



Neighborhood analysis of underplanted Korean pine demography in larch plantations: Implications for uneven-aged management in northeast China



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ABSTRACT

Quantifying the growth and survival of underplanted Korean pine (*Pinus koraiensis* Sieb. et Zucc.) in existing plantations provides a critical step toward developing an uneven-aged management system in northeast China. We conducted neighborhood analysis to quantify the effect of individual-level competition on the growth and survival of underplanted Korean pines in larch plantations (*Larix olgensis* A. Henry and *Larix kaempferi* [Lamb.] Carr.). The growth rate depended significantly on target tree size and the strength of competition from neighboring trees, whereas survival depended solely on tree size. The survival rate increased sharply with increasing tree size, and trees that had reached ca. 3 cm in diameter at a height of 0.3 m rarely died, even under strong competition. The effect of competition from neighbors on growth was determined by the neighboring tree's size and its spatial relationship with the target tree. Neighbors located near and southwest of the target tree produced stronger competition than trees at greater distances and different azimuths. Our simulation in which Korean pines were underplanted in strip openings showed that their growth rates increased with increasing strip width. The growth rate was also related to the strip's azimuth and the underplanting position within the opening. The results indicate that planting Korean pines in northwest to southeast strips would create a more heterogeneous size structure than planting in northeast to southwest strips. Our results suggest that spatial factors such as strip width, strip direction, and planting position strongly influence the development and productivity of uneven-aged Korean pine–larch stands.

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1. Introduction

Since 1949, China has implemented the largest afforestation program in the world, and has created the world's largest area of plantation forest (64.5 million ha; FAO, 2010). These plantations are beginning to play an important role in producing timber products for both domestic use and export (Wang et al., 2007), as well as in providing ecosystem services such as soil protection (Wang, 2004) and carbon storage (Fang et al., 2001). For these plantations to continue meeting China's economic and ecological objectives, the establishment of an uneven-aged management system has grown in importance (Liu et al., 2005; Lei et al., 2007; Shang et al., 2010). In contrast with a single-age plantation managed by clear-cutting, the uneven-aged system generates a more complex

forest structure (Schütz, 2002) that could produce higher timber revenue as well as a more steady flow of ecosystem services (Laiho et al., 2011).

In northeast China, one of the increasingly important ways to create uneven-aged stands is to underplant Korean pine (*Pinus koraiensis* Sieb. et Zucc.) in larch plantations after thinning (Shang et al., 2010). Larch species such as *Larix olgensis* A. Henry and *Larix kaempferi* (Lamb.) Carr. are the major plantation tree species in this region (Liu et al., 2005). Korean pine is an economically and ecologically important tree species in temperate and cool-temperate forests across East Asia (Piao et al., 2011). Korean pine contributes greatly to conserving regional biodiversity by serving as a food source for at least 22 wildlife species (Hutchins et al., 1996). Its wood and seeds (pine nuts) are an important revenue source for local residents (Piao et al., 2011). In northeast China, however, the tree density of Korean pine in natural forests has declined dramatically owing to excessive timber harvesting (Yu et al., 2011) and

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seed collection (Li et al., 2012). It has thus become increasingly important to secure this resource by means of planting (Liu and Wang, 2011; Li et al., 2012).

The growth and survival of understory trees depend strongly on the overstory canopy conditions (Kobe et al., 1995; Cole and Newton, 2009). Previous studies of underplanted trees have analyzed the effect of the post-thinning overstory structure on tree demography at a stand level (e.g., Maas-Hebner et al., 2005; Chan et al., 2006; Cole and Newton, 2009). However, to our knowledge, no study has focused on an individual-tree level. In managed forests, the intensity and spatial pattern of thinning drastically change the understory environment, which is primarily affected by the stem size of neighboring trees, the distance between a focal point (e.g., an individual target tree) and its neighbors, and the direction from that focal point to neighboring trees (Sprugel et al., 2009; Beaudet et al., 2011). Therefore, detailed modeling of the growth and survival of underplanted trees would require a distance-dependent individual-based approach.

In this study, we quantified the growth and survival of underplanted Korean pine in larch plantations by using neighborhood analysis. Neighborhood analysis is based on the assumption that fine-scale spatial competition among individual trees regulates forest dynamics (Canham and Uriarte, 2006). Our specific objectives were: (i) to quantify the effects of individual-level factors (i.e., tree size, distance between a neighboring tree and the target tree, and direction from a neighboring tree to the target tree) on the growth and survival of underplanted Korean pine, and (ii) to illustrate the response of Korean pine under varying conditions of size, density, and spatial distribution of the overstory larches. Our results represent a critical step toward securing China's Korean pine resource, and provide insights into managing the massive area of plantation forests in China by means of an uneven-aged system.

2. Materials and methods

2.1. Study site

We conducted our study in the Dabianguou Forest Farm of Qingyuan County, Liaoning Province, China (41°59' to 42°04'N, 124°59' to 125°10'E). The forest is located in a temperate zone (Yu et al., 2011). The mean annual temperature and annual precipitation are 5.0 °C and 700–800 mm, respectively (Shang et al., 2010). The typical soil type is a brown forest soil.

In June 2012, we established 12 study plots at the study site (Table S1). The plots were scattered across the study site (Fig. S1). The distance between plots ranged from 0.03 to 7.2 km, with a mean of 2.9 km. The elevation of the plots ranged from 448 to 544 m a.s.l. The plots were rectangular, with the area and the length of their sides ranging from 142 to 612 m² and from 10.5 to 25.5 m, respectively.

