Tree competition and species coexistence in a Quercus–Betula forest in the Dongling Mountains in northern China

Ji-hua Hou a,b, Xiang-cheng Mi a, Can-ran Liu a, Ke-ping Ma a,*

a Laboratory of Quantitative Vegetation Ecology, Institute of Botany, Chinese Academy of Sciences, Beijing 100093, China
b The Key Laboratory for Silviculture and Conservation of Ministry of Education, Beijing Forestry University, Beijing 100083, China

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ABSTRACT

The population size structure, growth dynamics and mode of competition among adult trees (≥ 4 cm DBH) of six abundant tree species in a 5 ha study plot of a temperate deciduous forest in the Dongling Mountains in northern China were investigated using diffusion and growth dynamics models. In the year of 2000, two dominant species, Quercus liaotungensis and Betula dahurica accounted for ca. 68.69% of the total basal area and 52.71% of the total density of adult plants. Q. liaotungensis, Populus davidiana and Acer mono exhibited inverse J-shaped DBH distributions whereas Betula dahurica, B. platyphylla and Salix caprea had unimodal DBH distributions. One-sided interspecific competition was detected between some species combinations at the scale of the 5 ha study plot, and the competitive effect was mainly size-dependent rather than from species-specific interactions with large individuals in the canopy layer out competing smaller individuals in the understory. Symmetric competition was found between Q. liaotungensis and A. mono only. However, considering the straight line relationship of \( G(t, x) - \sqrt{D(t, x)} \), which suggests that competitive asymmetry is very low or absent, combined with the relatively low mortality of trees with a DBH larger than 4 cm, we speculate that asymmetric interspecific competition was not important in structuring this tree community. Regeneration characteristics of each species are most likely important in regulating species coexistence and stand dynamics in this forest.

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1. Introduction

Competition is the interaction among individuals utilizing a limited resource resulting in reduced fitness in the competing individuals. As a primary mechanism of interaction among plants, competition can occur between species (interspecific competition) or among members of a species (intraspecific competition) utilizing a shared resource (Mackenzie et al., 1998). Competition plays an important role in population and community dynamics (Pacala and Weiner, 1991; Huston and DeAngelis, 1994; Oliver and Larson, 1996), and is thought to contribute to species coexistence and diversity (Bengtsson et al., 1994; Fargione and Tilman, 2002). Although the relationship of competition and coexistence among short-lived species has been studied in manipulated populations under controlled environmental conditions (e.g. Fowler, 1986; Tilman, 1994; Rösch et al., 1997; Stoll and Prati, 2001; Moora et al., 2003), it is much more challenging to characterize the competitive interactions among long-lived species such as trees (Simberloff, 1983; Keddy, 1989).

With the development of increasingly sophisticated competition models and regression techniques, there have been...
an increasing number of studies on competition in forest communities (Robert and Andrew, 2001; Leathwick, 2002; Berger and Hildenbrandt, 2003; Simard et al., 2004). These studies have considered intra- or interspecific competitive effects and the strength and mode of competitive interactions among plant species in non-manipulated multispecies communities (e.g. Hara et al., 1995; Kubota and Hara, 1995; Yoshida and Kamitani, 2000; Nishimura et al., 2002; Takahashi et al., 2003; Bauer et al., 2004). Some investigators have addressed the role of competition in regulating species coexistence in warm-temperate rainforests (e.g. Kohyama, 1993; Manabe et al., 2000). Thus, the role of competition in mixed forests is uncertain, and further studies are required to develop our understanding of the main mechanisms controlling the dynamics of these communities.

