



Effect of Forest Composition and Dynamics of Light on Seedlings and Saplings of Korean pine (*Pinus koraiensis*) in Northeastern China

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ABSTRACT

Natural regeneration of Korean pine (*Pinus koraiensis* Siebold & Zucc.) in northeastern China has often been problematic in mixed broad-leaved Korean pine forests (primary forest), but not in deciduous broad-leaved forests (secondary forest). Light transmittance, soil temperature, leaf area index (LAI), height and diameter of Korean pines were estimated in order to examine the contribution of composition and the dynamics of light to Korean pine regeneration in two forests. A spatial point pattern analysis was carried out to investigate the response of seedlings and saplings to light regimes and their relationship with mature trees, graded by size. We draw the following results: (1) light conditions were better in the secondary forest than in the primary forest in late spring (June and July) before the leaf expansion and the secondary forest received more light before leaf expansion and less light penetration in the early summer (August); (2) our spatial analysis indicated that seedlings are negatively correlated with saplings and exhibit a higher degree of clumping than saplings. Relationships of seedlings with mature pines and all sizes of other mature trees appeared random, whereas saplings were negatively associated with small, medium and large mature trees. Our findings suggest that the effect of forest composition on regeneration mainly occurred before the leaf expansion in late spring.

INTRODUCTION

Forest regeneration is critical to the evolution of forest ecosystems and an important measurement in regulating forest structure (Emborg 1998). Species in the regeneration layer have the potential to affect the composition of the forest community (Koehler 2000, Calvo et al. 2002, Hartman et al. 2005, Tang et al. 2013). In northeastern China, North Korea and the Russian Far East, Korean pine (*Pinus koraiensis* Siebold & Zucc.) dominates the temperate mixed broad-leaved Korean pine forests as a regional climax vegetation type (Hao et al. 2008). With mature Korean pines dominating in the canopy and large groups of seedlings on the forest floor, saplings are largely absent in the understory (Li et al. 2003, Zhao et al. 2013). Moreover, field data have revealed the successful regeneration of Korean pine in deciduous broad-leaved forests (Liu et al. 1987). Why the regeneration in these forests is so different? Which factors determine the survival of seedlings? Ding (1994) reported that the light requirement of seedlings increases over time with 100-259 Lux being the minimum light intensity for growth. Other researches on photosynthesis, canopy structure and characteristic of understory and some also proved the effect of light on seedling growth (Dai 1996, Li et al.

1991). But it could not explain the survival of seedlings in secondary forest, because the light is even lower in secondary forest especially after canopy closure (Yuan et al. 2008).

We hypothesised that the difference in regeneration is due to the various compositions between primary and secondary forests. Specifically, the considerable variation in light conditions in deciduous broad-leaved forests at the leaf expansion and defoliation stages, provides saplings with more light available than in primary forests. We limit our discussion to the period of leaf expansion (from April to August), because seedlings and saplings are more vital in the spring than in the fall (after September) (Lu et al. 1980).

The analysis of the spatial patterns may identify the underlying processes such as competition and regeneration (McIntyre et al. 2009, Wiegand et al. 2009). We expect that the response of seedlings and saplings to light can be detected from spatial patterns and their relationships with mature trees. Spatial point pattern analysis (SPPA) is applied to interpret these processes on the spatial patterns of trees (McIntyre et al. 2009, Martínez et al. 2013).

Given this hypothesis, forest structure, regeneration and light conditions in two forests were investigated to test the

relationship between forest composition and the light available in late spring. Spatial patterns of seedlings and saplings were analysed to explore the different responses to light, from their relationships with mature trees in primary and secondary forests.

