The spatial distribution of the needle area of planted *Larix olgensis* trees

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Abstract: The spatial distribution of leaf area largely governs both the structure and function of a tree crown. For a 16-year-old *Larix olgensis* plantation in the Maoershan Forest Farm, Heilongjiang Province, all needles from the branches in the nodal and internodal pseudowhors within the crown were destructively sampled. The crown was divided into several segments in the vertical and horizontal directions, resulting in different subregions. The needle area (NA) in each subregion was computed based on the needle mass per area (NMA). The vertical and horizontal distributions and their cumulative NA distributions were characterized by the Weibull distribution function and its cumulative form. A two-dimensional NA model was established by combining the two Weibull distribution functions of the vertical and horizontal distributions. The variations in the spatial distribution of NA among the different crown directions were discussed, and the influence of competition from neighboring trees on the spatial distribution of NA was analyzed. The results showed that the Weibull distribution function and its cumulative form performed well in describing the vertical and horizontal distributions and their cumulative distributions of NA. NA was generally concentrated upward within the crown, and this phenomenon was most obvious in dense stands with strong competition. The center of NA exhibited an inward shift in the horizontal direction within the crown but shifted outward with the increase in competition. The cumulative vertical and horizontal distributions of NA obviously varied with the different crown directions, and this variation was mainly associated with the light conditions. The two-dimensional NA patterns showed that the center of the NA generally shifted outward with the increase in the relative depth into the crown (RDINC), and more concentrated and more skewed patterns usually occurred under increased competition. Different crown directions exhibited different two-dimensional NA patterns, but the core driver was the different light conditions caused by the competition from neighboring trees, especially in closed stands.

Keywords: needle area; vertical distribution; horizontal distribution; two-dimensional pattern; crown competition index; *Larix olgensis*

1. Introduction

The spatial distribution of foliage (including mass and area) is one of the main determinants of crown structure [1,2] and function [3,4]. The spatial distribution of foliage influences the sapwood cross-sectional area (or area increment) [5-9], light transmittance [2,10,11], microenvironment [1,2,13], radial pattern of sap flux density [3] and photosynthetic productivity [14-16]. Vertical foliage distribution generally plays an important role in determining effective crowns, consisting of branches that could produce excess photosynthate to contribute to the growth of the main tree stem [18], which provides a reference for artificial pruning height in young forests [19].

Previous studies have generally simulated vertical foliage distribution with probability density distributions, in which β [1,15,20-22] and Weibull [4,23-27] distributions are widely used because they
are highly flexible. The β distribution has an advantage in that it is bounded at the extremities [28], and it is logically defined on an interval with fixed endpoints, that is, (0,1) [15]. The β distribution is equal to the relative depth into the crown (RDINC), with 0 being the tree tip and 1 being the crown base [22]. However, the β distribution does not have a cumulative distribution form, so some researchers have to compute it using the numerical integration method [9,15]. The Weibull distribution has the cumulative distribution form; thus, it is widely applied to model the cumulative distribution of foliage [10,16,29-31]. In contrast to vertical foliage distribution, there are few studies on horizontal foliage distribution [1,10,20,21,27,32]. However, similar to vertical foliage distribution, the horizontal distribution of foliage usually influences within-crown light environments [33], and many ecological and physiological models [1,34-36] rely on accurate characterizations of both horizontal and vertical distributions [10].

The two-dimensional distribution of foliage within a crown is important when establishing eco-physiological models of canopy photosynthesis [12,36]. Wang and Jarvis [1] first tried to simulate a two-dimensional distribution of leaf area density (LAD) by combining vertical and horizontal β distributions. Zhang et al. [21] modeled a two-dimensional distribution of LAD based on a quadratic trend surface function to achieve multiple integrals to further model the radiation transfer within the canopy [37].

For an individual tree, vertical foliage distribution is generally influenced by crown size, tree social position [7,20,22,25], stand density [10,31], tree health [22], crown ratio [31], species shade tolerance [8,38], and silvicultural treatments [29]. Previous studies on foliage distribution generally assumed that there was no significant difference among different horizontal directions [1,21,36]. However, during the actual measurement process, we found that the foliage distribution was inconsistent in reality. In addition, a recent study also suggested that foliage distributions differed among different quadrants, especially between southern and northern quadrants [27]. Some studies have proven that differences in branch size [39,40] and corresponding leaf photosynthetic traits [41] among different crown directions exist, which are probably derived from the distinct light conditions and unbalanced competition status from neighboring trees [40-42]. Thus, it is necessary to analyze the distribution of foliage in different crown directions, and it is important to accurately model light transmission and calculate the photosynthetic production of different crown directions. The objectives of this study are (i) to model the vertical and horizontal distribution, cumulative vertical and horizontal distribution and two-dimensional distribution of foliage with the Weibull probability density function; (ii) to analyze the differences in foliage area distributions among different crown directions; and (iii) to analyze the influence of competition from neighboring trees on the distribution of needle area (NA).