Quercus liaotungensis (also known as Q. wutaishanica) is a dominant tree species in the warm temperate zone of China. Oak dominated forests were once widely distributed across northern China, but only a few patches in the low hills and mountains of the region remain today (Chen, 1995). The protection, management and restoration of oak forests are urgently needed, but our understanding of population and community dynamics of these systems is limited. Previous studies have focused primarily on the regeneration properties and ecophysiology of this species and the dynamics of oak populations (e.g. Wang et al., 1999; Li and Ma, 2003; Hou et al. 2004a), but few reports have examined the interactions between and among species. Our recent work has implicated competition as a mechanism regulating the stand dynamics of a Q. liaotungensis and Betula dahurica dominated forest (Hou et al., 2004b). Thus we ask, is intra- and interspecific competition a critical process that facilitates species coexistence in this temperate deciduous forest? In order to elucidate this question, we undertook the present study. Specifically, we 1) quantified the population size structure of six abundant species; and 2) analyzed the growth dynamics of individual adult trees ≥ 4 cm DBH to assess intra- and interspecific competition among species in this forest.

### 2. Methods

#### 2.1. Study site and field measurements

The study site was located in the Dongling Mountains near the Beijing Forest Ecosystem Research Station (40°00’N, 115°26’E; 1300 m asl). The region has a temperate continental monsoon climate with a mean annual temperature of 4.8 °C (January −10.1 °C and July 18.3 °C) and annual precipitation of 612 mm year⁻¹, 78% of which occurs between June and August. Q. liaotungensis forests and Q. liaotungensis co-dominated forests are zonal climax communities. The study site is a mature (approximately 60 years old, with the largest oak tree about 100 years old), secondary forest dominated by Q. liaotungensis and B. dahurica that has been protected since the 1950s.

In July 2000, a permanent 5 ha plot (200 m × 250 m) was established that was further subdivided into 2000 contiguous 5 m × 5 m quadrats. Data were collected during July and August 2000. Within each quadrat, all live individuals were identified by species, tagged and mapped to the nearest 0.1 m. The diameters at breast height (DBH, 1.3 m above the ground), height, and crown diameters of all stems with DBH ≥ 4 cm were measured. The stem DBH of all tagged trees was re-measured in July 2003 and all dead trees and any new recruits that had entered the minimum size class ≥ 4 cm DBH were recorded.

#### 2.2. Data analysis

##### 2.2.1. Intra- and interspecific competition

The effects of intra- and interspecific competition on the growth rate (measured as the change in DBH) of six abundant species (> 200 individuals in the 5 ha study plot) were analyzed (see Table 1) based on the size-structured stochastic model (‘diffusion model’) (Hara, 1984) and growth dynamics model (cf. Yokozawa and Hara, 1992; Hara et al., 1995; Kubota and Hara, 1995). In the diffusion model (Eq. (1)),

\[
\frac{\partial}{\partial t} f(t,x) = \frac{1}{2}\frac{\partial^2}{\partial x^2} \left[ D(t,x)f(t,x) \right] - \frac{\partial}{\partial x} \left[ G(t,x)f(t,x) \right] - M(t,x)f(t,x) 
\]

#### Table 1 - The basal area and density of individual trees (DBH ≥ 4 cm) observed in 2000 and 2003, and the maximum tree size of each species in 2000 in a 5 ha plot in temperate forest in Dongling Mountain in northern China

<table>
<thead>
<tr>
<th>Species</th>
<th>Basal area (m² ha⁻¹)</th>
<th>Density (no. ha⁻¹)</th>
<th>Mortality (%·year⁻¹)</th>
<th>Recruitment (%·year⁻¹)</th>
<th>Maximum DBH (cm)</th>
<th>Species abbreviation</th>
</tr>
</thead>
<tbody>
<tr>
<td>Q. liaotungensis</td>
<td>7.68 8.58</td>
<td>158 160</td>
<td>0.26</td>
<td>0.68</td>
<td>62.0</td>
<td>Ql</td>
</tr>
<tr>
<td>B. dahurica</td>
<td>5.81 5.89</td>
<td>231 215</td>
<td>2.84</td>
<td>0.56</td>
<td>61.5</td>
<td>Bd</td>
</tr>
<tr>
<td>B. platyphylla</td>
<td>2.43 2.69</td>
<td>86 84</td>
<td>1.25</td>
<td>0.55</td>
<td>50.6</td>
<td>Bp</td>
</tr>
<tr>
<td>S. caprea</td>
<td>1.55 1.41</td>
<td>58 49</td>
<td>4.84</td>
<td>0.32</td>
<td>34.0</td>
<td>Sc</td>
</tr>
<tr>
<td>P. davidiana</td>
<td>0.85 1.00</td>
<td>95 94</td>
<td>2.29</td>
<td>2.08</td>
<td>33.1</td>
<td>Pd</td>
</tr>
<tr>
<td>A. mono</td>
<td>0.73 0.86</td>
<td>60 71</td>
<td>0.22</td>
<td>6.20</td>
<td>32.9</td>
<td>Am</td>
</tr>
<tr>
<td>Others</td>
<td>0.60 0.67</td>
<td>50 53</td>
<td>1.31</td>
<td>2.30</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>19.64 21.10</td>
<td>738 725</td>
<td>1.90</td>
<td>1.32</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