The most important criterion in choosing the study plots was to cover a wide range of overstory canopy conditions and stem sizes of the component trees. Plots 1–5 were stands in which Korean pines were underplanted in 2008 within the openings created by thinning in the larch plantations. The width of the strips in each plot was 4.5–7.5 m. The tree age of the larches in each plot ranged from 12 to 43 years. Plot 6 was a site where Korean pines were planted in a clear-cut at 2007. The height of all of the pine saplings in plots 1–6 was <1.3 m. We selected plots 1–5 and plot 6 as study plots to collect the data on pine saplings growing under a moderate canopy density and under no competitive stress, respectively. Plots 7–10 were two-storied stands with larch in the overstory and Korean pine in the understory. The overstory larches were distributed randomly in the stands as a result of thinning from below. The height of all larches and pines was ≥ 1.3 m. The diameter at breast

height (DBH) of the Korean pines in plots 7–10 ranged from 3.0 to 35.5 cm. We selected plots 7–10 to collect the data on small to medium-sized pines growing under a moderate canopy density. Plots 11 and 12 were Korean pine plantations. The stand ages were 20 and 43, respectively. The ranges of DBH in each plot were 9.4–24.3 cm and 18.8–37.2 cm, respectively. We selected plots 11 and 12 to collect data on medium-sized pines growing under moderate to high canopy density. Although plots 6, 11, and 12 did not have an uneven-aged structure, we chose them to fill the gaps in our data and to cover a broader array of forest attributes. The overstory larch species in plots 1–5 and 7–10 were either *L. olgensis* or *L. kaempferi*. Due to their similar morphological traits, however, we could not identify the species in the field.

2.2. Data collection

We measured the DBH for all trees with height ≥ 1.3 m within the study plots. The locations (*x–y* coordinates) of all saplings and trees were measured with 0.1-m accuracy using a compass, a clinometer, and a laser rangefinder. In plots 1–6, we measured the annual height growth of all Korean pine saplings (height <1.3 m) during the preceding years to the nearest 1 cm. In plots 7–12, we obtained increment cores from 4 to 6 Korean pines at the lowest possible height (0.3 m) in each plot. The cores were taken from two opposite directions from each tree. Using the cores, we measured the annual ring growth from 2007 to 2011 to the nearest 0.01 mm by means of a microscope with a stage micrometer. The mean value of the growth in the two core directions was used for our analyses. In total, we measured 181 annual height growths from 97 saplings and 150 annual diameter growths from 31 trees. Before our analysis, we estimated the diameter of the saplings in each year by using a diameter–height allometric equation (Eq. S1; Fig. S2), because diameter growth was used as a variable in subsequent analyses. Since the diameter growth in 2012 was not complete at the time of our measurements, we excluded these data from our analyses. The diameter of the sampled trees ranged from 0.183 to 29.686 cm, with a mean of 6.605 and an SD of 8.158. The diameter growth rate ranged from 0.44 to 11.72 mm year⁻¹, with a mean of 2.84 and an SD of 1.64 (Fig. S3).

We also counted the number of live and recently dead Korean pines in the study plots. Recently dead trees were defined as trees that had died since 2007. We identified these individuals in the field by examining the leaf retention and twig suppleness of each tree, similar to the sampling method described by Kobe et al. (1995). Because we could not identify the cause of the death, we simply recorded it as a binary variable (i.e., dead or alive). In total, we observed 43 recently dead saplings and 85 live saplings, and no recently dead trees and 148 live trees.

2.3. Statistical modeling

We used hierarchical Bayesian models to analyze the growth and survival of the Korean pines. In this section, we describe the model structure, starting from the simplest model that used the target tree's diameter as the sole explanatory variable, and subsequently discuss more complex models that included competition from neighbors as an explanatory variable.

Given that growth is non-negative, we assumed that the logarithm of the diameter growth rate (G_{ij} , mm year⁻¹, based on the diameter at 0.3 m above the ground) of target tree i in year j would follow a normal distribution:

$$\ln(G_{ij}) \sim \text{Normal}[\ln(\bar{G}_{ij}), \sigma] \quad (1)$$

where \bar{G}_{ij} is the expected annual diameter growth rate (mm year⁻¹) of the target tree, and σ is the variance of the diameter distribution.

We expressed the effect of the target tree's diameter on the relative growth rate using the Gompertz growth function (Zeide, 1993):

$$\ln \left(\bar{G}_{ij} / D_{ij}^{[t]} \right) = \alpha_0 + \alpha_1 D_{ij}^{[t]} + \varphi_{i_i} \quad (2)$$

where $D_{ij}^{[t]}$ is the diameter at 0.3 m above the ground (cm) of target tree i in year j , α_0 and α_1 are parameters, φ_{i_i} is a random parameter for individual trees, and I_i is the identification number for tree i (1, 2, ..., 128). We included φ_{i_i} in the model because we took up to five replicates of annual growth from each of the 128 sampled trees (i.e., pseudo-replication). The parameter was defined to have a hierarchical structure: $\varphi_z \sim \text{Normal}(0, \tau^2)$ and $\tau \sim \text{Uniform}(0, 10000)$, where $z = 1, 2, \dots, 128$ and τ is the variance of φ_z . Here, the value φ_z is estimated separately for individual trees, but still accounts for the variation among the trees.

We assumed that the survival status of target tree i , denoted S_i (where $S_i = 1$ and $S_i = 0$ correspond to live and dead trees, respectively), to follow a Bernoulli distribution:

$$S_i \sim \text{Bernoulli}(\bar{S}_i) \quad (3)$$

where \bar{S}_i is the expected annual survival rate (year^{-1}) of the target tree.