2. Materials and Methods

*Larix olgensis* is native to the Changbai Mountain area and the Laoyeling Mountain area of northeast China and is a medium-sized tree that can reach a height of 30 m and a diameter of more than 1 m. It is an apparently light-demanding but cold-resistant and drought-resistant tree species that has the advantages of fast growth and strong adaptability [43,44]. Thus, *Larix olgensis* has been one of the main reforestation tree species in northeastern China, especially in mountainous regions, and has been identified as a major fast-growing and high-yielding tree species in northeastern China [45]. The planted area and volume of *Larix olgensis* account for 36% and 37% of the total area and total volume, respectively, of all the plantations in northeastern China. *Larix olgensis* also has high economic value due to its wide application for housing, furniture, plywood, flooring, decorative and pulp purposes [46], and its plantations represent almost 38% of the commercial timber plantations in northeastern China [47].

2.1. Site description

The experiments were conducted at the Maoershan Forest Farm (127°18′0″E – 127°41′6″E and 45°22′0″N – 45°18′16″N), which was founded in 1958 in northeastern China. The total area of the forest farm exceeds 27,000 ha, including 26,067 ha forestland, with an average altitude of 400 m above sea
level. The site is characterized by a temperate continental monsoon climate with warm, wet summers and cold, dry winters. Dominated by Eutroboralfs [48], the area has a mean annual temperature of 2 °C but exhibits a large temperature difference throughout the year with a minimum temperature of −40 °C and a maximum temperature of 34 °C. The total forest coverage is approximately 83.3%, and 14.7% of this area consists of plantations.

2.2. Field measurements and sample selection

Three sample plots (20 m × 30 m) were established within pure and unthinned 16-year-old Larix olgensis plantations of the same habitat, with different stand densities of 2000, 2400 and 3200 trees ha−1. The diameter at breast height (DBH), tree height (H) and crown width (CW) were measured for each tree with a DBH greater than 5 cm, and the quadratic mean diameter (Dg) was calculated for each plot. Then, three sample trees with DBH values that were similar to the Dg of the corresponding plot were selected to represent the average state of the stand. The DBH, H, CW, and relative azimuth (AZI) of neighboring trees (the trees with crowns that were in contact with the target tree crown) to the target (AZI) were measured. Meanwhile, the distance between the target tree and the neighboring trees (DIS) was also measured to calculate the crown competition index of neighboring trees (CCI) [49]. The attributes of the sample trees and corresponding neighboring trees are listed in Table 1.

<table>
<thead>
<tr>
<th>Sample trees</th>
<th>Neighboring trees</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Tree no.</strong></td>
<td><strong>DBH (cm)</strong></td>
</tr>
<tr>
<td>1</td>
<td>10.8</td>
</tr>
<tr>
<td>2</td>
<td>11.2</td>
</tr>
<tr>
<td>3</td>
<td>10.9</td>
</tr>
</tbody>
</table>

Note: Tree no. = tree number, DBH = diameter at breast height, H = tree height, Mean CW = mean value of crown width of four directions, CL = crown length, AZI = azimuth, CCI = crown competition index of neighboring trees.

2.3. Measurement of needle biomass of the whole crown

At the end of the growing season (early September), three sample trees were cut down for measurement. In the vertical direction, the crown length (the distance from the tree tip to the base of its live crown, CL) of each sampled tree was divided into several segments based on the pseudowhorls [50] from top to bottom. In the horizontal direction, the CWs were divided into several...
segments at 0.3 m projected length intervals from the branch base to the branch tip. According to the above method, the crown was divided into different subregions (Figure 1). The branch diameter (BD), branch length (BH), branch chord length (BC), branch azimuth (φ), branch angle (θ) and depth into the crown (DINC) of all branches were measured. Afterward, all branches were cut to obtain the fresh weight of needles in each subregion by destructive sampling. We hypothesize that the ratio of dry weight to fresh weight (RDF) is not significantly different within the same vertical segment of the crown; thus, 20 g needle samples were randomly selected from each vertical segment and dried immediately after they were taken from the field to a constant weight at 105 °C and weighed to calculate the RDF.

Figure 1. A schematic diagram of the crown attributes of a Larix olgensis tree and the principle of subregion division.