STUDY SITES AND METHODS

Experimental design and site description: In 2010, two study sites were established in northern Changbai Mountain National Nature Reserve (CMNRR): one site was located in a mixed primary broad-leaved and Korean pine forest (128°05'51"E, 42°24'01"N, situated 776 m above sea level), while the other site was in a 1.5 ha aspen-birch secondary forest (128°06'01"E, 42°24'10"N, 756 m above sea level). CMNRR, as a flat terrace formed after volcanic eruptions, is located in a region bordering China and North Korea. The mean annual temperature of this region is 2.8°C–13.7°C for January as the coldest month and 19.6°C for July as the warmest month (Yang 1985). Total annual precipitation ranges from 600 mm to 900 mm, with the period of maximum precipitation occurring from June to August. The soil at the study site is a typical mountainous dark-brown soil. General information about the two sites is shown in Table 1.

METHODS

We established one 100 m × 100 m plot in the primary forest and a 60 m × 80 m plot in the secondary forest on 8 May 2010. Both plots were divided into 10 m × 10 m sub-plots, establishing 100 sub-plots in the primary forest and 48 sub-plots in the secondary forest. We measured the height of each living stem ≥ 1.5 m as well as the diameter at breast height (DBH). For shrubs, height and average coverage were estimated with a quadrat placed at the centre of each sub-plot. We also estimated the average height and cover-

age of the herb layer.

The age of the seedlings and saplings was estimated by the number of verticils or internodes, while the age of mature trees was estimated from tree rings. We also determined the locations, height and basal diameter of the seedlings and saplings. The population structure of the pines was grouped into three sub-groups according to their age, height and DBH: seedlings (age < 3 years old); saplings (age ≥ 3 years old and height < 1.5 m). Pines with an average height of ≥ 1.5 m and a DBH of < 5 cm were classified as saplings and all trees with height ≥ 1.5 m and DBH ≥ 5 cm were classed as mature. All trees, considered mature by this definition, recorded on site were classified into three size classes on the basis of their DBH, i.e., small trees: 5 to 10 cm; medium trees with DBH 10.1 to 40 cm and large trees with DBH > 40 cm. Mature trees were also classified into a deciduous broad-leaved group and an evergreen coniferous group.

In May and August of 2011, images of the forest canopy were obtained at both sites by using a digital camera (Canon EOS 50D) with a fisheye lens (Sigma EX-DC 4.5mm), positioned 1.1 m above ground level. Leaf area index (LAI) was extracted using Hemiview 2.1 (AT Delta-T Devices Ltd., Cambridge, UK). We opted for the LAI of each sub-plot centre to investigate the effect of canopy on density, mean diameter and mean height of the seedlings and saplings. Light transmittance was determined using a Unispec-SC (Hansatech, UK) spectrometer at a height of 1.8 m from May to August 2011. Temperature recorders (Oneset, USA) were buried in the topsoil of the secondary and primary forests to record the variation of the temperature.

Data analysis: One-way ANOVA was used to test the densities and basal areas between deciduous and evergreen trees in the two forest types. We conducted two tailed *t*-tests to com-

Table 1: General information on the two experimental forest stands*

| Variables | Primary forest | Secondary forest |
|---|-----------------------------------|------------------------------------|
| Age (year) | > 300 | > 80 |
| Korean pine seedlings (stems·ha ⁻¹) | 162 | 152 |
| Korean pine saplings (stems·ha ⁻¹) | 8 | 2,896 |
| Korean pine adults pine (stems·ha ⁻¹) | 90 | 15 |
| Total Korean pine (stems·ha ⁻¹) | 260 | 3,063 |
| Mean density of all adult trees (stems·ha ⁻¹) | 673.00 ± 30.87 (100) ^A | 1 368.75 ± 54.75 (48) ^B |
| Mean basal area of all adult trees (cm ² ·ha ⁻¹) | 630.16 ± 36.82 (100) ^A | 219.35 ± 82.80 (48) ^B |
| Mean height of tree layer (m) | 14.22 ± 0.22 (100) ^A | 12.82 ± 0.21 (48) ^B |
| Mean height of shrub layer (cm) | 45.10 ± 0.99 (400) ^A | 39.90 ± 1.44 (192) ^B |
| Mean height of herbal layer (cm) | 17.31 ± 0.38 (400) ^A | 15.92 ± 0.41 (192) ^B |
| Mean coverage of tree layer (%) | 68.10 ± 1.14 (100) | 65.50 ± 1.05 (48) |
| Mean coverage of shrub layer (%) | 24.98 ± 1.86 (400) ^A | 19.22 ± 1.74 (192) ^B |
| Mean coverage of herbal layer (%) | 34.90 ± 1.54 (400) | 33.80 ± 1.56 (192) |