We used a complementary log–log (CLL) link function to examine the effect of a target tree's diameter on its annual survival rate:

$$\text{cloglog}(\bar{S}_i) = \beta_0 + \beta_1 D_i^{[t]} + \ln(T_i) \quad (4)$$

Where $D_i^{[t]}$ is the initial diameter at 0.3 m above the ground (cm) of target tree i , T_i is the number of years after planting (4 years in plots 1–5, 5 years in plot 6) or the number of years chosen to define recently dead trees (i.e., 5 years), and β_0 and β_1 are parameters. The values of $D_i^{[t]}$ of the saplings in plots 1–6 were set to 0, since their heights were less than 0.3 m at the time of planting. For trees in plots 7–12, $D_i^{[t]}$ were estimated by using a diameter–DBH allometric equation (Eq. S2). The CLL link function allows the simultaneous use of data with different time intervals by means of an offset variable (Rose et al., 2006); the term $\ln(T_i)$ is the offset variable in Eq. (4).

For the remaining candidate models, the growth and survival of the target tree were predicted as functions of neighborhood competition as well as of the target tree's diameter:

$$\ln \left(\bar{G}_{ij} / D_{ij}^{[t]} \right) = \alpha_0 + \alpha_1 D_{ij}^{[t]} + \varphi_{i_i} + \alpha_2 \text{NCI}_i \quad (5)$$

$$\text{cloglog}(\bar{S}_i) = \beta_0 + \beta_1 D_i^{[t]} + \ln(T_i) + \beta_2 \text{NCI}_i \quad (6)$$

where NCI_i is a neighborhood competition index for target tree i , which is defined in detail in the rest of this section.

By modifying the functional form of NCI step by step, we tested three different hypotheses about how the strength of competition from neighbors on a target tree is determined. As the basis of all NCI equations, we used an index developed by Canham et al. (2004), in which the total competitive effect on a target tree is expressed as the summation of the effects of individual neighboring trees. Neighboring trees were defined as those individuals located within 10 m of a target tree. We selected this neighborhood radius on the basis of results from previous neighborhood analyses, which showed that the competitive effect of neighbors farther than 10 m from a target tree are negligible (Thorpe et al., 2010; Luu et al., 2013; Tatsumi et al., 2013). Under this definition, target trees located within 10 m of the nearest plot edge had incompletely mapped neighbors (i.e., some neighbors lay outside the plot). To account for this, we considered the plot to represent the surface of a torus; that is, each plot edge was connected to the edge on the opposite side of the plot. There are several alternative approaches to address such problems with censored neighborhood

data (Canham and Uriarte, 2006). However, we assumed that the use of a torus plot would be the most appropriate approach for our study, based on our observations in the field and in aerial photographs that the stand structure of the surrounding areas was similar to that inside the plots.

The simplest hypothesis that we tested assumed that the competition strength of an individual neighbor was determined by its DBH and by its distance from the target tree. The total competitive effect of neighbors on target tree i was expressed as follows:

$$\text{NCI}_i = \sum_{k \in N_i} \exp \left[\gamma_1 \ln \left(D_k^{[n]} \right) + \gamma_2 M_k \right] \quad (7)$$

where N_i is the set of identification numbers for the neighbors of target tree i , $D_k^{[n]}$ is the DBH (cm) of neighboring tree k , M_k is the distance (m) from the target tree to neighboring tree k , and γ_1 and γ_2 are parameters. For $D_k^{[n]}$, we used the DBH value in 2012 for all trees based on the assumption of a small proportional change in the DBH of neighbors in the most recent 5 years. We refer to Eq. (7) as the “simple NCI” model.

Many stand-level studies have shown strong evidence for the existence of an environmental gradient within an opening in the stand (e.g., Kuuluvainen, 1994; Canham et al., 1990), and thus the position of the target tree within an opening could have a considerable effect on sapling demography (Coates, 2000). To determine whether these findings extended to the level of individual trees, we tested a form of NCI that includes the azimuth between the target tree and neighbors as an explanatory variable (henceforth, the “azimuth-dependent NCI” model):

$$\text{NCI}'_i = \sum_{k \in N_i} \exp \left[\gamma_1 \ln \left(D_k^{[n]} \right) + \gamma_2 M_k + \ln \left(1 + \gamma_3 \cos \theta_k + \gamma_4 \sin \theta_k \right) \right] \quad (8)$$

where θ_k is the azimuth (measured clockwise from north, at 0°) of neighboring tree k as seen from a target tree, and γ_1 – γ_4 are parameters. The newly added term allows the competition strength of neighbors to fluctuate so that it has a peak at azimuth x and a minimum at the opposite azimuth, $x - 180^\circ$. The parameters γ_3 and γ_4 determine the value of x as well as the magnitude of the variation in the competition strength.

The last hypothesis that we tested (henceforth, the “full NCI” model) was whether the diameter of the target tree ($D_i^{[t]}$) has an influence on NCI. The effect of $D_i^{[t]}$ may be negative (i.e., small trees are more affected by competition than large trees) as a result of asymmetric competition (Weiner and Thomas, 1986), or positive, which reflects the change in shade tolerance in response to changes in the life history stage (Sun et al., 2009; Yu et al., 2011):

$$\text{NCI}''_i = \sum_{k \in N_i} \exp \left[\gamma_1 \ln \left(D_k^{[n]} \right) + \gamma_2 M_k + \ln \left(1 + \gamma_3 \cos \theta_k + \gamma_4 \sin \theta_k \right) + \gamma_5 D_i^{[t]} \right] \quad (9)$$

where γ_5 is a parameter.

