Variations of leaf inclination angle distribution with height over the growing season and light exposure for eight broadleaf tree species

Kairi Raabe \textsuperscript{a,}\textsuperscript{*}, Jan Pisek \textsuperscript{b}, Oliver Sonnentag \textsuperscript{b}, Kalju Annuk \textsuperscript{a}

\textsuperscript{a} Tartu Observatory, 51602 Tõrvarre, Tartumaa, Estonia
\textsuperscript{b} Département de géographie, Université de Montréal, Montréal, QC, Canada

1. Introduction

Understanding light interception by vegetation canopies is of paramount importance for estimating canopy productivity (Niinemets, 2010). There are several strategies for plants to optimize canopy light interception, including increasing total foliar area or increasing the efficiency of light harvesting per unit canopy leaf area. However, due to the high biomass costs for leaf exposure it is inevitable that parts of the foliage will remain shaded and thus unable to realize their full productivity potential (Niinemets and Fleck, 2002). Adjusting the leaf inclination angle distribution to improve the transmission of light through the canopy provides an important way to maximize the light availability throughout the entire vertical profile of a plant canopy.

The probability of the transmission of a beam of light in the direction \( \theta \) through a horizontally homogenous canopy can be described by Beer's law (Monsi and Saeki, 1953, 2005):

\[
P(\theta) = \exp\left[-G(\theta)\frac{L}{\cos \theta}\right]
\]

where \( P \) denotes the gap probability, \( L \) denotes the effective leaf area index (Jonckheere et al., 2004), \( \theta \) is the view zenith angle, and \( G \) is the ‘G-function’ defined as the projection coefficient of foliage area on the plane perpendicular to the view direction (Ross, 1981). The quantification of G-function requires knowledge of the leaf inclination angle density distribution function \( f(\theta_i) \), where the leaf inclination angle \( \theta_i \) is defined as the angle between the leaf surface normal and the zenith (Fig. 1).

Despite its importance for radiative transfer, relatively few measurements of leaf inclination angle distributions have been reported for different tree species. Compilation of larger datasets has been hampered due to difficulties in consistently applying existing methods to tree canopies, the unsatisfactory ability of these methods to reproduce measurements, and expensive logistical costs. Recently, Ryu et al. (2010) proposed a robust and affordable method based on digital photography that allows reproducible and consistent measurements of leaf inclination angles. Pisek et al. (2010) showed the method to be capable of providing results comparable to manual clinometer measurements while being simple and affordable, not requiring direct access to the actual leaves of the tree species of interest. However, presently the method is difficult to automate, and substantial user interaction is required to identify suitable leaves to measure leaf inclination angles. It has not been examined yet how user subjectivity might affect leaf inclination angle distribution estimates obtained with digital photography as proposed by Ryu et al. (2010).

It has been noted previously that leaf inclination angle distributions might change with canopy height (e.g. Hutchinson et al., 1986), light exposure (McMillen and McClendon, 1979; Kull et al., 1999; Utsugi et al., 2006) and season (Hosoi and Omasa, 2009; Pisek et al., 2013). However, to the best of our knowledge, no previous study has examined concurrent changes in leaf inclination angle distribution throughout the growing season at
different levels of the canopy. The goal of this study is to examine changes at different heights within the tree canopy over the course of the growing season. To meet this goal the leaf inclination angle distributions of eight deciduous broadleaf tree species commonly found in temperate and hemiboreal ecoclimatic regions of Europe and North America were estimated at several heights throughout the growing seasons of 2011 and 2013.

The study has three objectives. First, the robustness of the digital camera method to measure leaf inclination angle is tested in terms of its sensitivity to subjectivity. Second, we report on the vertical and seasonal changes in leaf inclination angle distributions of eight common broadleaf tree species. Third, we examine how the leaf inclination angle distribution along vertical profiles might vary depending on site-specific environmental conditions by comparing the leaf inclination angle distributions along vertical profiles for the same tree species in stand-alone trees or tree groups and in closed forest stands.