*Only species with density ≥ 50 trees ha⁻¹ in 2000 are listed, and species are ranked by basal area in 2000.*
\( f(t, x) \) is the size distribution function of size \( x \) at time \( t \), and \( G(t, x), D(t, x) \) and \( M(t, x) \) are the mean absolute growth rate, the variance of absolute growth rate, and the mortality rate of individuals of size \( x \) at time \( t \), respectively. The \( G(t, x) \) and \( M(t, x) \) functions represent averaged size-dependent species characteristics, whereas the \( D(t, x) \) function represents variation in species characteristics caused by environmental heterogeneity, genetic variation, and variation in the effect of neighborhood competition due to the spatial distribution of individuals. The recruitment rate, \( R(t) \), is the number of individuals entering the population per unit time through the minimum size of the population, \( x_{\min} \), and gives a boundary condition for Eq. (1). Values of \( G(t, x), D(t, x) \) and \( M(t, x) \) were estimated directly from DBH growth data for individual trees of the six abundant species. Individuals of the six species were divided into about 10 DBH size classes, each size class with at least 10 individuals. For each DBH size class, the means and variances of DBH increments from 2000 to 2003 were calculated as well as the mortality rate (i.e., number of dead stems in 3 years/number of initial live stems in 2000). These calculations provided values for \( G(t, x), D(t, x) \) and \( M(t, x) \), respectively, when \( x \) was given as a midpoint value of each DBH size class at time \( t = 2000 \).

The growth model was developed for multi-species forests (Hara, 1992; Yokozawa and Hara, 1992; Hara et al., 1995) to examine the effects of intra- and inter-specific competition on the growth rate of each of \( N \) species, \( k = 1, 2, \ldots, N \):

\[
G_i(t, x) = \frac{x_d - \sum_{j=1}^{N} c_{ij} G_j(t, x) - \sum_{j=1}^{N} c_{ij} G_i(t, x_{\min})}{\Delta x}
\]

(2)

where \( G_i(t, x) \) is the absolute growth rate (DBH increment per year) of species \( k \) of size \( x \) at time \( t \), and \( G_i(t, x) \) is the cumulative basal area (cm\(^2\) m\(^{-2}\)) of neighboring trees of species \( i \) at time \( t \) with DBH > \( x \), and \( x_{\min} \) is the minimal size in the stand. The coefficients \( \Delta x, c_{ij} \), and \( c_{ij} \), are constants. To examine spatial distribution effects on individual growth rates (i.e., distant neighbors have smaller effects on the growth of a focal individual than close neighbors), the distance between individuals was incorporated into the model. Thus, the \( C_i(t, x) \) function in Eq. (2) was given by the following equation,

\[
C_i(t, x) = \sum_{j=1}^{N} \delta_{ij} (y_{ij})^2 (s_{ij})^{-1}
\]