2.4. Parameter estimation and model selection

To estimate the posterior distributions of the parameters, we used the Markov-chain Monte Carlo (MCMC) method implemented by the OpenBUGS 3.2.2 software (Lunn et al., 2009) via the R2OpenBUGS package (Sturtz et al., 2005) in the R 3.0.2 software (R Core Team, 2013). For each model, we obtained posterior samples using three independent MCMC samplings, in each of which 500 values were sampled with a 100-step interval after a burn-in period of 1000 MCMC steps. The convergence of the MCMC calculations was confirmed by evaluating the Gelman and Rubin \hat{R} parameter (Gelman et al., 2004). Convergence occurred when the \hat{R} value of all the model parameters was less than 1.1.

We used subjective priors for the prior distributions of the parameters γ_1 and γ_2 to support their convergence (Table S2). We set their mean and variance based on the results of our previous study (Tatsumi et al., 2013), in which we analyzed the neighborhood competition by using NCI with a similar functional form as in Eq. (7). Although the previous study was conducted in a different region (a cool-temperate forest in Japan; Tatsumi et al., 2013), we assumed that the change in the neighbor's competition strength in response to its DBH (determined by parameter γ_1) and to its distance from the target tree (parameter γ_2) would not differ dramatically between the sites. We used non-informative priors for other parameters (Table S2).

For model selection, we first fitted four candidate models, defined on the basis of combinations of the two response variables (growth and survival) and two NCI models (without NCI and simple NCI), to the data (Table 1, combined models 1–4). When any of the combined models that included the simple NCI (combined models 2–4) was selected, we further tested the significance of adopting the modified form of NCI (azimuth-dependent NCI and full NCI). We used the deviance information criterion (DIC; Spiegelhalter et al., 2002) for model selection. The combined model with the lowest DIC value was considered the best model. Models with a DIC value within 4 units of the lowest DIC value were also considered to have substantial support (McCarthy, 2007).

2.5. Simulating the competitive effects of neighbors on Korean pine demography

The demography of the target tree was expected to have a wide range of values under a potentially infinite number of possible combinations of neighbor parameter values (i.e., DBH, distance, and azimuth). To illustrate the effect on tree demography under such diverse conditions, we conducted simulations that assumed two different potential management scenarios at the study site: (i) Korean pine underplanted in the larch plantation with a uniform distribution of larch (Fig. 1A), and (ii) Korean pine underplanted in the openings created by strip thinning in the larch plantations (Fig. 1B and C). In scenario i, we simulated the growth of Korean pine under a range of larch DBHs (10–40 cm) and larch densities (defined as the shortest distance between individual trees, 2–5 m). In addition to these two factors, scenario ii also considered the effects of strip width (4–14 m) and strip direction (from northeast to southwest or from northwest to southeast). The simulations predicted the growth of a Korean pine with a diameter of 2 cm located at 2 m from each edge of the strip openings (a, b, c, and d in Fig. 1). We used the best selected model and the associated parameter estimates for the prediction.

3. Results

3.1. Model selection and goodness of fit

All of the associated parameters of the tested models adequately converged ($\hat{R} < 1.1$). The best model selected on the basis

of the DIC value was the model in which growth and survival were expressed by using the azimuth-dependent NCI and no NCI, respectively (Table 1, combined model 5, DIC = 503.8). In addition to model 5, the model that expressed growth and survival using simple NCI and no NCI, respectively (combined model 2, DIC = 504.9), and the model that expressed both variables using simple NCI (combined model 4, DIC = 505.8) had substantial support. Table 2 shows the parameter estimates for combined model 5. Posterior distributions of the parameters that determine the influence of azimuth (γ_3 and γ_4) included a value of 0. This indicates that, although the model selection based on DIC suggests these extra parameters are warranted, it does not mean that the combined model 5 is better than models 2 and 4 (which lack the azimuth parameter) in an absolute sense.

Combined model 5 and its parameter estimates provided a good fit to the observed data; the R^2 value between observed and predicted growth was 0.670 (Fig. 2), and the accuracy of the live–dead classification was 69.2% (Table S3, trees with a predicted survival rate of $\hat{S}_i \geq 0.5$ were classified as live). Combined models 2 and 4 provided comparable fit to the growth rate ($R^2 = 0.666$ and 0.668 , respectively) and the same classification accuracy for survival rate (69.2%).

3.2. Effects of target tree diameter and competition strength on growth and survival

Fig. 3 shows the effects of target tree diameter and competition strength on growth and survival, estimated by using combined model 5. The estimated NCI value ranged from 0 to 261.8, with a mean of 106.4 and an SD of 71.7. The relative diameter growth rate of the target tree was negatively correlated with the tree's diameter and NCI (Fig. 3A). The predicted survival rate increased sharply with increasing diameter (Fig. 3B). This result reflects the fact that all of the dead trees we observed during our field measurements had an initial height smaller than 0.3 m (i.e., $D_i^{(t)} = 0$).

3.3. Effects of neighboring tree's diameter and location on competition strength

In combined model 5, the competition strength of an individual neighbor was explained by its DBH, its distance from the target tree, and its azimuth from the target tree. The competition strength of the neighbor increased with increasing DBH (Fig. 4A). For example, a neighbor with a 30-cm DBH exerted 3.9 times the competition strength of a neighbor with a 10-cm DBH. The competition strength decreased rapidly with increasing distance from the target tree (Fig. 4B). For instance, a neighbor located 1 m from the target tree had 5.5 times the strength of a neighbor located 5 m away, and 45.4 times that of a neighbor located 10 m away. The competition strength peaked when a neighbor was located at an azimuth of 223.9° from the target tree and reached its minimum at 43.9° (Fig. 4C), which almost exactly corresponded to southwest and northeast directions, respectively. For example, neighbors with an azimuth of southeast (135°), southwest (225°), and northwest

Table 1

Differences in the deviance information criterion (Δ DIC) between the combined models of Korean pine growth and survival. Δ DIC for the model with the lowest DIC is 0.