2.4. Calculation of NA

The NA of coniferous tree species is generally difficult to measure and estimate due to the small sizes and irregular geometries of the needles. In recent studies, the method used to measure the needle surface area involved defining the cross-section of a needle as a simple geometric shape [1,51,52], such as a triangle for Pinus koraiensis, square for Picea, and rectangles for both Abies nephrolepis and Larix gmelinii. However, this method ignores the variation in the sizes and shapes of cross-sections with the position of the needle and is usually accompanied by large measurement errors. Thus, some authors measured the projected needle surface area by scanning, such as in
previous studies on *Pinus sylvestris* [53] and *Larix decidua* [54]. In this study, we selected the second method (scanning) because *Larix olgensis* needles are so small that large errors may occur when measuring the length, width and thickness. Moreover, the mean width to thickness ratio for *Larix olgensis* needles is greater than four, which is close to a flat shape.

Once the fresh weight of the needle was measured, 10 groups of 0.1 g needles were randomly selected in each vertical segment. Then, all sample groups were scanned and surveyed with image analysis software (Image-Pro Plus 6.0, Media Cybernetics, Bethesda, MD, USA) in the laboratory, resulting in a projected leaf area. The needle mass per area (NMA) was calculated by dividing the projected leaf area by the corresponding needle dry mass. Finally, the NA in each subregion could be calculated as follows:

\[
\text{NA}_{ij} = \text{RDF}_j \times \text{NMA}_{ij} \times \text{WF}_{ij}
\]  \hspace{1cm} (1)

where \(i\) is the subregion number, \(j\) is the vertical segment number, and WF is the fresh weight of the needle.

To describe the NA distribution of each crown direction, we divided the crown into four directions, with the azimuth of a branch ranging from 315 to 360 and from 0 to 45 defined as north, from 45 to 135 defined as east, from 135 to 225 defined as south, and from 225 to 315 defined as west.

### 2.5. Description of NA distribution functions

In this study, we intend to simulate the vertical and horizontal distributions and cumulative vertical and horizontal distributions using the same type of distribution function. Thus, we select the Weibull probability density function to fit the NA distribution and cumulative NA distribution of the proportion of NA to total NA.

NA distribution function:

\[
P(x) = \frac{c}{b} \left(\frac{x}{b}\right)^{c-1} \times \exp \left[-\left(\frac{x}{b}\right)^c\right]
\]  \hspace{1cm} (2)

where \(P(x)\) is the proportion of NA at a specific RDINC to the total NA of the whole crown, and \(b\) and \(c\) are the scale and shape parameters, respectively.

Cumulative NA distribution function:

\[
P(x) = 1 - \exp \left[-\left(\frac{x}{b}\right)^c\right]
\]  \hspace{1cm} (3)

where \(b\) and \(c\) are described above.

### 2.6. Description of the two-dimensional regression equation of NA

Wang and Jarvis [1] first established a two-dimensional regression equation for LAD during a study of the crown structure of Sitka spruce. These authors suggested that if LAD varied in both the vertical and horizontal directions, the LAD within the crown could be calculated by combining two \(\beta\) distributions. Thus, we established a two-dimensional regression equation by combining two Weibull distributions (vertical distribution and horizontal distribution) based on the same theory as Wang and Jarvis [1]:

\[
\text{NA}(h,r) = \text{NA}_T \times a_0 \times \left(\frac{h}{b_1}\right)^{c_1-1} \times \exp \left[-\left(\frac{h}{b_1}\right)^{c_1}\right] \times \left(\frac{r}{b_2}\right)^{c_2-1} \times \exp \left[-\left(\frac{r}{b_2}\right)^{c_2}\right]
\]  \hspace{1cm} (4)

where \(\text{NA}\) is the needle area, \(h\) and \(r\) are the relative crown height (1-RDINC) and relative radial distance (ratio of projective length from tip to stem junction to CW), respectively, \(\text{NA}_T\) is the total NA of the whole-tree crown, and \(a_0, b_1, b_2, c_1\) and \(c_2\) are estimated coefficients.

In this study, maximum likelihood estimates of the coefficients of the distribution functions (Eq. 2 and Eq. 3) were determined using Gauss-Newton, and the coefficients of the regression model were determined via nonlinear least squares, which was carried out using R software (version 3.5.1). The
performance of the Weibull distribution and cumulative Weibull distribution were validated by the Chi-square test [55]. The coefficient of determination ($R^2$) and root mean square error (RMSE) were used to evaluate the performance of the regression equations (Eq. 4).