(3)

if \( y_{ij} > x, \delta_{ij} = 1 \); if \( y_{ij} \leq x, \delta_{ij} = 0 \)

where \( y_{ij} \) denotes DBH of the \( j \)th individual of species \( i \) with \( m_i \) individuals and \( s_{ij} \) denotes the distance from the \( j \)th individual to the focal individual of species \( k \) with DBH \( x \) in a circular neighborhood of radius \( S \) m with the focal individual being at the center. Thus, the term \( c_{ij} C_i(t, x) \) with \( c_{ij} > 0 \) in Eq. (2) expresses the effect of suppression on the growth of a focal tree of species \( k \) with DBH \( x \) due only to individual trees of species \( i \) with DBH > \( x \) present in the neighborhood; hence, the coefficient \( c_{ij} (> 0) \) measures the one-sided competitive effect of species \( i \) on species \( k \) (i.e., suppression only by larger individuals). Similarly, \( c_{ij} C_i(t, x) \) with \( c_{ij} > 0 \) expresses the suppression on species \( k \) by all the trees of species \( i \) (both larger and smaller individuals) present in the neighborhood such that the coefficient \( c_{ij} (> 0) \) measures the symmetric competitive effect of species \( i \) on species \( k \). The response of species \( k \) is represented by \( G_k(t, x) \). The direction of the competitive effect is from species \( i \) to species \( k \) if \( c_{ij} > 0 \) or \( c_{ij} < 0 \) for \( G_k(t, x) \). Moreover, if \( c_{ij} > 0 \) or \( c_{ij} < 0 \) holds for \( G_i(t, x) \), the direction of interspecific competition is symmetric (two-sided); otherwise \( c_{ij} = 0 \) and \( c_{ij} = 0 \) for \( G_i(t, x) \), the competitive direction is one-sided from species \( i \) to species \( k \). If \( c_{ij} < 0 \) or \( c_{ij} > 0 \), interspecific relationships are positive (non-competitive) such that the relative growth rate, \( RGR = G(t, x)/x \), of the individual for species \( k \) increases with the abundance of species \( i \) in the same neighborhood. For \( i = k, c_{ij} \), or \( c_{ij} \) are indicators of intraspecific competition, and the competitive direction is also determined by the coefficients of \( c_{ij} \) and \( c_{ij} \), the same mode as mentioned above (symmetric, asymmetric or one-sided).

Eq. (2) includes time \( t \) in \( c_i(t, x) \) and \( c_i(x_{\min}) \). To estimate the coefficients for Eq. (2) from the 3 years of data, it was assumed that the phase average (or ensemble average) was identical to the time average as in thermal physics and statistical dynamics (e.g., see Kittel, 1969). Similar studies have been conducted in various types of forests (e.g., Hara et al., 1995; Kubota and Hara, 1995; Yoshida and Kamitani, 2000). This assumption is reasonable here because the forest under study can be regarded as a mature forest, and climatic conditions over the 3-year study were typical when compared to the 10-year average for the area (Moving t-test, \( t = -0.9239, 0.0139 \) for mean annual temperature and mean total annual precipitation, respectively) (see Afifi and Azen, 1972 for details of this approach).

Multiple linear regressions were used to examine the relationship of growth rates to model parameters of competitive interactions. The DBH increment of each individual tree was used as the dependent variable for \( G_k(t, x) \) and \( x' \), \( x' C_i(t, x) \) and \( x' C_i(t, x_{\min}) \) \((i = 1, 2, \ldots, N) \) were the explanatory variables in Eq. (2) for each of the six abundant species (see Table 1 and Fig. 1) and for the other species combined (i.e., \( N = 7 \)). A forward stepwise method (explanatory variables are entered or removed stepwise one at a time) was used. The \( P \)-value used to enter and to remove an explanatory variable was set at 0.05 or 0.1, respectively. Individual trees within a \((200 - 5) \times (200 - 5) \) m\(^2\) in the center of the 5 ha study plot were used for the analysis. The dependent variables were In-, square-root- or Freeman–Tukey-transformed to have a constant variance of residuals. Extreme outliers were excluded.

### Estimation of the \( G(t, x) \)–\( \sqrt{D(t, x)} \) Relationship and \( M(t, x) \) Function

The \( G(t, x) \)–\( \sqrt{D(t, x)} \) relationships can provide useful information about intra- and inter-specific competition. Usually, a concave relationship suggests strongly asymmetric competition, whereas a straight line \( G(t, x) \)–\( \sqrt{D(t, x)} \) relationship suggests that the degree of competitive asymmetry is very low or absent (Hara et al., 1991; Kubota and Hara, 1995).