Combined model number	NCI used in the model		Equation numbers		DIC	Δ DIC
	Growth	Survival	Growth	Survival		
1	Without NCI	Without NCI	2	4	522.9	19.1
2	Simple NCI	Without NCI	5 and 7	4	504.9	1.1
3	Without NCI	Simple NCI	2	6 and 7	525.0	21.2
4	Simple NCI	Simple NCI	5 and 7	6 and 7	505.8	2.0
5	Azimuth-dependent NCI	Without NCI	5 and 8	4	503.8	0
6	Full NCI	Without NCI	5 and 9	4	512.3	8.5

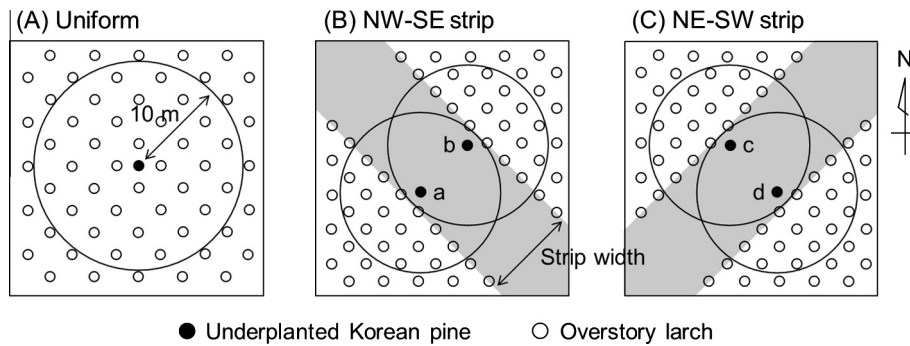


Fig. 1. Schematic representation of the spatial distributions of individual trees that were considered in the simulations. Circles with a 10-m radius represent the range in which the trees were considered to be competitive neighbors. The gray areas represent strip openings, which were oriented (B) from northwest to southeast and (C) northeast to southwest.

Table 2
Summary of the posterior distribution of the parameters for the selected model (Table 1, combined model 5).

Parameter	Description	Mean	Credible interval	
			2.5%	97.5%
α_0	Y-intercept of the growth model	1.844	1.645	2.043
α_1	Effect of target tree's diameter on its growth rate	-0.123	-0.142	-0.102
α_2	Effect of NCI on growth rate	-0.008	-0.015	-0.004
β_0	Y-intercept of the survival model	-1.330	-1.559	-1.114
β_1	Effect of target tree diameter on the survival rate	0.928	0.179	2.345
γ_1	Effect of a neighboring tree's DBH on NCI	1.232	1.022	1.447
γ_2	Effect of distance on NCI	-0.424	-0.506	-0.338
γ_3	Effect of azimuth on NCI	-0.112	-0.991	0.786
γ_4	Effect of azimuth on NCI	-0.108	-1.036	0.922
τ	Standard deviation of parameter φ	0.564	0.490	0.648
σ	Standard deviation of growth rate	0.346	0.382	0.316

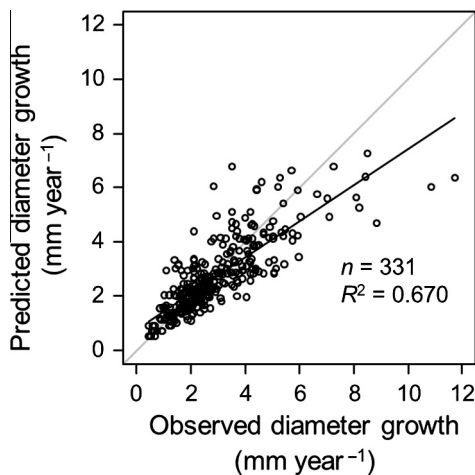


Fig. 2. Relationship between the observed diameter growth and the diameter growth predicted using the best selected model (Table 1, combined model 5) and mean values of each parameter estimate (Table 2). The dark line represents the regression line. The light line represents $y = x$.

(315°) exerted 1.2, 1.4, and 1.2 times the competition strength, respectively, of a neighbor located northeast (45°).

3.4. Effects of the size, density, and spatial distribution of the larch overstory on the growth of Korean pine

Under a uniform spatial distribution of larch, the predicted diameter growth of underplanted Korean pine decreased with

increasing DBH and density of the neighboring larches (Fig. 5). The decrease in response to DBH was faster at higher larch densities. Korean pine growth decreased non-linearly with increasing larch DBH at a larch density of 2–4 m between trees, but decreased almost linearly at a larch density of 5 m between trees.

The predicted diameter growth of the underplanted Korean pine in openings differed as a function of larch DBH, larch density, strip width, and position within the opening (Fig. 6). All else being equal, Korean pines planted under small larches (10-cm DBH; Fig. 6A and B) had better growth than those planted under large larches (30-cm DBH; Fig. 6C and D). The growth of Korean pine under dense larch (3-m spacing; Fig. 6A and C) was smaller than that under sparse larch (5-m spacing; Fig. 6B and D).

The growth rate increased with increasing strip width, and reached equilibrium at a width of 12 m under all conditions. The increase in growth with increasing strip width was larger in stands with larch that had a large DBH and a high density (Fig. 6C; an increase from 2.0 mm year⁻¹ at a width of 4 m to between 4.0 and 4.9 mm year⁻¹ at a width of 14 m) than in stands with larch that had a small DBH and a low density (Fig. 6B; from 8.4 mm year⁻¹ to between 8.9 and 9.1 mm year⁻¹).