Note*: Values in the table are means ± standard error (SE); sample sizes are given in parentheses. *t* tests were used and no significant differences were found for the mean layer height and coverage at an α level of 0.05 in the two forests; capital letters of the mean density and basal areas indicate a significant difference at an α level of 0.01.

pare density, basal area, layer height and cover between the two forests. We also used paired *t*-tests to distinguish between the light transmittance in the two forests. The relationship between LAI and height and DBH of juveniles were tested by using Pearson's correlation coefficients. Statistical analyses were performed using SPSS.18.0 (IBM SPSS Inc., USA).

Spatial patterns and species relationships were characterized by Ripley's *K* function (Diggle 2003, Illian et al. 2008). In the cumulative distribution of this *K*-function, large-scale information may include small-scale information (Wiegand et al. 2004, Schurr et al. 2004, George et al. 2006, Wiegand et al. 2007). The *O*-ring statistic can separate classes with specific distances (Wiegand et al. 2004). In our study, the univariate *O*-ring statistic was used for analysing the spatial patterns of seedlings, saplings and mature trees in both forests, while the bivariate *O*-ring statistic was used for analyzing the effect of the various tree sizes on seedlings, saplings and their relationships with mature trees, seedlings and saplings at different scales.

The spatial patterns were analysed using the grid-based software Programita (Wiegand et al. 2004, Wiegand et al. 2007). In order to estimate the pairwise correlation functions, we used a ring width of 2 m and 99 Monte Carlo simulations to generate 99% confidence envelopes.

RESULTS

Forest structure and composition: In our study the primary forest had a higher mean basal area ($t = 10.613$, $p < 0.001$) but a lower mean density of mature trees ($t = 11.948$, $p < 0.0001$) compared with the secondary forest. The higher mean height of trees ($t = 4.603$, $p < 0.0001$), shrubs ($t = 2.984$, $p < 0.01$) and herb layers ($t = 2.487$, $p < 0.05$) suggests a better community development in the primary forest than in the secondary forest (see Table 1).

The density of deciduous trees was higher than that of the evergreen trees in both primary and secondary forests. The deciduous broad-leaved trees were considered to be the largest group with only seven mature Korean pines found on a site measuring 0.48 ha in the secondary forest (Fig. 1A). The primary evergreen forest showed the largest mean basal area among the forests (Fig. 1B).

Light conditions and their dynamics: Light transmittance was lower in the primary forest than in the secondary forest before August (Figs. 2A and 2B). After the leaves expanded completely during August (Fig. 2C), light transmittance was little higher in the primary forest than in the secondary forest. The soil temperature was the same tendency with light transmittance. The soil temperature was higher in secondary forest than in primary from April to August. The largest soil temperature difference occurred in June. After August,

the soil temperatures had no significant difference in two forests (Fig. 2D). The fisheye image of the forest canopy also showed a higher mean LAI ($t = 2.015$, $p < 0.05$) in the secondary forest, indicating that denser canopies were created in the secondary forest in August.

Pearson's correlation coefficients showed that the light distribution of LAI was not correlated with density, height and diameter of juveniles in May and August in two forests ($p > 0.05$).

Spatial pattern of seedlings and saplings: The spatial pattern of the seedlings displayed a strong aggregation from 0 to 40 m in the primary forest (Fig. 3A). By comparison, seedlings were aggregated at 2-5 m, 12 m, 16-18 m and 23-26 m in the secondary forest (Fig. 3B). Saplings in the secondary forest indicate strong clumping at all scales (Fig. 3C). The correlation between seedlings and saplings was negative at most scales (Fig. 3D).