3. Results

3.1. Vertical distribution of NA

The parameter estimates and the Chi-square test results of the Weibull distribution fitted to the vertical distribution of NA for three sample trees are presented in Table 2. The Chi-square test indicated that all of the vertical distributions of NA satisfied the null hypothesis ($\alpha = 0.05$). Figure 2 shows that the observed NA was distributed almost perfectly on the lines of estimated NA. Hence, the Weibull distribution was suitable for describing the vertical distribution of NA within the crown. The peak NA in the vertical direction (PNAV) within the crown in each direction was also calculated from the Weibull distribution (Table 2). As we conjectured, the PNAVs within the crown differed in different directions, although most were maintained within a range of 0.4 to 0.6. The predicted vertical distributions of NA in the four directions (east, south, west and north) for three sample trees are shown in Figure 3. For tree 1, the PNAVs of the four directions were below the crown midpoint and were not significantly different (Figure 3a). For tree 2, the vertical distribution of NA in the four directions exhibited an upward shift, and the PNAVs were also similar (Figure 3b). For tree 3, the PNAVs in the four directions fluctuated more obviously than those in the first two trees, and PNAV differences were greater than 0.2 between the west and south directions with the RDINC (Figure 3c).

Interestingly, the peak of the total NA of tree 3 was almost equal to that of tree 1, although the PNAVs in different directions were absolutely different between the two trees. The PNAVs among the four directions in an individual tree were different, but the difference was not significantly correlated with direction.

Table 2 Parameter estimates and Chi-square test of the Weibull function fitted to the vertical distribution of NA in different directions

<table>
<thead>
<tr>
<th>Tree no.</th>
<th>Direction</th>
<th>Parameters</th>
<th>$\chi^2$</th>
<th>$\chi^2_{a=0.05}$</th>
<th>RDINC value of maximum NA</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>$b$</td>
<td>$c$</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>East</td>
<td>0.615</td>
<td>3.129</td>
<td>1.516</td>
<td>11.070</td>
</tr>
<tr>
<td></td>
<td>South</td>
<td>0.645</td>
<td>3.162</td>
<td>6.909</td>
<td>11.070</td>
</tr>
<tr>
<td></td>
<td>West</td>
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<td>2.823</td>
<td>3.421</td>
<td>11.070</td>
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<tr>
<td></td>
<td>North</td>
<td>0.589</td>
<td>2.551</td>
<td>1.635</td>
<td>11.070</td>
</tr>
<tr>
<td></td>
<td>Total</td>
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<td>2.925</td>
<td>7.859</td>
<td>11.070</td>
</tr>
<tr>
<td>2</td>
<td>East</td>
<td>0.485</td>
<td>2.472</td>
<td>2.560</td>
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</tr>
<tr>
<td></td>
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<td>0.504</td>
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<td>6.825</td>
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<tr>
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<td>2.777</td>
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<tr>
<td></td>
<td>North</td>
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<td>3.208</td>
<td>1.630</td>
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</tr>
<tr>
<td></td>
<td>Total</td>
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<td>2.851</td>
<td>7.063</td>
<td>12.592</td>
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</tr>
<tr>
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</tr>
<tr>
<td></td>
<td>West</td>
<td>0.492</td>
<td>3.153</td>
<td>3.073</td>
<td>9.488</td>
</tr>
<tr>
<td></td>
<td>North</td>
<td>0.601</td>
<td>2.939</td>
<td>1.548</td>
<td>11.070</td>
</tr>
</tbody>
</table>
Note: Tree no. = tree number, RDINC = relative depth into crown, NA = needle area.

**Figure 2.** Description of observed NA and corresponding estimated NA for three sample trees: (a) tree 1; (b) tree 2 and (c) tree 3.

**Figure 3.** Vertical distribution of predicted NA, according to RDINC at intervals of 0.1 in different directions for three sample trees: (a) tree 1; (b) tree 2 and (c) tree 3.

The predicted cumulative vertical distribution of NA in four directions within the crown for three sample trees is shown in Figure 4. For tree 1, the cumulative needle areas (CNAs) in four directions all demonstrated an increase with increasing RDINC, but the total NA in four directions exhibited significantly different values of 12.4 m² in the south, 9.2 m² in the west, 5.2 m² in the north and 4.9 m² in the east, which indicated that the NA was more concentrated in the south and west directions of the crown. For tree 2, the CNAs in four directions also demonstrated a pattern similar to that shown in tree 1 that increased with increasing RDINC, but the rate of increase approached zero in the lower sections of the crown. The total NAs in the four directions were 15.1 m² in the south, 9.0 m² in the west, 7.8 m² in the north and 5.3 m² in the east. Tree 2 showed a similar concentrated tendency as tree 1, where the NAs in the south and west directions of the crown were greater than...
the NAs in the east and north directions. For tree 3, although the CNAs in the four directions also increased with increasing RDINC as in the first two trees, the difference in the total NAs among the four directions was smaller. In addition, the order of the total NAs in the four directions differed from the orders for the first two trees: 9.5 m² in the east, 8.0 m² in the west, 6.3 m² in the north and 5.9 m² in the east. The total NA of the whole crown exhibited "S curve" vertical patterns that were similar between tree 1 and tree 2, but the pattern for tree 3 was slightly different. The rates of increase along RDINC in tree 1 and tree 2 were smaller in the upper crown but greater in the lower crown than those in tree 3.