2. Methods and materials

2.1. Study sites

The seasonal and vertical changes in leaf inclination angles were monitored at five different sites: Tartu Observatory, Tõravere, Tartumaa, Estonia (58.27° N; 26.46° E), henceforth referred to as Tõravere; Järvselja, Tartumaa, Estonia (56.27° N; 27.32° E); Tartu, Tartumaa, Estonia (58.38° N; 26.72° E); Kõpu, Viljandimaa, Estonia (58.33° N; 25.30° E); and the Harvard Forest Environmental Measurement Site, Petersham, MA, USA (42.54° N; 72.17° W). In the following text all sites except for Tõravere are referred to by the name first listed.

Leaf inclination angle measurements for five broadleaf tree species in Estonia were made on images taken four times between May and September 2013 at approximately monthly intervals (Table 1). At Tõravere, leaf inclination angles were measured for a gray alder (Alnus incana) plantation (established in 2000); trees planted in a regular 1 m × 1 m grid; mean tree height (H) 16 m; effective L = 2.13, for silver birch (Betula pendula Roth; H = 23 m) and horse-chestnut (Aesculus hippocastanum) trees (H = 20 m). In Tartu, leaf inclination angles were measured for Norway maple (Acer platanoides; H = 20 m) and in Kõpu for an individual aspen (Populus tremula; H = 10 m). Except for A. incana, all trees were located in open parks as stand-alone trees or small clusters of trees.

Additionally, leaf inclination angles were measured for four broadleaf tree species in natural forests. Silver birch (B. pendula Roth) was monitored in Järvselja at the peak of the growing season (08/08/2013) and during senescence (09.21/2013). At Harvard Forest, leaf inclination angles were monitored for red oak (Quercus rubra), red maple (Acer rubrum) and yellow birch (Betula alleghaniensis) trees at monthly intervals throughout the 2011 growing season (May–September; Table 1). The trees were located in a 50–70 year-old mixed-hardwood forest stand (H = 25 m; L = 5.5) near the micrometeorological tower at Harvard Forest. The leaf inclination angle measurements for Harvard Forest were previously shown at the whole-tree level (Pisek et al., 2013).

2.2. Leaf inclination angle measurements and data processing

Leaf inclination angles were measured from images obtained using the leveled digital camera method introduced by Ryu et al. (2010) and validated by Pisek et al. (2011). A series of leveled digital images of the tree crown was taken during calm conditions to prevent wind effects on leaves (Tadrist et al., 2014). The crowns of the trees were reached from poles, ladders, windows of tall buildings, and observational towers. We used a Sony Cyber-shot DSC-HX200V in Tartu and Kõpu, Canon EOS 40D in Tõravere, Canon PowerShot A610 in Järvselja and a Pentax K100D digital single-lens reflex (DSLR) camera at Harvard Forest. None of the lenses used at any of the sites were evaluated for distortions.

To examine the influence of user subjectivity on resulting leaf inclination angle distributions, four tree species were chosen: gray alder (A. incana) from a plantation in Tõravere; Moreton Bay chestnut (Castanopsis australis) and purple trailing lantana (Lantana montevidensis) from the Botanical gardens, Monaco; and olive (Olea europaea) from a public park in Villefranche-sur-Mer, France (Table 1). The leaf inclination angles of each tree species were measured at the whole tree level, i.e., images were not categorized

