bungeana steppe community. *Chinese Journal of Ecology* 13(3):62–67.

Li SF, Liu WD, Su JR, Zhang ZJ. 2011. Niches and interspecific associations of dominant tree populations at different restoration stages of monsoonal broad-leaved evergreen forest [in Chinese]. *Chinese Journal of Ecology* 30:508–515.

Lin YM, Wu CZ, Hong W, Ji GZ, Hu XS, Wu JL. 2005. Study on the scale effect of interspecific association of species in tree layer of the rare plant *Tsuga longibracteata* community [in Chinese]. *Guangxi Flora* 25:526–532.

Liu T, Zhao XJ, Jia YM. 2008. Spatial pattern of population recruitment of *C. ewersmanniana* in south of Gurbantunggut desert [in Chinese]. *Journal of Desert Research* 28:258–264.

Liu XY, Yu XX, Chen LH. 2009. Interspecific association and niche research of natural forest in Beijing mountainous area [in Chinese]. *Journal of Northwest Forestry University* 24(5):26–30.

Liu XZ, Lu YC, Zhou YH, Meng JH, Zhang XQ, Lei XD. 2011. The influence of soil conditions on regeneration establishment for degraded secondary forest restoration, Southern China. *Forest Ecology and Management* 261(11):1771–1780.

Liu ZG, Ji LZ, Hao ZQ, Zhu JJ, Kang HZ. 2004. Effect of cone-picking on natural regeneration of Korean pine in Changbai Mountain Nature Reserve [in Chinese]. *Chinese Journal of Applied Ecology* 15(6):958–962.

Miller TE. 1994. Direct and indirect species interactions in an early old-field plant community. *American Naturalist* 143:1007–1025.

Moeller DA. 2004. Facilitative interactions among plants via shared pollinators. *Ecology* 85:3289–3301.

Mori AS, Komiyama A. 2008. Differential survival among life-stages contributes to co-dominance of *Abies mariesii* and *Abies veitchii* in a subalpine old-growth forest. *Journal of Vegetation Science* 19:239–244.

Newbery DM, Renshaw E, Brünig EF. 1986. Spatial pattern of trees in kerangas forest, Sarawak. *Vegetatio* 65:77–89.

Palmer TM, Stanton ML,Young TP. 2003. Competition and coexistence: Exploring mechanisms that restrict and maintain diversity within mutualist guilds. *American Naturalist* 162:63–79.

Peng SL, Zhou HC, Guo SC. 1999. Studies on the changes in interspecific association of zonal vegetation in Dinghushan [in Chinese]. *Acta Botanica Sinica* 41:1239–1244.

Prokonev MH, Zhai RK. 1964. Regeneration of *P. koraiensis* Nakai under forest canopy [in Chinese]. *Practical Forestry Technology* 19:7–8.

Richard KK, Corine FV. 2011. Conspecific density dependence in seedlings varies with species shade tolerance in a wet tropical forest. *Ecology Letters* 14: 503–510.

Rousset O, Lepart J. 2000. Positive and negative interactions at different life stages of a colonizing species (*Quercus humilis*). *Journal of Ecology* 88:401–412.

Schupp EW, Jordano P. 2011. The full path of Janzen-Connell effects: genetic tracking of seeds to adult plant recruitment. *Molecular Ecology* 20(19):3953–3955.

Shu M, Tie N, Xi QH, Liu WJ. 2008. Study on the spatial distribution pattern of *Larix gmelinii* forest. *Forest Resources Management* 3:86–89.

Silvera K, Skillman JB, Dalling JW. 2003. Seed germination, seedling growth and habitat partitioning in two morphotypes of the tropical pioneer tree *Trema micrantha* in a seasonal forest in Panama. *Journal of Tropical Ecology* 19:27–34.

Sugita H, Tani M. 2001. Differences in microhabitat-related regeneration patterns between two subalpine conifers, *Tsuga diversifolia* and *Abies mariesii*, on Mount Hayachine, northern Honshu, Japan. *Ecological Research* 16:423–433.

Takahashi K, Homma K, Vetrova VP, Florenzev S, Hara T. 2001. Stand structure and regeneration in a Kamchatka mixed boreal forest. *Journal of Vegetation Science* 12:627–634.

Tang LN, Li AX, Shao GF. 2011. Landscape-level forest ecosystem conservation on Changbai Mountain, China and North Korea (DPRK). *Mountain Research and Development* 31(2):169–175.

Wang ZF, Peng SL, Liu SZ, Li Z. 2003. Spatial pattern of *Cryptocarya chinensis* life stages in lower subtropical forest [in Chinese]. *Botanical Bulletin of Academia Sinica* 44:159–166.

Wootton JT. 1994. The nature and consequences of indirect effects in ecological communities. *Annual Review of Ecology and Systematic*s 25:443–466.

Wright SJ, Muller-Landau HC, Calderon O, Hernandez A. 2005. Annual and spatial variation in seedfall and seedling recruitment in a neotropical forest. *Ecology* 86:848–860.

Xu HC. 2001. *Natural Forests of* Pinus koraiensis *in China* [in Chinese]. Beijing, China: Forestry Press.

Yang JL, Wang H, Wang L. 2007. Spatial distribution pattern and interspecific association of main tree species in *Pinus tabulaeformis* forest in Ziwuling Mountains [in Chinese]. *Acta Botanica Boreali-Occidentalia Sinica* 27:0791–0796.

Yu SL, Ma KP, Liu CR, et al. 2002. Neighbor diversity and interspecific association of Quercus mongolica. *Chinese Journal of Applied Ecology* 13(3): 271–274 (in Chinese).

Zhang JT. 2004. *Quantitative Ecology* [in Chinese]. Beijing, , China: Science Press.

Zhang ZH, Hu G, Zhu JD, Luo DH, Ni J. 2010. Spatial patterns and interspecific associations of dominant tree species in two old-growth karst forests, SW China. *Ecological Research* 25(6):1151–1160.

Zhang ZY, Tao DD, Li DZ. 2003. An analysis of interspecific associations of *Pinus squamata* with other dominant woody species in community succession [in Chinese]. *Biodiversity Science* 11:125–131.