![Diagram showing cumulative vertical distribution of predicted NA, according to the RDINC at intervals of 0.1, in different directions for three sample trees: (a) tree 1; (b) tree 2 and (c) tree 3.](image)

**Figure 4.** Cumulative vertical distribution of predicted NA, according to the RDINC at intervals of 0.1, in different directions for three sample trees: (a) tree 1; (b) tree 2 and (c) tree 3.

### 3.2. Horizontal distribution of NA

The parameter estimates and the Chi-square test results of the Weibull distribution fitted to the horizontal distribution of NA for three sample trees are presented in Table 3. The Chi-square test indicated that all of the horizontal distributions of NA satisfied the null hypothesis (α = 0.05). Figure 5 shows that the observed NA was distributed almost perfectly on the lines of the estimated NA. Hence, the Weibull distribution was also suitable for describing the horizontal distribution of NA within the crown. The peak NA in the horizontal direction (PNAH) within the crown in each direction was also calculated from the Weibull distribution (Table 3). The PNAHs within the crown in different directions (east, south, west and north) were concentrated within the range of 0.15 to 0.30, and the ratio of the projective length from tip to stem junction to crown width (RRD) exhibited little difference. The RRD values of the PNAHs were usually greater in the south direction than in other directions, but in the other directions, the order of the RRD values of the PNAHs was not associated with direction. The predicted horizontal distribution of NA in the four directions for three sample trees is shown in Figure 6. The RRD values of the PNAHs of the total NA for three sample trees were 0.19 (tree 1), 0.22 (tree 2) and 0.23 (tree 3), respectively, which indicated that the horizontal distribution of total NA of the whole crown exhibited inside shifts for all three sample trees, but this phenomenon was most obvious in tree 1. The difference in PNAHs among the four directions was obvious in tree 1 and tree 2 but weak in tree 3 because the coefficients of variation (CVs) of the PNAHs among the four directions were 0.29, 0.32 and 0.14 for tree 1, tree 2 and tree 3, respectively.

**Table 3.** Parameter estimates and Chi-square test of the Weibull function fitted to the horizontal distribution of NA in different directions.

<table>
<thead>
<tr>
<th>Tree no.</th>
<th>Direction</th>
<th>Parameters</th>
<th>$\chi^2$</th>
<th>$\chi^2$ at 0.05</th>
<th>RRD value of</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
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<td></td>
<td></td>
<td></td>
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</tbody>
</table>
### Table 1: Observed and Estimated Needle Area for Three Sample Trees

<table>
<thead>
<tr>
<th></th>
<th>b</th>
<th>c</th>
<th>Maximum NA</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>0.282</td>
<td>2.276</td>
<td>5.991</td>
</tr>
<tr>
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</tr>
<tr>
<td>2</td>
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<td>7.815</td>
</tr>
<tr>
<td>2</td>
<td>0.242</td>
<td>1.749</td>
<td>7.815</td>
</tr>
<tr>
<td>Total</td>
<td>0.335</td>
<td>1.670</td>
<td>9.488</td>
</tr>
<tr>
<td>3</td>
<td>0.304</td>
<td>1.770</td>
<td>7.815</td>
</tr>
<tr>
<td>3</td>
<td>0.382</td>
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<td>7.815</td>
</tr>
<tr>
<td>3</td>
<td>0.310</td>
<td>1.752</td>
<td>9.488</td>
</tr>
<tr>
<td>West</td>
<td>0.286</td>
<td>2.177</td>
<td>5.991</td>
</tr>
<tr>
<td>Total</td>
<td>0.333</td>
<td>1.775</td>
<td>9.488</td>
</tr>
<tr>
<td>East</td>
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<td>1.944</td>
<td>9.488</td>
</tr>
<tr>
<td>South</td>
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<td>1.996</td>
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<tr>
<td>Total</td>
<td>0.351</td>
<td>1.827</td>
<td>9.488</td>
</tr>
</tbody>
</table>

Note: Tree no. = tree number, RRD = ratio of the projective length from tip to stem junction to crown width, NA = needle area.