**Table 1**

<table>
<thead>
<tr>
<th>Tree species name</th>
<th>Location</th>
<th>Date of acquisition</th>
</tr>
</thead>
<tbody>
<tr>
<td>Acer platanoides</td>
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<td>06/01/13, 06/15/13, 07/31/13, 09/08/13</td>
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<td>Acer rubrum</td>
<td>Harvard Forest, USA</td>
<td>05/17/11, 06/14/11, 05/07/11, 08/11/11, 09/02/11</td>
</tr>
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<td>Aesculus hippocastanum</td>
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<td>Alnus incana</td>
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</tr>
<tr>
<td>Betula alleghaniensis</td>
<td>Harvard Forest, USA</td>
<td>05/17/11, 06/14/11, 05/07/11, 08/11/11, 09/02/11</td>
</tr>
<tr>
<td>Betula pendula Roth</td>
<td>Tõravere, Estonia</td>
<td>05/16/13, 06/13/13, 08/11/13, 09/05/13</td>
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<tr>
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<td>08/08/13, 09/21/13</td>
</tr>
<tr>
<td>Castanopsis australis</td>
<td>Monaco-ville, Monaco</td>
<td>07/08/12</td>
</tr>
<tr>
<td>Lantana montevidensis</td>
<td>Monaco-ville, Monaco</td>
<td>07/08/12</td>
</tr>
<tr>
<td>Olea europaea</td>
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<td>07/10/12</td>
</tr>
<tr>
<td>Populus tremula</td>
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<td>05/17/11, 06/14/11, 07/05/11, 08/11/11, 09/02/11</td>
</tr>
</tbody>
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according to different height levels but a combination of photos from all height levels was used. The images were visually inspected for the presence of leaves with their surfaces oriented approximately perpendicular to the viewing direction of the digital camera (Fig. 1). The inclination angles of suitable leaves were measured using the public domain image processing software ImageJ (http://imagej.nih.gov/ij/). It has been suggested that hundreds of leaves should be measured to obtain an accurate representation of the leaf inclination angles (Kucharik et al., 1998). However, a more recent study suggests that around 75 leaves may be sufficient to obtain a representative leaf inclination angle distribution (Pisek et al., 2013). In the current work, approximately 100 leaves were measured whenever possible.

The leaf inclination angle distribution was estimated assuming a uniform distribution of leaf azimuth and leaf inclination angle being independent of leaf size. The measured leaf inclination angles were fitted with the two-parameter Beta distribution (Goel and Strebel, 1984), which was shown to be the best suited for describing the probability density of $\theta_L$ (by Wang et al., 2007):

$$f(t) = \frac{1}{B(\mu, \nu)}(1 - t)^{\mu - 1}t^{\nu - 1}$$

(2)

where $t = 2\theta_L / \pi$. The Beta-distribution function $B(\mu, \nu)$ is defined as

$$B(\mu, \nu) = \int_0^1 (1 - x)^{\mu - 1}x^{\nu - 1}dx = \frac{\Gamma(\mu)\Gamma(\nu)}{\Gamma(\mu + \nu)}$$

(3)

where $\Gamma$ is the Gamma function and $\mu$ and $\nu$ are two parameters calculated as

$$\mu = (1 - \bar{t})(\frac{\sigma_0^2}{\sigma_t^2} - 1)$$

(4)

$$\nu = \bar{t}(\frac{\sigma_0^2}{\sigma_t^2} - 1)$$

(5)

where $\sigma_0^2$ is the maximum standard deviation with expected mean $\bar{t}(\frac{\sigma_0^2}{\sigma_t^2} - 1)$ and $\sigma_t^2$ is variance of $t$ (Wang et al., 2007).

Following Goel (1988), leaf inclination angle distributions can be described using six common functions based on empirical evidence of the natural variation of leaf normal distributions and mathematical considerations: planophile, plagiophile, uniform, spherical, erectophile and extremophile (Fig. 2). For spherical canopies, the relative frequency of leaf inclination angles is the same as the relative frequency of the inclinations of the surface elements of a sphere; for uniform canopies, the proportion of leaf inclination angles is the same at any angle; planophile canopies are characterized by a predominance of horizontally oriented leaves; plagiophile canopies are dominated by inclined leaves, erectophile canopies are dominated by vertically oriented leaves, and extremophile canopies by high frequencies of both horizontally and vertically oriented leaves (Lemeur and Blad, 1974). As these classical distributions are widely used and easier to interpret than the parameter values of the Beta distribution, all measured leaf inclination angle distributions were classified by finding the classical distribution type closest to it. For each leaf inclination angle distribution, its deviation from the distributions suggested by de Wit ($f_{deWit}(\theta_L)$) was quantified using a modified version of the inclination index provided by Ross (1975):

$$\chi_t = \int_0^{\pi/2} |f(\theta_L) - f_{deWit}(\theta_L)|d\theta_L$$

(6)

2.3. User subjectivity

In order to assess the robustness of the leveled digital camera method in terms of its sensitivity to user subjectivity, ten users
measured leaf inclination angles from four image sets. Among them were the lead author and two co-authors of the paper, three students from the Université de Montréal and four students from the University of Tartu. Their previous experience with the method ranged from beginners with no prior knowledge of leaf inclination angle measurements to experts well acquainted with the leveled digital camera method. The results were compared in terms of the respective mean leaf inclination angles, their standard deviations and resulting Beta distributions.