In the primary forest, the relationship between seedlings and mature pines, as well as, the spatial pattern of mature pines was random at most scales (Figs. 3E and 3F). Seedlings were randomly associated with small, medium and large trees at most scales in the primary forest (Figs. 4A to 4C) and similar relationships of seedlings with mature trees were found in the secondary forest (Figs. 4D to 4F). Saplings were negatively associated with trees in the secondary forest (Figs. 4G to 4I) suggesting the effect of mature trees on saplings.

DISCUSSION

Effect of forest composition on light conditions: Our study indicated that the light transmittance of the secondary forest was higher than that of the primary forest before leaf

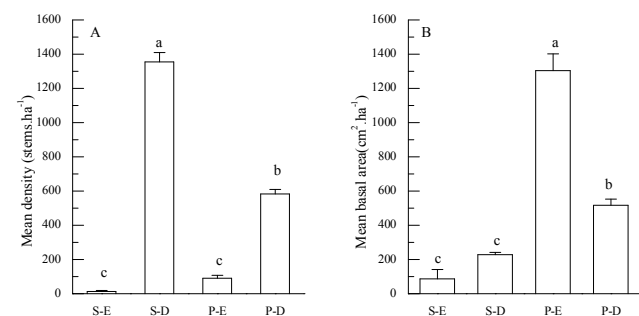


Fig. 1: Relationships between mean density and mean basal area of mature trees in different groups. Fig. 1A: Mean density of deciduous and evergreen groups in the two forests. The four groups are: secondary evergreen group (S-E; $n=48$), primary evergreen group (P-E; $n=100$), secondary deciduous group (S-D; $n=48$) and primary deciduous group (P-D; $n=100$). Fig. 1B: Mean basal area of deciduous and evergreen groups in the two forests. The four classes are: secondary evergreen group (S-E; $n=48$), primary evergreen group (P-E; $n=100$), secondary deciduous group (S-D; $n=48$) and primary deciduous group (P-D; $n=100$). Bars represent means \pm 1 standard error and letters indicate differences at an α level of 0.05.

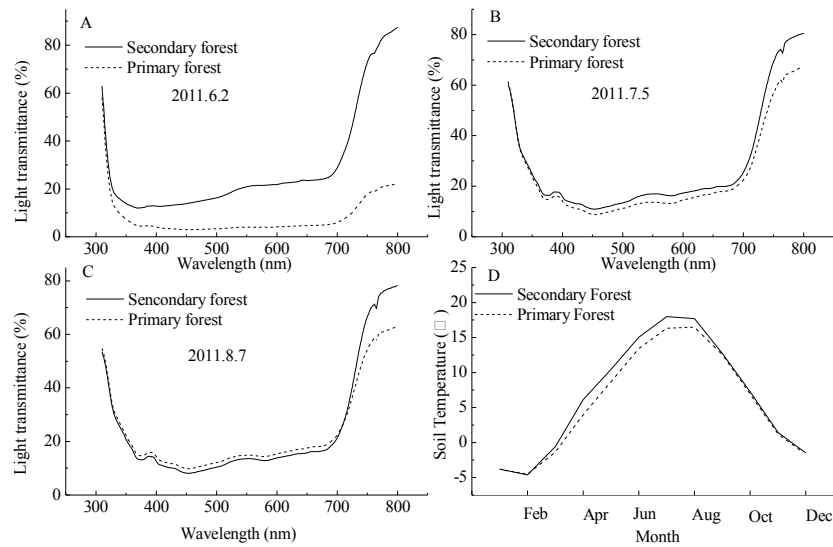


Fig. 2: Light transmittance under secondary and primary forests in June, July and August, respectively (A-C).
Fig. 2D The variation of soil temperature in secondary and primary forests in 2011.