![Figure 5](https://example.com/figure5.png)

**Figure 5.** Description of observed NA and corresponding estimated NA for three sample trees: (a) tree 1; (b) tree 2 and (c) tree 3.
The predicted cumulative horizontal distribution of NA in the four directions within the crown for three sample trees is shown in Figure 7. The CNA inside the crown (RRD < 0.5) of the three sample trees all increased with increasing RRD, but there was almost no increase outside the crown (RRD > 0.5), which indicated that most of the NA was concentrated inside the crown. The ratios of CNA within the RRD range from 0 to 0.5 to the total NA of the whole crown were 0.86, 0.87 and 0.85 for tree 1, tree 2 and tree 3, respectively, which further validated that the horizontal distribution of NA exhibited an inside shift. The horizontal distributions of CNA also exhibited obvious variations in different directions. For tree 1 and tree 2, the total NA in the south direction was significantly greater than that in other directions, but for tree 3, the total NA in the east direction was the greatest.

Figure 7. Cumulative horizontal distribution of predicted NA according to the RDINC at intervals of 0.1 in different directions for three sample trees: (a) tree 1; (b) tree 2 and (c) tree 3.

3.3. Two-dimensional pattern of NA

The parameter estimates and the goodness of fit ($R^2$ and RMSE) of the two-dimensional regression model of directional and total NA for three sample trees are presented in Table 4. The large $R^2$ values and small RMSE values reflected that the two-dimensional regression models could fit the two-dimensional NA patterns well. The predicted two-dimensional patterns of directional and total NA for the three sample trees are shown in Figure 8. The two-dimensional patterns of NA exhibited an obvious difference among the three sample trees. Although most of the NA was concentrated in the middle of the vertical direction and inside the horizontal direction in both tree 1 and tree 3, the degree of concentration of tree 1 was stronger than that of tree 3. However, the two-dimensional NA pattern of tree 2 exhibited a more obvious upper shift and an inside shift than exhibited by tree 1 and tree 3. Different crown directions generally exhibited different two-dimensional NA distribution patterns, which was mainly reflected in the concentration degree and concentration position. For tree 1, there was no significant difference in the positions of NA concentration among the four crown directions, and the concentration degrees were stronger in the south and west directions than in the east and north directions. For tree 2, the positions of NA concentration among the four crown directions were also similar, but the concentration degrees were stronger in the south and north directions than in the east and west directions. For tree 3, the positions of NA concentration in the east and south directions were lower in the vertical direction and the middle in the horizontal direction, but the positions of NA concentration in the west and north directions were in the upper part in the vertical direction and inside in the horizontal direction. The degrees of NA concentration were also markedly different in the different directions and descended in the order of south, west, north and east.

Table 4 Fitting results of a two-dimensional model of directional and total NA for three planted Larix olgensis trees
<table>
<thead>
<tr>
<th>Tree no.</th>
<th>Directions</th>
<th>Estimated coefficients</th>
<th>( R^2 )</th>
<th>RMSE</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>( a_0 )</td>
<td>( c_1 )</td>
<td>( b_1 )</td>
</tr>
<tr>
<td>1</td>
<td>East</td>
<td>0.100</td>
<td>2.218</td>
<td>0.598</td>
</tr>
<tr>
<td></td>
<td>South</td>
<td>0.203</td>
<td>2.487</td>
<td>0.563</td>
</tr>
<tr>
<td></td>
<td>West</td>
<td>0.170</td>
<td>3.255</td>
<td>0.611</td>
</tr>
<tr>
<td></td>
<td>North</td>
<td>0.102</td>
<td>2.392</td>
<td>0.795</td>
</tr>
<tr>
<td></td>
<td>Total</td>
<td>0.129</td>
<td>2.478</td>
<td>0.610</td>
</tr>
<tr>
<td>2</td>
<td>East</td>
<td>0.120</td>
<td>2.681</td>
<td>0.744</td>
</tr>
<tr>
<td></td>
<td>South</td>
<td>0.493</td>
<td>7.193</td>
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</tr>
<tr>
<td></td>
<td>West</td>
<td>0.143</td>
<td>3.535</td>
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<td></td>
<td>North</td>
<td>0.156</td>
<td>5.834</td>
<td>0.657</td>
</tr>
<tr>
<td></td>
<td>Total</td>
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<td>4.241</td>
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<td>3</td>
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<td>1.856</td>
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<tr>
<td></td>
<td>South</td>
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<td>3.820</td>
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</tr>
<tr>
<td></td>
<td>West</td>
<td>0.146</td>
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</tr>
<tr>
<td></td>
<td>North</td>
<td>0.107</td>
<td>3.599</td>
<td>0.613</td>
</tr>
<tr>
<td></td>
<td>Total</td>
<td>0.356</td>
<td>2.164</td>
<td>0.590</td>
</tr>
</tbody>
</table>