The growth of Korean pine also differed among the four positions within the strip openings. Korean pine underplanted at the southwestern edge of the northwest to southeast strip (edge a, Fig. 1) grew least, whereas pine underplanted at the northeastern edge of the same strip (edge b) grew most (Fig. 6). The difference in growth rate between the two edges reached 0.2–0.8 mm year⁻¹ at a strip width of ≥ 12 m. The growth at both edges in the northeast to southwest strip was intermediate between the values in the northwest to southeast strip, and was slightly larger at the northwestern edge (edge c) than at the southeastern edge (edge d).

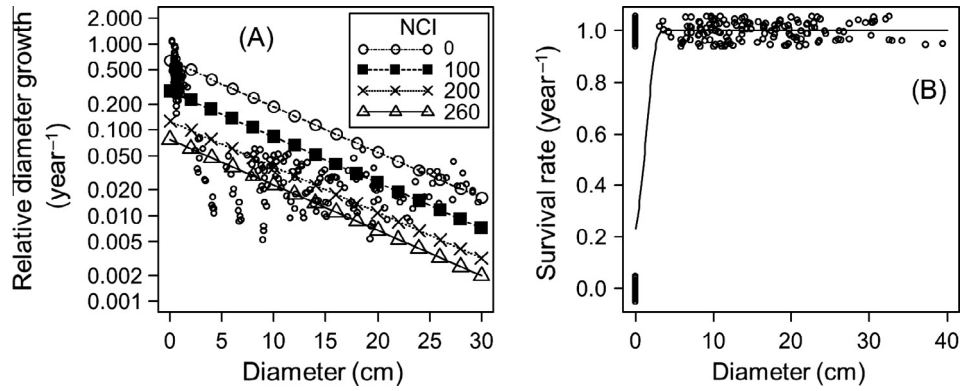


Fig. 3. (A) Effects of the target tree's diameter at 0.3 m above the ground and the neighborhood competition index (NCI) on relative diameter growth and (B) effect of the target tree's diameter on its survival rate. The lines represent the values predicted by using the selected model (Table 1, combined model 5). Circles represent the observed values. In the left panel, the lines are drawn across the range of estimated NCI values (0–261.8). In the right panel, small random numbers were added to the survival rate to lessen overlapping of the data points.

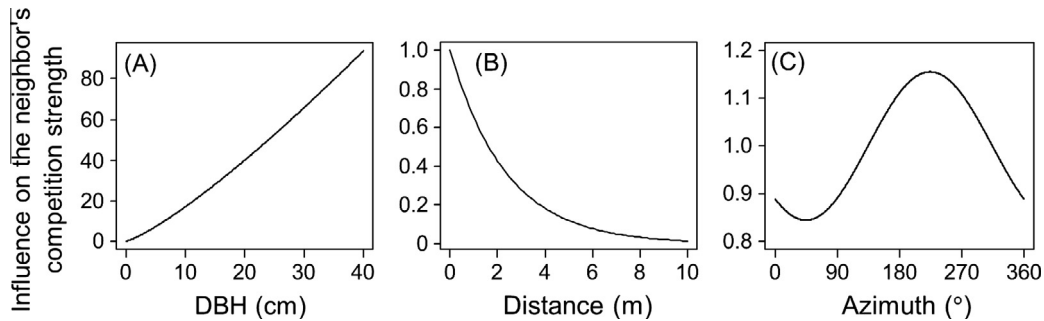


Fig. 4. The influence of the neighboring tree's (A) DBH, (B) distance from the target tree, and (C) azimuth from the target tree on the neighbor's competition strength. Each panel shows how the relative strength of an individual neighbor changes in response to the value of the variable on the x-axis when the values of the other two variables are held constant. The three panels correspond to the three variables in Eq. (8): (A) $(D^m)^{\gamma_1}$, (B) $\exp(\gamma_2 M)$, and (C) $1 + \gamma_3 \cos \theta + \gamma_4 \sin \theta$ (see the main text for a description of the variables). The selected model (Table 1, combined model 5) and the mean values of each parameter estimate (Table 2) were used for the prediction.

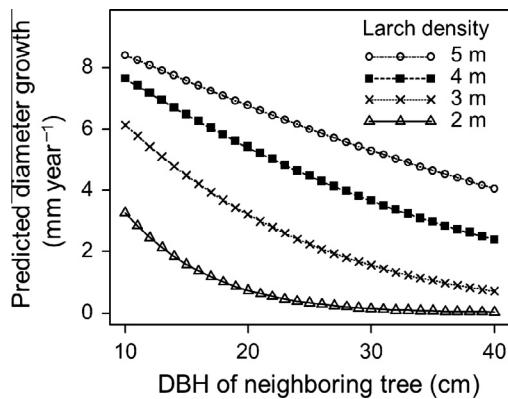


Fig. 5. Predicted diameter growth of a Korean pine sapling (with a diameter of 2 cm at 0.3 m above the ground) as a function of the DBH of the neighboring larch tree and larch density. Larch density was defined as the shortest distance between individual larches. Larches were distributed uniformly around the Korean pine (see Fig. 1A). The best selected model (Table 1, combined model 5) was used for prediction.

