

SPATIAL PATTERNS OF CANOPY LEAVES OF SAPLINGS OF FOUR WOODY SPECIES IN A FOREST ENVIRONMENT

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ABSTRACT. The spatial patterns of canopy leaves of saplings of four woody species in a natural secondary forest of northeastern China were analyzed. Four saplings displayed leaf area in higher layers with larger positive inclination angles more than that of the other layers. However, this proportion declined gradually along with descending sapling height, and the leaf area with smaller inclination angles gradually increased. Along the gradient of azimuth angle, the frequency distribution patterns of the leaves of four saplings were irregular and stochastic to some extent. The leaf area density curves of two saplings were parabola-shaped along the gradient of sapling height, and in the middle layers the leaf area densities were higher than those of lower and top layers in sequence. Applying the formulae of Levins (1968) and Shannon and Weaver (1949), as well as the formulae of Schoener (1970) and Pianka (1974), the characteristics of leaf populations of four saplings distributed along the gradients of inclination and azimuth angles, were further analyzed. The significance of these adaptive characteristics in understanding the dynamic properties and regeneration process of the forest community are discussed.

Key words: canopy, forest environment, leaf, sapling, spatial pattern

INTRODUCTION

Plant forms, often diverse and striking, are objects of both aesthetic wonder and scientific curiosity (Waller 1986). The physical form of a plant embodies its behavior and at least partially reflects its circumstances of growth. Plants often are limited in their responses by structural or architectural constraints which in turn depend upon the attributes of other plants in the vicinity (Maynard Smith & Price 1973). The way leaves are arranged in the crown obviously affects their efficiency, and different patterns of arrangement would be favored in different environments (Waller 1986). A large number of leaves growing in an orderly fashion on an elaborately branched structure forms a canopy that greatly enhances the interception of light, and also considerably interferes with the photosynthetic rates and growth of understory plants, including the offspring of the trees. In such seriously reduced light, some species cannot live; others not only survive, but can opportunistically grow and complete their life history.

Research on the adaptive characteristics and the mechanisms of growth of understory saplings contribute greatly to an understanding of the dynamic properties of forest communities

and an assessment of the process of forest regeneration. The successful colonization and establishment of saplings in the forest environment relies to a great extent on the functioning of their leaf systems as light-collectors and energy-transmitters; the assimilative capacity of a plant is linked directly to its ability to acquire water, light and nutrients, and the process itself serves as an integrator of "success" in a given habitat (Mooney 1986). Older methods developed by many investigators for studying canopy structure were reviewed by Kumura (1975), and their feasibilities have been tested repeatedly. Furthermore many newer methods have been devised (e.g., Perry et al. 1988, Walklate 1989, McIntyre et al. 1990, Welles & Norman 1991, Yamamoto & Itoh 1997). The impacts of canopy structure on growth and survival of understory plants and their corresponding responses to the availability of light were emphasized by Young and Smith (1979), Ustin et al. (1984), Canham (1988), Pfitsch and Percy (1992), Bonser (1994), Holmes (1995), Lieffers (1995), O'Connell (1995). Additional studies have focused on the impact of canopy structure and/or distribution of foliage in relation to the production of the whole plant (e.g., Horn 1971, Hallé et al. 1978, Cody 1984, Ardhana et al. 1988, Hollinger 1989, Jack & Long 1992, Kuuluvainen 1992, Ellsworth & Reich 1993, Herbert 1992, Schmid & Bazzaz

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1994). Analyses of crown structure and heterogeneity of the microsite are central to understanding the ecological and evolutionary importance of phenotypic plasticity and acclimation to light in plants (Chazdon et al. 1988).

The present study analyzes the spatial distribution of leaves in canopies of understory saplings of four species in natural secondary forest from northeastern China.