Note: Tree no. = tree number, RDINC = relative depth into crown, NA = needle area. \( R^2 \) = coefficient of determination, RMSE = root mean square error.
Figure 8. The results of the simulation of two-dimensional NA for the whole and different directions of crowns for three sample trees.
4. Discussion

In past studies, the foliage area or foliage mass of the subregions within the crown or the whole crown was mainly obtained by two methods: 1) calculated using the foliage removed from sample branches [3,27,31,38]; 2) estimated by establishing regression models at the branch level [4,8,9,12,15,16,29,30]. Then, these estimations could be accumulated to the desired scale. Regression models have been proven to perform well [4,16], but validations at large scales, such as subregions within crowns or whole crowns, still could not be conducted due to the lack of actual measurement data for all branches. For Larix olgensis tree species, there are usually small branches (delayed by one or more years behind the main branches, [31]) in nodal/internodal pseudowhorls that have proportions of branches and needles that are abnormal compared with the main branches. This phenomenon was also reported in Schneider et al. [9], who found that nodal foliage was more abundant than internodal foliage. The NPBs were generally ignored when selecting branch samples, and consequently, the estimation of the needle mass of these NPBs usually has a large error. In this study, all of the branches were destructively cut, and all of the needles in each branch were picked and weighed to obtain the actual needle mass, despite the measurements being very time consuming. We also estimated the needle masses of the NPBs using the form from Maguire and Bennett [15], which was confirmed to be the best branch-level leaf area equation that depended on the data from the main branches. The results showed that the absolute relative error of the crown needle mass was approximately 23.7%, indicating that sampling only the main branches was inaccurate for modeling the NPBs.

Many previous studies suggested that the foliage distribution usually exhibited a unimodal curve [31,56] and was not distributed symmetrically within the crown [57]. Some of these studies suggested that the vertical distribution of foliage was skewed upward toward the top of the crown [8,16,25,31,57]. In contrast, others reported that the center of foliage was located below the crown midpoint [7,15,38]. Foliage development is predominantly dependent on light [22,25,56], which is closely associated with the growing space [38]. In this study, the stand density of tree 1 was low (2000 trees ha$^{-1}$), which resulted in weak competition (Table 1). Thus, the vertical distribution of NA for tree 1 exhibited a downward shift (Figure 3a), which was a direct result of the long and wide crowns that were permitted by the ample space and light resources. This result was in concordance with the results of other works [38]. However, the center of NA for tree 2 significantly shifted upward toward the top of the crown (Figure 3b) with the increase in stand density (2400 trees ha$^{-1}$). This discrepancy probably arises because of the stronger competition in the lower crown [31], which leads to an appropriate assignment of NA to favorable light environments in response to shading by neighbors in crowded stands [25]. This result appears to be consistent with the results of previous studies that suggested that foliage was typically shifted upward in crowns growing in dense stands relative to the foliage distribution in crowns growing in open stands [25,30,38]. In contrast, the vertical distribution of NA for tree 3, which grew in a very dense stand (3400 trees ha$^{-1}$), appeared to be at odds with the above rule indicating that the center of NA was located below the crown midpoint (Figure 3c). This effect presumably arises from the fierce competition of branches between tree 3 and the neighboring trees due to the increased CCI value (Table 1). Many branches in the lower crown died due to the lack of light resources, which resulted in a smaller crown ratio (defined as the ratio between crown length and tree height). Consequently, the center of NA shifted downward [58]. In summary, the differences in the vertical foliage distribution are related to the strategies used to capture light [25].

Our results showed that different crown directions also showed different amounts of plasticity in the shift in foliage distribution within the crown. The CNAs in the south and west crowns were higher than those in the north and east, respectively, for tree 1 and tree 2 (Figure 4a and 4b), which was consistent with the local sunshine duration that descended in the south, west, east and north [59]. Gao et al. [40] found a similar relationship when modeling crown profiles and suggested that it is necessary to consider the differences caused by different directions when analyzing the crown structure. However, the CNA for tree 3 did not follow this rule. The CNAs in the east and south were greater than those in the west and north (Figure 4c), which showed a negative correlation with CCI.
This result was in concordance with a previous study that suggested that the competitions from neighboring trees were the core factor influencing the CNA in dense stands [60].