The \( G(t, x) \)–\( \sqrt{D(t, x)} \) relationship was obtained from these estimated values for each species. A second-order polynomial regression was applied to the \( G(t, x) \)–\( \sqrt{D(t, x)} \) relationship, where each value was weighted with the sample number of each size class. If the second-order term was not significantly different from 0 (\( P > 0.05 \)), simple linear regression was applied.
2.2.3. Spatial associations among tree species

To get information on the spatial relationships among the six species, we examined their bivariate spatial interactions using the $L_{12}(t)$ function, a transformation of the $K_{12}(t)$ function: $L_{12}(t) = \sqrt{K_{12}(t)/\pi} - t$ (see Diggle, 1983; Upton and Fingleton, 1985 for details). The population independence hypothesis was adopted. A value of $L_{12}(t) = 0$ indicates that the two groups are spatially independent, and values of $L_{12}(t) > 0$ indicate an attractive effect, whilst values of $L_{12}(t) < 0$ indicate a repulsive (negative) effect (Mateu et al., 1998; Goreaud and Pélissier, 2003). The calculations were computed using the ADE-4 package (Thioulouse et al., 1997) in the ADE-4 home-page (http://pbil.univ-lyon1.fr/ADE-4/).

3. Results

3.1. Size structure, growth and mortality

The forest was dominated by two species, Q. liaotungensis and B. dahurica, which accounted for ca. 68.69% of the total basal area of woody stems $\geq 4$ cm in DBH (19.6 m$^2$ ha$^{-1}$) in 2000 (Table 1). Betula platyphylla, Salix caprea, Populus davidiana and Acer mono were canopy species. The density of individuals $\geq 4$ cm DBH was 738 trees ha$^{-1}$, and Q. liaotungensis and B. dahurica accounted for 52.71% of the total number of individuals. Total tree density decreased from 738 to 725 trees ha$^{-1}$ during 2000–2003, but total basal area increased in the corresponding period (Table 2). Most of the six species showed an increase in basal area except S. caprea which declined due to its high mortality. Recruitment and mortality rates were 1.32% and 1.90% year$^{-1}$, respectively, for the stand. The recruitment rate exceeded mortality for Q. liaotungensis and A. mono.

The size frequency distributions differed among the six species. Q. liaotungensis had an inverse J-shaped DBH distribution with a decline in the 4–8 cm DBH size class. P. davidiana and A. mono also showed strong inverse J-shaped patterns. These three species had abundant numbers of seedlings, saplings and adults. In contrast, B. dahurica, B. platyphylla and S. caprea showed unimodal DBH distribution with few seedlings or saplings (Fig. 1).

The directly estimated $G(t, x)$ for DBH ($= x$) differed significantly among the six abundant tree species (ANCOVA with the covariate ln $x$, Fig. 2). There were significant differences
in the $G(t, x)$ function between $P. davidiana$ and other species, and between $A. mono$ and other species ($P < 0.05$), but no significant differences were found between other combinations (Scheffé test, Table 2). The growth rates of $P. davidiana$ and $A. mono$ were significantly lower than the other species. There were significant differences in the $G(t, x) - \sqrt{D(t, x)}$ relationship between the following species pairs: $P. davidiana$ and $B. dahurica$, $A. mono$ and $B. dahurica$, $B. dahurica$ and $B. platyphylla$ combinations (ANCOVA, $P < 0.05$; Table 2 and Fig. 3).

However, there were no significant differences detected among other combinations (Scheffé test, Table 2). The $G(t, x) - \sqrt{D(t, x)}$ relationship for all six species was linear suggesting that tree competition was symmetric or absent in these species. There were no significant differences in the $M(t, x)$ function based on DBH except for the species combinations with $S. caprea$ (Table 2 and Fig. 4).