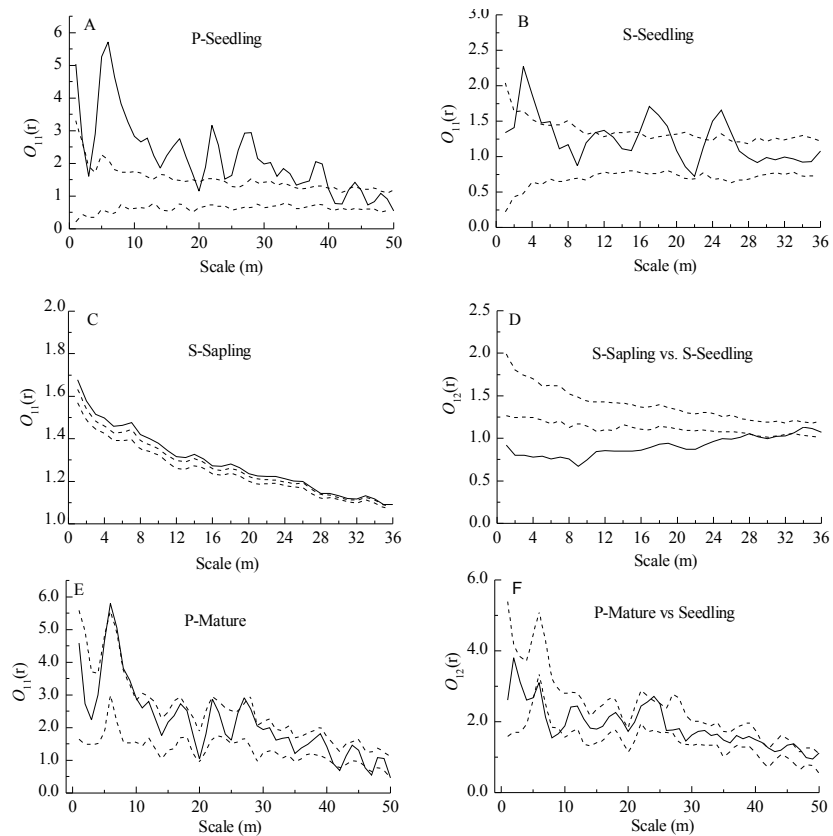


Fig. 3: Univariate analysis of primary seedlings (A), secondary seedlings (B), secondary saplings (C) and primary mature pines (E). Bivariate analysis of saplings and seedlings in the secondary forest (D) and seedlings and mature pines in the primary forest (F). Black lines indicate the ring statistics $O(r)$; thin dashed lines indicate the upper and lower limits of the 99% confidence envelope. The points of the univariate analysis above the upper envelope indicate clumped, within the envelope indicate randomness, and below indicate regular. The points of the bivariate analysis above the upper envelope indicate positive relationship, the points between the envelopes indicate no spatial relationship, while the points below the lower envelope indicate a negative relationship.