Both horizontal foliage distribution and vertical distribution play important roles in the determination of light interception [33]. The plasticity of horizontal foliage distribution is also an important component in the adaptive response to stand competition [27]. Our results showed that the peaks of NA were usually concentrated inside the crown (Figure 6), which was in accordance with other studies on Tsuga heterophylla, Pseudotsuga menziesii and Abies grandis [20], Pinus taeda [10], Cunninghamia lanceolata [21] and Larix occidentalis [27]. However, the center of the NA shifted toward the outside with the increase in stand density (Figure 6, Table 3), which was consistent with the results of previous studies that suggested that branches in the shade extend laterally to expose themselves to more sunlight [10,16]. Our results showed that the difference in the horizontal distribution of NA among different directions was obvious (Figure 6). A similar finding was reported in a Larix occidentalis study, in which the horizontal foliage distribution along a branch was significantly different at different directions within the crown [27]. In most species, horizontal foliage distribution also depends on vertical branch position in the crown, total crown length and social position [10,20,32]; however, all of the factors are related to maximizing the use of light resources.

Wang and Jarvis [1] first simulated the two-dimensional patterns of LAD by combining the β distribution functions of vertical and horizontal distributions. Similarly, we established a two-dimensional model of NA (Eq. 4) by combining the Weibull distribution functions of the vertical and horizontal distributions, which exhibited good performance (Table 4). The predicted two-dimensional patterns of total NA (Figure 8) showed that the center of NA usually shifted toward the outside with the increase in RDINC, which was consistent with the results of previous studies [10,20,27], indicating that trees tended to maximize the light available to the needles in the lower crown by minimizing self-shading. The center of NA shifted upper in the crown (Figure 8) with the increase in competition from neighboring trees (Table 1). This shift was probably because the competition between trees became stronger (Table 1) with the increase in stand density, and this phenomenon generally occurred in the low crown first. Trees in open stands easily obtain ample space and light resources for branch development, which results in a wider development of branches in low crowns. However, an overly dense stand may cause extensive branch mortality in the lower crown and lead to a short CL (Table 1), which is why the center of NA for tree 3 seemed to shift downward with the increase in competition [10]. For individual trees, the two-dimensional pattern of NA also varied with different crown directions, and the difference became more obvious with the increase in competition (or stand density) (Figure 8). As a result, stronger competition usually caused a more nonuniform distribution of needles to allow more light to penetrate deep into the crown. Thus, the skewed pattern of NA within a crown reflected the excellent adaptability of trees.

To date, there have been many studies on foliage distribution, but some of them have made a mistake about the meaning of “distribution”. Generally, the foliage distribution should be described by probability distribution functions (β distribution function, Weibull distribution function, etc.) that have fixed endpoints (0, 1) that correspond to the top and bottom of a live crown. However, some studies used the distribution functions only as equations and fit the foliage distribution using nonlinear regression [10,21,27,29,31]. The parameter estimation methods used for distribution functions and regression equations are maximum likelihood estimation and nonlinear least squares, respectively, which are definitely different from each other. In our opinion, it is more reasonable to refer to the “vertical or horizontal patterns of foliage” rather than “vertical or horizontal distributions of foliage” when using a regression method. In this study, we use the Weibull distribution function, which has a cumulative distribution form, to uniformly characterize the spatial distributions of NA, including the vertical/horizontal distribution and cumulative vertical/horizontal distribution. A two-dimensional model for NA was similarly established based on the Weibull distribution function to describe the two-dimensional patterns of NA within the crown.

5. Conclusions
The vertical and horizontal distributions of NA were simulated by the Weibull distribution function, and the cumulative Weibull distribution function was used to simulate the cumulative vertical and horizontal distributions of NA. All of the above distributions performed well. A two-dimensional NA model was also established based on the Weibull distribution function and exhibited a good fitting result. For a closed stand, the center of NA generally showed an upward shift in the vertical direction in the crown, and this phenomenon became more obvious with the increase in competition. Most of the NA was concentrated inside the crown in the horizontal direction, but this center shifted outward with the increase in competition. The cumulative vertical and horizontal distributions obviously varied among the different crown directions, and this difference was mainly associated with the light conditions. The two-dimensional NA patterns showed that the center of the NA generally shifted outward with the increase in RDINC. Stronger competition will lead to a more concentrated and more skewed two-dimensional NA pattern. Different crown directions exhibited different two-dimensional NA patterns, but the core driver was the different light conditions caused by competition from neighboring trees.

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**Author Contributions:** Qiang Liu undertook data analysis and wrote most of the paper. Qiang Liu and Longfei Xie collected and analysed the data. Fengri Li supervised and coordinated the research paper, designed and installed the experiment, made some measurements, and contributed to the writing of the paper.

**Conflicts of Interest:** The authors declare no conflict of interest.

**References**