MATERIALS AND METHODS

The study site was the Experimental Forest Farm of Northeast Forestry University, Heilongjiang Province, northeastern China (45°20'–25'N, 127°30'–34'E). In this area, the mean annual temperature averages 2.8°C and the mean annual precipitation is 724 mm; sunshine occurs 2471.3 hours per year and the frost-free period is 120 days. The regional climax vegetation is a mixture of broadleaf trees and Korean pine. Originally, such forest was extensively distributed in northeastern China. However, beginning in 1903, this vast area of virgin forest was destroyed by foreign colonizers during a half-century, and secondary succession followed. For several decades, there was natural recovery and typical secondary forest formed; it is now extensively distributed in this area. The main constituent trees are broadleaf trees of large statures and extensive crowns. Gaps in this forest are small to moderate in size and there are a considerable number of regenerating seedlings and saplings aggregatively distributed on the forest floor (Chen 1992). Our investigation was conducted in a typical hardwood secondary forest with the following characteristics: tree density 1124/ha; mean stand height, 16.4 m; mean diameter of trees 15.8 cm; average age of trees, 28 years. There were four species of saplings selected for our survey: *Fraxinus mandshurica* Rupr., *Phellodendron amurense* Rupr., *Quercus mongolica* Fisch. ex Turcz., and *Acer mono* Maxim., all of which are common regenerating species on the forest floor. These four species are also mid- to late-successional trees and are often found as components of climax forest (Chen 1992).

The four species of saplings grew in small gaps (3 to 5 m diameter). The neighboring understory shrubs were all below the height of saplings. Nearby overstory trees were all hardwoods over 15 m high. The photon flux density in the surveyed sites was 20–40% of full light. For each species, the spatial patterns of canopy leaves of a typical sapling was measured and analyzed in detail. The height of the saplings sampled ranged from 108 to 152 cm. Leaf areas were measured with leaf area meters (CAC 100,

Japan) and the angles of inclination and azimuth of leaves were measured with a high precision compass (NJ 830, China). The telescopic sight of the compass was turned both vertically and horizontally to parallel the leaf blade as exactly as possible, so that the turning angles were geometrically equal to the respective angles of inclination and azimuth of the leaf blades. Angles were expressed as positive or negative depending on whether they tilted above or below the horizontal plane. The unevenness of leaf blades, such as minor twists and wrinkles were ignored. The height of every leaf above ground surface also was recorded. The leaves were then numbered and stored in small plastic bags until their surface areas could be measured.

When analyzing the spatial patterns of the canopy leaves, measurements were clustered at intervals (12° for inclination angles and 45° for azimuth angles), so that any possible small errors in measurement would not affect the results. The canopies were divided into two or three layers (more for *Fraxinus mandshurica* and *Phellodendron amurense*) for convenience of analysis. The crown volumes at different layers were approximated from the formulae of a circular cone and frustum of a cone for the upper and lower layers respectively. The diameters of the bottoms of the circular cone and frustum of a cone at different layers of the crowns were averaged from measurements in four different directions. Modifications of the following formulae (see review by Kumura 1975) were used to analyze the distribution patterns of leaves:

$$G_{Lj}(Z, \theta_{Lj}) = \frac{\sum g_i(Z, \theta_{Lji})}{\sum g_i(Z, \theta_{Lj})}$$

where i refers to individual leaves; j refers to layers; Z refers to heights; θ indicates inclination angles; $\sum g_i(Z, \theta_{Lji})$ stands for the total area of the leaves whose inclination angle is within the interval $\Delta\theta_L$ in a given layer; $\sum g_i(Z, \theta_{Lj})$ refers to the total area of leaves for the whole plant and $G_{Lj}(Z, \theta_{Lj})$ indicates frequency. If one substitutes θ for ψ (azimuth angle of the leaf blade) in the above formula, then:

$$G_{Lj}(Z, \psi_{Lj}) = \frac{\sum g_i(Z, \psi_{Lji})}{\sum g_i(Z, \psi_{Lj})}$$

where $\sum g_i(Z, \psi_{Lji})$ refers to the total area of the leaves whose azimuth angle is within the interval $\Delta\psi_L$ in a given layer; $\sum g_i(Z, \psi_{Lj})$ refers to the total area of the leaves with various azimuth angles for the whole plant; $G_{Lj}(Z, \psi_{Lj})$ refers to frequency.