### Table 2 – Statistical results for post hoc tests of the relationship between DBH in 2000 and $G(t, x)$, between $G(t, x)$ and $D(t, x)$, and between DBH in 2000 and $M(t, x)$ among six abundant species (the results are expressed as $P$-values; blanks indicate non-significant differences by Scheffé tests). Species codes are as for Table 1.

<table>
<thead>
<tr>
<th>Species code</th>
<th>DBH in 2000 vs. $G(t, x)$</th>
<th>$G(t, x)$ vs. $D(t, x)$</th>
<th>DBH in 2000 vs. $M(t, x)$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ql</td>
<td>Bd</td>
<td>Bp</td>
<td>Sc</td>
</tr>
<tr>
<td>Ql</td>
<td>0.000</td>
<td>0.001</td>
<td>0.031</td>
</tr>
<tr>
<td>Bd</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bp</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sc</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pd</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Am</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

### Fig. 2 – The relationships between DBH in 2000 and the mean annual absolute growth rate $G(t, x)$ of DBH from 2000 to 2003 for six abundant tree species. ▽: Q. liaotungensis, ▼: B. dahurica, ●: B. platyphylla, ○: S. caprea, □: P. davidiana, ○: A. mono.

### Fig. 3 – The relationship between mean absolute growth rate $G(t, x)$ of DBH from 2000 to 2003 and square-root of the variance in absolute growth rate $D(t, x)$ of DBH for six abundant species. Symbols are as shown in Fig. 2. The $G(t, x)$ and $D(t, x)$ values were directly estimated from the field data. The linear regression for all the species together was: $\sqrt{D(t, x)} = (0.0032 \pm 0.0279) + (0.8028 \pm 0.0867) G(t, x)$, $R = 0.7671$, $P < 0.0001$.

### Fig. 4 – The relationship between DBH in 2000 and observed mortality rates from 2000 to 2003 for the six abundant species. △: Q. liaotungensis, ●: B. dahurica, ●: B. platyphylla, ○: S. caprea, □: P. davidiana, ○: A. mono.
The effects of intra- and interspecific competition on growth rates were examined by multiple linear regression analysis. For each species \( k (k = 1, 2, \ldots, 6) \), one to two explanatory variables out of 15 entered into the regression were significant \((P < 0.05)\) (Table 3). The direction of interspecific competition was generally one-sided: from S. caprea to B. platyphylla and to B. dahurica, from B. dahurica to Q. liaotungensis, from Q. liaotungensis to A. mono, and from A. mono to P. davidiana. In all cases, interspecific competitive effects were asymmetric, with the exception of competitive interactions between Q. liaotungensis and A. mono which were symmetric. No evidence of intraspecific competition was detected in any of the species. For all six species, the coefficient \( a_0 \) was entered first in the stepwise regression and was significantly correlated with \( G_k (t, x) \) \((P < 0.001)\), indicating the strong size effects on the growth of the six species.

### 3.2. Growth and mode of tree competition

Bivariate analysis of the six species was conducted at the scale of 0–100 m. Repulsive effects were detected between Q. liaotungensis and four other species: Q. liaotungensis vs. B. dahurica at small scales (0–5 m), and Q. liaotungensis vs. B. platyphylla, S. caprea, and P. davidiana at relatively larger scales (5–35 m) (Table 3). Attraction effects were found between B. platyphylla and S. caprea only at the scale of 15–55 m. At other scales, these species were spatially independent.

### 4. Discussion

#### 4.1. Interspecific competition between adult trees

In the present work, one-sided interspecific competition was found between some species of adult trees (≥4 cm DBH) in this temperate forest (Table 4). The one exception was for Q. liaotungensis and A. mono where symmetric competition was found to predominate. Asymmetric competition for nutrients and light was due to size differences among individuals, rather than species differences, which should lead to size-dependent growth and mortality (Ford and Diggie, 1981; Hara, 1985; Schmitt et al., 1987). Higher mortality rates \( M (t, x) \) among smaller sized individuals (Fig. 4) offered further evidence of size-dependent growth and mortality.