4. Discussion

4.1. Effects of target tree diameter on growth and survival

The target tree's diameter had a significant direct effect on its relative growth rate (Fig. 3A). On the other hand, the results of the model selection between models 5 and 6 (Table 1) showed

no clear evidence for a change in NCI with a change in the target tree's diameter, which indirectly affects growth. Many neighborhood analyses have supported the hypothesis that the strength of competition from neighbors decreases with increasing target tree diameter (e.g., Canham et al., 2004; Zhao et al., 2006; Thorpe et al., 2010). This decline most likely reflects the fact that smaller trees suffer greater shading than larger trees under a given set of neighboring conditions, an effect known as asymmetric competition (Weiner and Thomas, 1986). We assume that the decline was not clear in our study owing to the successional traits of Korean pine, which requires higher levels of light as the tree grows (Sun et al., 2009; Yu et al., 2011). This change in light requirements suggests that the sensitivity to NCI should increase with increasing target tree diameter. Such an increase in sensitivity may have canceled out the decrease in NCI that would occur as a result of asymmetric competition.

The DIC value of model 2 and 5 was slightly smaller than that of model 4 (Table 1), and the accuracy of the live–dead classification was identical for these three models (Table S3). These results suggest that the survival rate is unaffected by the strength of competition from neighbors and is determined solely by the target tree's diameter. However, this hypothesis requires further verification because there was only a small difference in DIC among the three models. Moreover, the influence of competition may have been masked by other factors that cause pine death, such as white pine blister rust (caused by *Cronartium ribicola* J.C. Fisch. in Rabh.; Zhang et al., 2010) and rodent damage (Xu, 2001). We could not examine such differences in the cause of death in our analyses because we

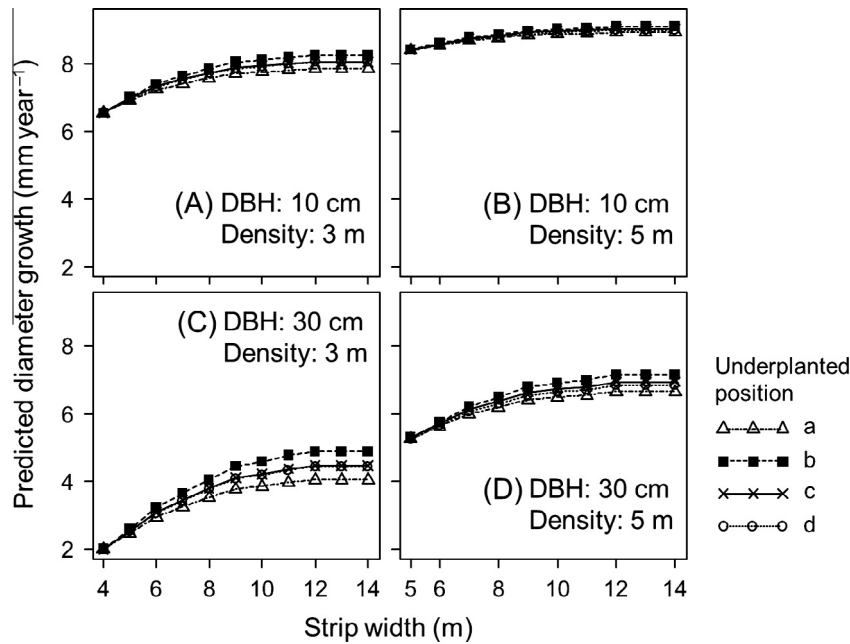


Fig. 6. Predicted diameter growth of a Korean pine sapling (with a diameter of 2 cm at 0.3 m above the ground) as a function of the neighboring larch's DBH, the larch density, the strip width, and the underplanting position within the strip. Larch density was defined as the shortest distance between individual larches. The four lines show the growth of Korean pine underplanted at different positions within the strip opening (a, b, c, and d in Fig. 1). The best selected model (Table 1, combined model 5) was used for the prediction.

did not collect data to support such an analysis. Further study will be necessary to understand the importance and generality of the competitive effect on survival rate.

The target tree's diameter sharply influenced the survival rate (Fig. 3B). This result agrees with the results from previous studies, which showed that Korean pine has a remarkably high risk of mortality during the early stage of its life history (height <0.3 m; Miyaki, 1987; Ishikawa and Okitsu, 2002) but high survival rates during subsequent stages (Li et al., 2012). We thus hypothesize that once a Korean pine reaches a certain size (ca. 3 cm in diameter; Fig. 3B), few trees will die, even under strong competition that causes them to grow slowly. This hypothesis is further supported by an earlier finding that Korean pine saplings (about 6 cm in diameter) in old-growth forests could survive under a closed canopy for up to 100 years (Ishikawa and Okitsu, 2002).

4.2. Effects of the neighboring tree's diameter and location on competition strength

The model selection results showed that the competition strength of an individual neighbor is affected significantly by its DBH and by its distance from the target tree. The competition strength increased with increasing DBH (Fig. 4A) and decreased steeply with increasing distance from a target tree (Fig. 4B). Such trends in the response to DBH and distance are consistent with the results from previous neighborhood analyses (e.g., Canham et al., 2004; Thorpe et al., 2010; Tatsumi et al., 2013). In addition, the strength of the competition from neighbors located farther than 10 m from a target tree was negligible; these trees only had about 2% of the strength of a neighbor located 1 m away (Fig. 4B). This result confirms our assumption in the Methods that individual trees located within 10 m of a target tree should be considered to be competitive neighbors.

The DIC value of model 5 was slightly smaller than those of model 2 and 4 (Table 1). This suggests that the neighbor's competition strength would vary in response to the azimuth from the target tree. However, statistical evidence for this finding was not

compelling; there was only a small difference in the DIC and R^2 values among the three models. A key question is whether the extra parameters that determine the influence of azimuth (i.e., γ_3 and γ_4) could be justified. A previous stand-level study in the northern hemisphere that analyzed the influence of azimuth using categorical variables ("north", "south", and "middle") showed that trees located near the southern edge of an opening had smaller growth rates (Coates, 2000). This finding roughly corresponds to our results that neighbors located southwest of a target tree produced the strongest competition (Fig. 4C). Also, an environmental gradient related to light and heat follows the northeast to southwest direction (Canham et al., 1990; McCune and Keon, 2002). Given the high latitude and cold environment of our study area, it makes sense from a forest meteorology perspective that neighbors southwest of a target tree would produce the strongest competition, since they would block the high levels of light and heat coming from this direction. Therefore, we believe it is reasonable to accept the model that incorporates parameters γ_3 and γ_4 (Table 1, model 5) as the best model.