Synthesizing the above two formulae, then:

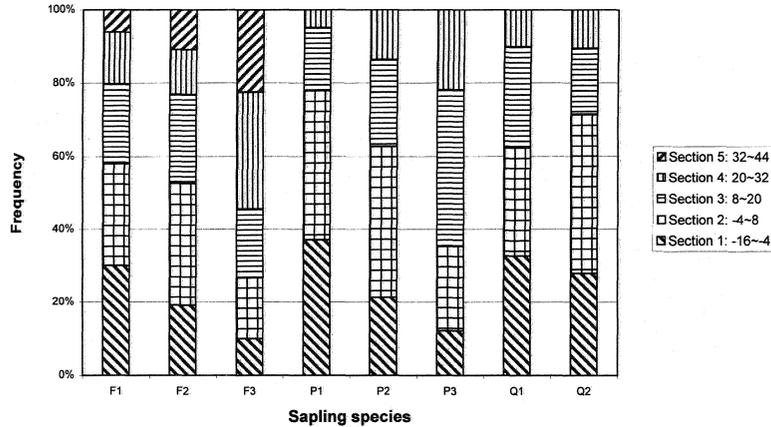


FIGURE 1. Spatial distribution of the canopy leaves of four sapling species along a gradient of angle of inclination. F, P, Q, A refer to saplings of *Fraxinus mandshurica*, *Phellodendron amurense*, *Quercus mongolica*, *Acer mono* respectively; 1, 2, 3 refer to the different layers of the saplings, F1 (32–72 cm), F2 (72–112 cm), F3 (112–152 cm); P1 (20–52 cm), P2 (52–84 cm), P3 (84–116 cm); Q1 (31–72 cm), Q2 (71–111 cm); A1 (28–68 cm), A2 (68–108 cm). The angles of inclination in which the leaf populations of 4 saplings grew were classified into 5 sections at intervals of 12°.

$$G_{L_j}(Z, \theta_{L_j}, \psi_{L_j}) = \frac{\sum g_i(Z, \theta_{L_{ji}}, \psi_{L_{ji}})}{\sum g_i(Z, \theta_{L_j}, \psi_{L_j})}$$

where $\sum g_i(Z, \theta_{L_{ji}}, \psi_{L_{ji}})$ refers to the total area of the leaves whose angles of inclination and azimuth are within the interval $\Delta\theta_L$ and $\Delta\psi_L$ in a given layer; $\sum g_i(Z, \theta_{L_j}, \psi_{L_j})$ refers to the total area of the leaves with various inclination and azimuth angles for the whole plant and $G_{L_j}(Z, \psi_{L_j})$ refers to frequency.

Leaf area density is the leaf area per unit crown volume. It usually varies with plant height, so it may be defined as:

$$U_{L_i}(Z_i) = S(Z_i)/V_i$$

where $U_{L_i}(Z_i)$ refers to the leaf area density; $S(Z_i)$ and V_i refer respectively to the total leaf area and crown volume at a given height Z_i .

The following four formulae were used for analyzing the distributive patterns of leaves in the sapling crowns:

$$B_i = \frac{1}{\sum p_{ij}^2} \quad (\text{Levins 1968})$$

$$B_i' = -\sum p_{ij} \log p_{ij} \quad (\text{Shannon \& Weaver 1949})$$

where p_{ij} refers to the percentage of the leaves within certain intervals of inclination angle ($\Delta\theta_L$) or azimuth angle ($\Delta\psi_L$) in a given crown layer. Formulae B_i and B_i' were comparatively used for calculating the distributive breadths of the leaves along the gradients of inclination and azimuth angles in the crown layers.

$$S_i = 1 - \frac{1}{2} \sum |p_{ij} - p_{hi}| \quad (\text{Schoener 1970})$$

$$S_i' = \frac{\sum p_{ij} p_{hi}}{[\sum p_{ij}^2 \sum p_{hi}^2]^{1/2}} \quad (\text{Pianka 1974})$$

where p_{ij} and p_{hi} refer to the percentage of the leaves within certain intervals of angles of inclination or azimuth in different crown layers. Formula S_i is also known as Czekanowski's Index. Formulae S_i and S_i' were comparatively used for calculating the similarity in distribution of the leaves respectively along the gradients of angles inclination and azimuth between two different layers.