### Table 3 – The competition effects of species \( i \) on DBH increment of individual trees of species \( k \) from 2000 to 2003 \([G_k (t, x)]\) in the 5 ha permanent plot of the temperate forest, in Dongling Mountain in northern China

<table>
<thead>
<tr>
<th>( G_k (t, x) )</th>
<th>( a_0 )</th>
<th>( Q_l (t = 1) )</th>
<th>( Bd (t = 2) )</th>
<th>( Bp (t = 3) )</th>
<th>( Sc (t = 4) )</th>
<th>( Pd (t = 5) )</th>
<th>( Am (t = 6) )</th>
<th>Adjusted ( r^2 ) for final model</th>
<th>Increase in ( r^2 ) for ( a_0 )</th>
</tr>
</thead>
<tbody>
<tr>
<td>( Q_l (k = 1) )</td>
<td>0.001</td>
<td>0.080</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.762</td>
<td>0.759</td>
</tr>
<tr>
<td>( Bd (k = 2) )</td>
<td>0.000</td>
<td></td>
<td>0.017</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.512</td>
<td>0.507</td>
</tr>
<tr>
<td>( Bp (k = 3) )</td>
<td>0.000</td>
<td></td>
<td>0.010</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.630</td>
<td>0.672</td>
</tr>
<tr>
<td>( Sc (k = 4) )</td>
<td>0.001</td>
<td></td>
<td></td>
<td>0.011</td>
<td></td>
<td></td>
<td></td>
<td>0.595</td>
<td>0.587</td>
</tr>
<tr>
<td>( Pd (k = 5) )</td>
<td>0.001</td>
<td></td>
<td></td>
<td></td>
<td>0.011</td>
<td></td>
<td></td>
<td>0.595</td>
<td>0.587</td>
</tr>
<tr>
<td>( Am (k = 6) )</td>
<td>0.001</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.011</td>
<td></td>
<td>0.595</td>
<td>0.587</td>
</tr>
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The effects were expressed by the P-values of \( a_0 \) (size effect), \( C_1 \) (one-sided competitive effect) and \( C_2 \) (symmetric competitive effect) in Eq. (2) for each abundant species, \( k \). Multiple linear regression analysis was conducted using forward stepwise method. The DBH increment was either ln-, square-root- or Freeman-Tukey-transformed to have a constant variance of residuals. The \( r^2 \)-values for the final models were d.f.-adjusted. Blank indicates explanatory variable was not entered into the regression \( (i.e., \text{the coefficients is 0}) \). Species codes are as for Table 1.

### Table 4 – Spatial associations among the six abundant species using binary point pattern analysis \( L_{1,2} (t) \) in the 5 ha plot in Dongling Mountain in northern China. The significant departure from independent association is considered based on 1000 Monte Carlo simulations. Bivariate analyses of six species were conducted at the scale of 0–100 m. A and R denote significant \((P < 0.01)\) attraction or repulsion effect at the scale \( t \), respectively; and – denotes an independent association at the scale \( t \) \((P < 0.01)\)

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evidence of asymmetric competition in this forest. Similar patterns of competition also have been found in a warm-temperate evergreen broad-leaved forest (Nishimura et al., 2002) and a warm-temperate rain forest (Kohyama, 1992, 1993). However, considering the straight-line relationship of $G(t, x) \sim \frac{DN(t, x)}{x}$ and relatively low mortality of trees larger than 4 cm DBH, we speculated that asymmetric interspecific competition was too weak to act as an important force structuring this tree community. And trees could grow and survive once over 4 cm in DBH. Interspecific competition also was found to have minor effects on the growth rates of adult trees in a deciduous broad-leaved forest and conifer-hardwood mixed forest in Japan (Hara et al., 1995; Kubota and Hara, 1995; Takahashi et al., 2003). A possible reason for the weak competition in this forest might be the low density of trees (738 trees ha$^{-1}$ in 2000).