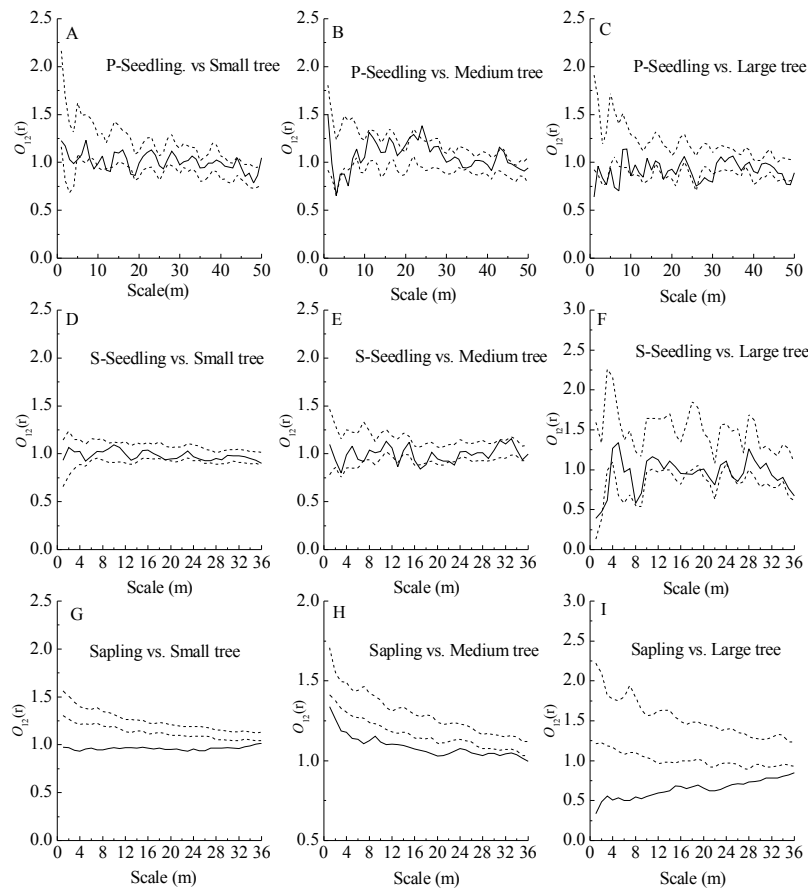


Fig. 4: Bivariate analyses of the correlation between saplings and seedlings at different sizes of mature trees in the primary and secondary forests. A-C: the relationship of seedlings to small, medium and large trees in the primary forest; D-F: the seedlings grown in the secondary forest; G-I: the relationships of saplings with three sizes of mature trees in the secondary forest.

expansion, which is consistent with the previous study (Wang et al. 1993). After leaf expansion, poor light conditions were observed in the secondary forest, which differed from other observations (Liu et al. 1987). Our study, at least uncovered the similarity in light conditions in both the primary and secondary forest after leaf expansion. The soil temperature dynamics also convince the difference of microclimate in two forests. This dramatic change in the light available in the secondary forest could be attributed to the distinct compositions of evergreen and deciduous trees (Fig. 1). No distinct forest gaps were found in our inventory, therefore, more temporal gaps were maintained by numerous deciduous broad-leaved trees before leaf expansion, but more shading, created by many broad overlapping leaves of several deciduous trees, may increase the darkness in the secondary forests after the leaves have completely expanded.

Relationship between light availability and development of seedlings and saplings: The largest difference between the primary and secondary forests observed in our study was

the availability of light in late spring prior to leaf expansion. However, this factor has not affected the seedling density. In the case of both seedlings and saplings, we found no relation between LAI and density, height and diameter. Controlled experiments of planting seeds or seedlings under different canopies may be more effective than field observations to uncover the effect of light on recruitment.

Spatial pattern of seedlings and saplings: In our study we observed that seedlings and saplings were aggregated and saplings repelled by all sizes of mature trees. By comparison, seedlings were not associated with all sizes of mature trees in either forest. These spatial patterns suggest that seedlings and saplings elicit different responses to mature trees.

Saplings only grow when they are distantly located from mature trees and only compete with adjacent seedlings. The negative relationships with all sizes of mature trees indicate that saplings are sensitive to shading, which is consistent with other study (Ding et al. 1994).

Previous studies have shown that the height and diam-

eter of saplings increase only in late spring (Li et al. 1987, Li et al. 1991). Szwagrzyk et al. (2001) observed a similar pattern of light demand in an experimental beech forest. Based on this discussion and our investigation, we further conclude that the light availability in secondary forests during leaf expansion in late spring, meets the light demand of the saplings. However, canopy closure in the primary forest over an entire year cannot meet this demand for light, resulting in the failure of regeneration.

We conclude that a successful regeneration is mainly driven by a higher demand for light on the part of saplings and for more temporal gaps created by deciduous trees in secondary forests. Deciduous broad-leaved forests, therefore, show their importance in the regeneration of secondary forests. Analyzing the relationship of seedlings and saplings with various sizes of mature trees could differentiate the responses to shadings between seedlings and saplings. Further field studies are needed on seedling cultivation to characterize the survival rates of seedlings and saplings, biomass accumulation, rates of photosynthesis.

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