4.3. Effects of the size, density, and spatial distribution of the larch overstory on the growth of Korean pine

The simulation results illustrated quantitative differences in the growth of the underplanted Korean pine under different combinations of larch DBH and density (defined as the shortest distance between individual larches), strip width, and position within the openings (Figs. 5 and 6). The growth increased with increasing strip width, but reached equilibrium at a strip width of 12 m. This equilibrium reflects the fact that distant neighbors exert a relatively small competitive effect, so removal of these neighbors by thinning has little significance for the growth of the target tree.

We found remarkable differences in growth rate among the different positions within the openings. Korean pine at the southwestern and northeastern edges of the northwest to southeast strips (edges a and b, Fig. 1) showed the smallest and largest growth, respectively (Fig. 6). The growth rates at both edges of

the northeast to southwest strips (edges c and d) were similar, and were between those in the northwest to southeast strip. The effect of these differences in annual growth rate on diameter will grow larger with time as a result of the multiplicative effect (i.e., a given growth rate per unit diameter produces more growth at greater diameters). Thus, these differences in growth rate might lead to considerable changes in future stand attributes such as the diameter-class distribution and the stand's vertical structure. More specifically, underplanted Korean pine in northwest to southeast strips will likely develop a gradient of size, with large trees at the northeastern edge and small trees at the southwestern edge. This gradient of size may become particularly evident in a stand with large DBH and high larch density, as the difference in growth rate between the two edges increased with increasing larch DBH and density (Fig. 6). In contrast, in northeast to southwest strips, the size variation among individual Korean pines will be relatively small, and the overall stand is likely to become a two-storied stand with a larch overstory and a Korean pine understory.

4.4. Further model development

More than two-thirds of the variations in growth ($R^2 = 0.67$, Fig. 2) and in survival (correct live–dead classification = 69.2%, Table S3) were explained by two variables: The size of the target tree and the strength of the competition from neighbors. In addition to these variables, previous studies have reported that factors such as topographic conditions (Li and Zhou, 1991) and climate (Yu et al., 2013) can strongly affect growth and survival. Soil characteristics, tree age, and past management operations would likely have a substantial influence as well. Moreover, previous neighborhood analyses have reported significant interspecific differences in competitive strength (Canham et al., 2004; Zhao et al., 2006; Thorpe et al., 2010). Including these factors in future models may explain much of the remaining one-third of the variation.

We analyzed the temporal response of the growth and survival of individual Korean pines, but could not forecast the future dynamics and economic productivity of the entire stand. Our results show that the growth of underplanted Korean pine increases in response to thinning of the overstory larch (Figs. 5 and 6). However, given that growth of the residual larches might also be increased by thinning, the growth promotion for Korean pine caused by thinning will probably diminish over time. Another economic consideration is how to predict the revenue from Korean pine seeds (pine nuts), since the silvicultural objective for Korean pine stands has recently shifted from timber to seed production (Yu et al., 2011). Future research could address these forest-dynamics and economic considerations by integrating additional models that predict larch stand dynamics and the seed productivity of Korean pines into our model. Such an integrated model could offer deeper insights into long-term competitive interactions between the Korean pines and the larches, and may help managers to develop silvicultural systems with higher total income from Korean pine seeds and larch timber.

4.5. Management implications

Chinese foresters have both economic and ecological objectives in developing and managing uneven-aged Korean pine–larch stands. Each of these objectives can be further divided into two interests. The two economic interests are to produce Korean pine seeds and larch timber. The two ecological interests are to secure the Korean pine resource and to prevent large clear-cuts. Here, optimizing these economic and ecological objectives requires a trade-off, which arises from the trade-off between the thinning intensity for larch and its effect on the growth of underplanted Korean pine (Figs. 5 and 6). Specifically, an increase in thinning

intensity for the larch will likely improve the future Korean pine resource and its seed production, but will decrease the number of residual larch trees after thinning and the future production of larch timber.

Our results provide new insights that will help managers to quantitatively determine which of the conflicting interests to satisfy, and to what extent. One remarkable feature of this study is that we revealed the responses of Korean pine to various larch spatial patterns and underplanting positions at an individual-tree level. So, for example, if the management objectives are to secure the Korean pine resource, to produce seeds, and to make the stand structure relatively homogeneous, then our results suggest that managers should create wide strips by thinning, and orient the strips in a northeast to southwest direction. If, on the other hand, the objectives are to provide ecosystem services such as soil protection, to produce larch timber, and to create a heterogeneous stand structure, then our results suggest that creating narrow strips oriented in a northwest to southeast direction would be preferable.

However, we stress that these management implications should be generalized cautiously. This study was conducted in a single region, and thus the results may be site-specific to some extent. Also, some of our findings were inconclusive. Specifically, there was only small statistical support for the results that the survival rate was unaffected by competition, and that the neighbor's competition strength varied with azimuth ($\Delta DIC \leq 2.0$; Table 1). These results should be verified using a larger dataset collected from a wider area. We expect that the accumulation of additional field data and further individual-based analyses would reveal the uneven-aged management regime that best suits the economic and ecological objectives for the plantations in northeast China.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.foreco.2014.03.022>.

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