The weak interspecific competitive interactions among trees were reflected in their spatial distribution patterns. A repulsive spatial association at small scales (< 5 m) was found between adult trees of Q. liaotungensis and B. dahurica suggesting the existence of interspecific competition only between these two species. No other interspecific competitive interactions were inferred based on the spatial analyses; however, these results seemed inconsistent with the growth dynamic results. This failure could be due to other factors, such as habitat patchiness, which obscured spatial associations caused by competition-based assembly rules (Callaway, 1998). However, the repulsive spatial associations between Q. liaotungensis and the four other species at large scales indicated that Q. liaotungensis preferred different establishment sites as compared to the other species. Q. liaotungensis is a xerophytic species and was located mainly on mountain ridge tops and south-facing slopes in our permanent plot. Little is known about the habitat preferences of the other five species, and further studies on their ecological properties are needed.

4.2. Size structure and stand dynamics

Given that interspecific competition was weak in this forest, the question arises: what processes control the stand dynamics of this forest? The forest structure analysis, such as the shape of the size frequency distribution, provided useful information on the ecological characteristics of this forest (Knowles and Grant, 1983; Nakashizuka, 1991). Analysis of growth pattern of the six species suggested that though there were some significant differences in the growth rates among the six abundant tree species, their relatively high growth rates might indicate that the growth rate is not a limiting factor for regeneration capacity in this forest. Similarly, there were few significant differences in the mortality patterns of the six species. But size had a strong effect on an individual’s growth (Tables 2 and 4 and Figs. 3 and 4). These results suggest that growth or mortality would contribute little to species coexistence in this forest. However, there were distinct differences in regeneration properties of the six tree species. Two of the dominant species, Q. liaotungensis and B. dahurica, had different regeneration patterns (Table 4 and Fig. 1). Q. liaotungensis had an inverse J-shaped DBH distribution with a small decline in saplings in the 4–8 cm DBH size class. This decline might be the result of high mortality of saplings due to intense competitive effects from siblings or canopy individuals (Wang et al., 1999), or could be an artifact of the change in methods used to measure tree size, from height measurements of individuals < 4 cm DBH to DBH measurements of individuals ≥ 4 cm DBH (Gao et al., 2001). Similar population size structures and regeneration patterns were reported for other Q. liaotungensis forests and Q. ilex forests (Wang et al., 1999; Pulido et al., 2001). Nevertheless, the abundant seedling and sapling populations of Q. liaotungensis indicate continuous regeneration that should ensure the long-term persistence of the population. In contrast, B. dahurica showed a unimodal distribution with an abundant number of adult trees in the 4–16 cm DBH size class but very few seedlings (Fig. 1). The paucity of seedlings and the high mortality rate of young B. dahurica trees indicated that the present environmental conditions of the stand are not favorable for the establishment and recruitment of this species from seeds. B. dahurica most likely requires large-scale disturbances for a new cohort of seedlings to become established resulting in temporal patterns of intermittent regeneration. B. dahurica had a large sapling population probably due to its ability to regenerate by sprouting (Zhou and Zu, 1997).

The population size structure of B. platypylla and S. caprea indicate a lack of seedlings and saplings in these populations. The small number of A. mono and P. davidiana adult trees were restricted to small size classes suggested their recent establishment in this stand. The large number of seedlings and saplings of these two species combined with their increasing numbers of adults suggested that if A. mono and P. davidiana reach maturity they could threaten the dominance of Q. liaotungensis and B. dahurica in this stand.

In summary, the above analyses suggested that the recruitment over 4 cm DBH might be a determinant process in the stand dynamics of this forest, and the process from seeds to seedlings/saplings and from seedlings/saplings to adults requires more attention in further studies.

It has been shown in temperate forests that the role of competition in species coexistence becomes weaker with increasing latitude and regeneration processes increasingly important in regulating species coexistence (Hara et al., 1995; Kubota and Hara, 1995; Takahashi et al., 2001; Nishimura et al., 2002). Compared to a warm temperate rain forest reported by Kohyama (1993), the role of competition in regulating species coexistence is weaker in this Q. liaotungensis–B. dahurica codominated temperate deciduous forest. Combining our size structure and spatial analyses, we confirm that competition in this forest plays a weak role in regulating species coexistence. Regeneration properties of each species, especially recruitment limitations, may be the key factor affecting the dynamics of species coexistence in this forest.

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