RESULTS

Spatial Patterns and Leaf Area Densities

The crowns of *Fraxinus mandshurica* and *Phellodendron amurense* saplings were classified into three layers at intervals of 40 cm and 32 cm respectively, and the crowns of *Quercus mongolica* and *Acer mono* saplings both were classified into two layers at an interval of 40 cm. The spatial patterns of canopy leaves along the gradients in angle of inclination are shown for different layers in FIGURE 1.

In the upper layers, the area of leaves with relatively large positive angles of inclination was greater than in the other layers, but with decrease in sapling height, this value declined gradually, and the areas with smaller, or negative, inclination angles increased accordingly.

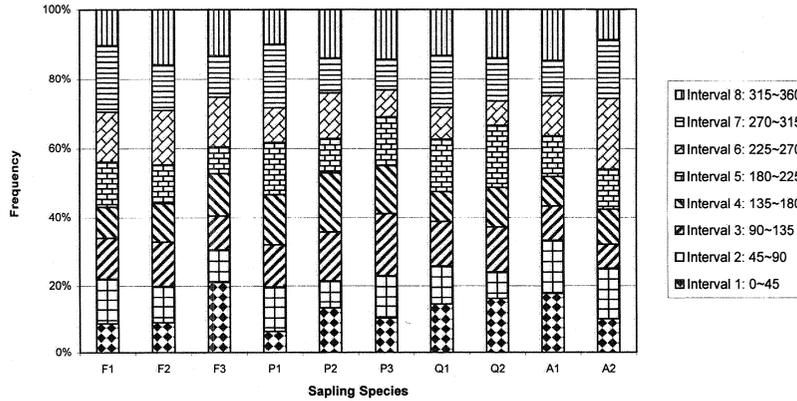


FIGURE 2. The spatial distribution of the canopy leaves of four saplings along a gradient of angle of azimuth. F, P, Q, A and 1, 2, 3 see also FIGURE 1. The azimuth angle was classified into 8 intervals of 45°.

FIGURE 2 shows that along the gradient of azimuth angle, the frequency distributions of the leaves of the four species of saplings were irregular and somewhat stochastic.

FIGURE 3 shows that the curves of leaf area density (LAD) of *Fraxinus mandshurica* and *Phellodendron amurense* saplings were parabolic along the gradient of sapling height. In both species, the LAD of the middle layer was higher than that of either the lower or top layers.

Mathematical Analysis of the Distributive Characteristics of Leaf Populations Along Gradients of Angles of Inclination and Azimuth

The formulae of Levins (1968), Shannon and Weaver (1949), Schoener (1970) and Pianka (1974) were used to analyze the characteristics of leaf populations of the four species of saplings along the gradients in angles of inclination and azimuth (FIGURE 4 and FIGURE 5).

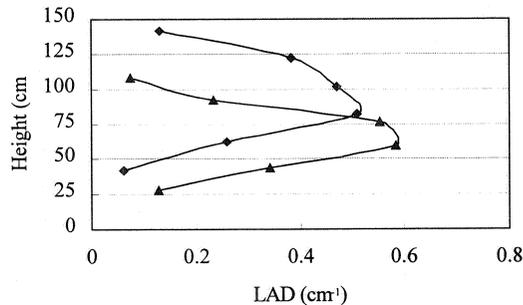


FIGURE 3. The spatial patterns of leaf area densities (LAD) of *Fraxinus mandshurica* (◆) and *Phellodendron amurense* (▲) saplings in relation of sapling height.

FIGURE 4 implies that in all crown layers, the leaves of all four species had a wider distribution along the gradient in azimuth angle than along the gradient in inclination angle. The results calculated from the formulae of Levins (1968) and Shannon and Weaver (1949) significantly correlated and reflected the same tendency; however, the values calculated by the former were always larger than those calculated by the later. In most cases, the distribution of the leaves of all four species was broader in the middle layers than in the other layers, both along the gradients of angle of inclination and of azimuth. Among the four saplings, the distributive breadths of leaf populations in different layers,

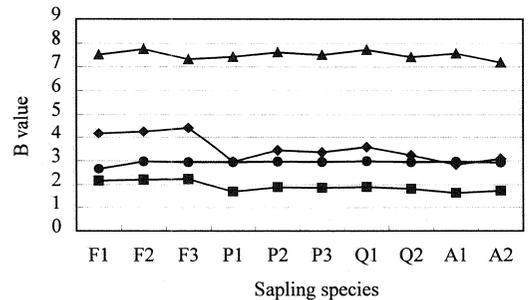


FIGURE 4. The distribution breadths of the leaf populations of four saplings along the gradients of angles of inclination and azimuth. F, P, Q, A and 1, 2, 3 see also FIGURE 1. B1i and B1a, as well as B2i and B2a refer to the values of distribution breadths of the leaf populations, calculated from the formulae of Levins (1968) and Shannon and Weaver (1949) along the gradients of angles of inclination (i) and azimuth (a) respectively. The correlation coefficient between B1i (◆) and B1a (▲) is 0.996, and that between B2i (■) and B2a (●) is 0.992.

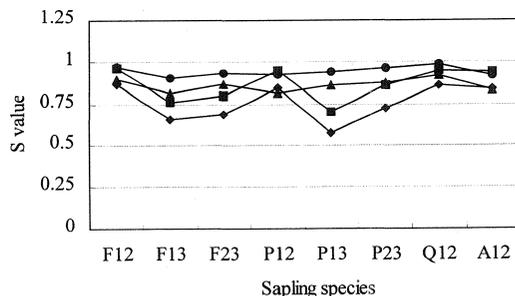


FIGURE 5. The interrelationships of the leaf populations' distributions between layers of four saplings along gradients of angles of inclination and azimuth. F, P, Q, A and 1, 2, 3 see also FIGURE 1. S1i and S1a, as well as S2i and S2a refer to the values of distribution similarity calculated from the formulae of Schoener (1970) and Pianka (1974) along gradients of the angles of inclination (i) and azimuth (a) respectively. The correlation coefficient between S1i (◆) and S1a (▲) is 0.995, and that between S2i (■) and S2a (●) is 0.943.

from *Fraxinus mandshurica* to *Acer mono* slightly declined.

FIGURE 5 shows some difference in the distributive similarities between different layers of leaf populations of the four species along the gradients in angles of inclination and azimuth. The results calculated from both formulae significantly correlated and reflected basically the same tendency. The values derived from Pianka's (1974) formula were usually slightly higher than those from Schoener's (1970).

DISCUSSION

Leafless tree canopies can intercept as much as 30% of incident radiation (Collins et al. 1985). Below a completely closed canopy, PAR may be as low as 1–5% of that in the open (Anderson 1964, Chazdon & Pearcy 1991). Sunflecks contribute relatively little radiation beneath late successional species (<10% of total understory PAR), but represent a major fraction (40–50%) of radiation beneath less shade-tolerant species (Canham 1995). However, the amount of light in the understory is heterogeneous; when seedlings or saplings live in different places in the forest, they probably encounter very different temporal fluctuations in sunlight. In a dense forest, sunflecks (patches of sunlight that pass through discontinuities in the canopy and travel through the forest as the sun moves) can change the photon flux density (PFD) impinging on a leaf near the forest floor over tenfold within seconds (Pearcy 1988). Occasional severe interference of the upper canopy by wind

also can change the PFD supply on the forest floor considerably (Li pers. obs.). Thus, sunflecks and wind both can affect the carbon metabolism of lower leaves in dense forest that are shaded by the upper canopy.

Many woodland species can respond to moderate increase in light levels caused by sunflecks, e.g., as increase in PFD up to 10% of ambient light can enhance population growth in a number of species (Reader & Bricker 1992) and significantly higher rates of flowering and seed production have been observed in populations of woodland species growing in gaps (Barkham 1980, MaCall & Primack 1987, Whigham & O'Neill 1988, Whigham et al. 1993). Therefore, these species may show positive responses to increases in light, even in gaps of small to moderate size. For plants growing in an understory with no gaps, or with very small ones, the capacity to utilize the available light is important. Changes in growth forms of leaves and in leaf-display are a common way in which plants increase their net photosynthetic ability. Organs within a leaf are positioned in ways that maximize absorption of radiation, and so are the leaves within an individual plant (Mooney 1986). Wilson (1960) classified patterns of arrangement of leaves into regular, random and clumped types (see also Kumura 1975). In our study, the leaves in the upper layers tended to be vertically oriented whereas those in the lower layers were more horizontal, even drooping. In the relatively high latitudes of the northern hemisphere, the incident sunlight does not always strike the earth surface perpendicularly, thus, the more vertically oriented leaves in the upper layers of plants can collect relatively more light both in forest and in the open. Normally, the photosynthetic capacity of a leaf changes with its age as well as with seasons. The highest photosynthetic rates are attained prior to or near maximal leaf expansion, after which fixation capacity begins to decline (Sestak 1985). Almost all young leaves are concentrated at the top of the tree or at the apex of branches, and the old leaves are located inside the crown or in the lower layers. In our study, this was true of all four species of saplings. Because of this, the upper leaves absorb sunlight maximally, thereby enhancing photosynthetic rates; the lower leaves absorb scattered light and/or transmitted light filtered through the upper canopy. The inclination of leaves of all four species of saplings is an adaptation to the environment in which they live.

Plants have the capacity to proliferate absorptive tissues in patches of high resource concentration (e.g., Hutchings 1988, Gross et al. 1993). Woody species can display their foliage away

from neighboring plants (e.g., Canham 1988, Koike 1989, Holmes 1995). However, if the habitat is not greatly heterogeneous, no obvious orientation in plant growth forms will appear. This might at least partially explain the stochastic distribution of the understory saplings' leaves along the gradient of azimuth angle in our study. Herbert (1992) demonstrated that total instantaneous photosynthetic rate of a plant was most sensitive to random orientation of leaves in the top canopy layer and less sensitive to the orientation of those in the lower layers.

The net photosynthesis of entire canopies can be described conveniently in terms of leaf area index (LAI), but leaf area density (LAD) expressed as total leaf area per unit of crown volume, often is also a useful measure. In saplings of *Fraxinus mandshurica* and *Phellodendron amurense*, the LADs of the middle layers of the canopies were higher than those of either the lower or the top layers. From an ecophysiological viewpoint, this pattern would greatly benefit the understory of saplings in a forest. In an individual plant with low LAD, much of the light passes through the upper canopy and if there is no lower layer of leaves, this filtered light is lost. At higher LAD, much of the light can be absorbed by the leaves, but then much of the resulting photosynthate may be wasted in the course of respiration of the shaded, non-photosynthesizing leaves. There would seem to be an optimal LAD at which net photosynthesis reaches a maximum. This optimal LAD is altered by different light conditions and with different canopy architecture. It also varies interspecifically. In a forest environment, light is usually insufficient for the growth and development of understory plants. Thus, efficient acquisition of available light is of utmost importance. *Fraxinus mandshurica* and *Phellodendron amurense* saplings achieve maximal usage of light by having relatively fewer leaves in the top layers of crowns but with those leaves having relatively large positive angles of inclination. In the middle layers, there are more leaves and they have a diversity of angles of inclination and azimuth. Finally, in the lower layers, there are few leaves but these have relatively large negative angles of inclination. This architecture of the canopy enhances the efficient acquisition of light at all levels. The upper layers with more perpendicular leaves can opportunistically absorb incident sunflecks. Light filtered through the upper layer can be absorbed by the middle layer of leaves where the foliage has a diversity of angles of inclination and azimuth. Only a very small proportion of incident light penetrates to the lower layer of leaves and the most common type of light there would be scattered light (both reflect-

ed and transmitted). In the lower layer, leaves with relatively large negative angles of inclination would be more efficient in interception of these kinds of light.

When leaves of barley become more perpendicular to the ground surface, the lower leaves remain above their compensation points (Pearce et al. 1967), but in a forest understory, the situation is different, because in most cases, the photon flux density available for the lower shaded leaves is very low, even lower than their light compensation points (Chen 1992), as a result, high respiration rates will waste photosynthate. Accordingly, redundant leaves self-thin, thereby maintaining energy balance (Li pers. obs.). For the remaining shaded leaves with very low photosynthetic rate, perhaps increasing leaf span may be the most productive option (Chabot & Hicks 1980) and therefore in the lower layers, both the numbers of leaves and the LADs declined. This basically is in accordance with the simple economic model described by Fitter (1986). This style of canopy architecture might be regarded as a special way of efficiently and competitively utilizing limited light resource in forest understory.

In northeastern China, *Fraxinus mandshurica* and *Phellodendron amurense* saplings (especially the former) are extensively distributed in natural secondary forest. In many sites, they also have become the main constituent species in the upper layers, replacing the pioneer species (e.g., *Populus davidiana* Dode and *Betula platyphylla* Suk.) after nearly a century of secondary succession (Chen 1992). All four species showed relatively few, large and thin leaves in the understory, compared with those grown in full light (Li unpubl. data). Thinner leaves are more economical to produce than are thicker ones, because, by increasing specific leaf area, a plant can increase the amount of incident light interception without a concomitant increase in biomass invested in leaf tissue (Poorter & Remkes 1990, Shipley 1995). Also, the maintenance cost of thinner leaves is low because they have fewer mesophyll cells than thicker leaves (Boardman 1977, Chabot et al. 1979). Thicker leaves can maintain higher photosynthetic rates than thinner leaves, but in order to sustain a positive carbon balance under light conditions suboptimal for photosynthesis, the more economical option for plants is to produce thinner leaves (Chabot et al. 1979).

The formulae of Shannon and Weaver (1949), Levins (1968), Schoener (1970) and Pianka (1974), as well as many other formulae, have been widely used in the measurement of niches, and their potential applications have been discussed in depth by many authors (e.g., Colwell

1971, Hurlbert 1978, Petraitis 1979, Abrams 1980, Feinsinger et al. 1981). The behavior of leaves also can be described and analyzed by the application of niche theory. The different positions of leaves in the plant crown, and the various angles of inclination and azimuth actually reflect the capacity for utilizing various ecological resources. So applying the methods commonly used in measuring niche parameters to describe the spatial distribution of leaves is theoretically feasible. In all crown layers, along the gradient in azimuth angle, the leaf populations of all four species of saplings had relatively greater breadth of distribution than those along the gradient in inclination angle. The underlying reason might be that the leaf populations of all four species of saplings can utilize the whole 360° of azimuth, but they can only partially use the entire 180° of inclination. The results calculated from both formulae showed basically the same tendency; however, the values derived from Levins' (1968) were always higher than those from the formula of Shannon and Weaver (1949). In the present case, Levins' (1968) formula appeared to be better than that of Shannon and Weaver (1949), because the former could be seen more intuitively. In most cases, in the middle layers, the distributive breadths of the leaf populations of all four saplings species were relatively large in comparison to those of the other layers along both gradients. The reasons for this might be that in the middle layers, leaves were more diversified and greater in number than those of the other layers. Generally, sapling size positively correlated with its leaf population size, and larger leaf populations tended toward greater diversity. From *Fraxinus mandshurica* to *Acer mono*, the sapling size decreased gradually and distributive breadths of leaf populations also slightly declined.

Along the gradients in the angles of inclination and azimuth, the measurement of interrelationships between layers of leaves of the four saplings species showed some difference, and the results calculated from both types of formulae reflected the same tendency and were significantly correlated. However, it is difficult to evaluate the relative merits of the two formulae. The leaf population of a plant is like a sensitive, wide-angled automatic light receiver adjusting to three-dimensional space according to ambient light condition; leaves not only dexterously regulate incident angles in ways that maximize the amount of various types of light absorbed, but they also can avoid self-shading. The divergence in the distributions of leaf populations between layers is a case in point.

All four species of saplings that presently grow naturally in the secondary forest commu-

nities of northeastern China are also the main constituent species in the regional climax (Chen 1992). They are shade-tolerant to some degree and rely on plasticity in morphology, anatomy and physiology, and their saplings can survive and opportunistically grow in forests with relatively few gaps. In many densely vegetated environments, leaves serve both as the plant's solar collector or "feeding site system" (Bell 1984, Li 1993) and as their weapons for interfering with the growth of neighboring plants (Waller 1986). Only when forest saplings can efficiently take advantage of all the resources available to them are they likely to avoid being overtopped by their neighbors and competitively suppressed.

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