2.4. Changes in leaf inclination angle distribution with height over the growing season

Vertical changes in leaf inclination angle distributions over the growing season were examined for five broadleaf tree species in Estonia. The images were taken at several height levels and grouped into three broad height categories – bottom, middle, and top of canopy – dividing the canopy into three approximately equal parts. However, for top of canopy measurements images from the top-most 2–3 m were used. Photos were taken from close range or with large zoom, thus significant vertical overlapping of photos did not occur. The leaf inclination angles measured from each image set were fitted with the Beta distribution and matched with the closest de Wit’s theoretical leaf inclination angle distributions. Since all of the five observed tree species were located in open areas, four additional tree species from natural forests were studied to assess the effects of different exposure to light. These included *B. pendula* Roth from Järvselja, and *A. rubrum, B. alleghaniensis,* and *Q. rubra* from Harvard Forest. Similarly, leaf inclination angles were measured several times over the growing season and grouped accordingly into the three broad height levels (Table 1). The obtained leaf inclination angle distributions were compared with the results from the five tree species monitored at mostly open locations in Estonia.

3. Results and discussion

3.1. User subjectivity

Generally, it can be seen that the method is quite robust in providing the same distributions of De Wit (1965) irrespective of the user and their previous experience with measuring leaf inclination angles (Tables 2 and 3). For *C. australis* all ten users estimated planophile leaf inclination angle distributions, with the mean leaf inclination angle varying between 26.36 and 32.16°. *L. montevidensis* was estimated to be uniform in nearly all cases with one spherical exception. Leaf inclination angle distributions for *A. incana* were predominantly planophile with two of the datasets showing plagiophile results. The mean leaf inclination angles for the two tree species were between 36.72 and 54.09°, and 29.27 and 40.52°, respectively. It should be noted that for *L. montevidensis* the suggested minimum sample size of 75 leaves was not always reached (Table 3), as the pool of available photos was not sufficient for all users to identify enough suitable leaves.

The only tree species for which differing leaf inclination angle distributions were obtained among the ten users was *O. europaea*. Results varied evenly between spherical, plagiophile and uniform, with mean leaf inclination angles ranging between 42.64° and 54.44°. The most likely cause is the long, narrow shape of the leaves, which can be easily misidentified while searching for leaves oriented perpendicular to the viewing direction. Repeated measurements for this species carried out by the two experienced users consistently resulted in a spherical distribution with the mean leaf inclination angle between 51.24° (standard deviation = 21.17°) and 55.63° (standard deviation = 17.96°), suggesting that the lack of agreement among users is likely due to lack of previous experience with the method. Despite the discrepancy for *O. europaea* the leveled digital camera method can be considered relatively robust for most broadleaved species, however it should be used with care for plants with elongated leaves.

3.2. Changes in leaf inclination angle distributions with height over the growing season

*A. hippocastanum* remained mostly plagiophile throughout the growing season with little variation in height (Fig. 3). Noticeable was a change toward planophile in June when changes in leaf inclination angles were observed over the entire vertical profile with the most pronounced deviation from plagiophile at the canopy top (Fig. 3D). In spring the variation was caused by the fact that the leaves initially emerged pointing downwards and gradually became more horizontally oriented until fully expanded in early summer. *Aesculus* has been shown to senesce early and to have
Aesculus hippocastanum

Acer platanoides

Fig. 3. Seasonal and vertical variation of leaf inclination angle distribution for Aesculus hippocastanum.

Fig. 4. Seasonal and vertical variation of leaf inclination angle distribution for Acer platanoides.

short leaf longevity (Augspurger and Bartlett, 2003), together most likely resulting in weakening of leaves in the second half of the season and the turn toward plagiophile, especially in the well-exposed canopy top.

A. platanoides was strongly planophile over the entire vertical profile throughout most of the growing season (Fig. 4). The only difference can be seen at the canopy top in spring and autumn (Fig. 4B). Early in spring the top started out as plagiophile. Similar to A. hippocastanum, the leaves of A. platanoides emerged oriented downwards and became more horizontally oriented when fully expanded. This change is visible only at the canopy top because by mid-May leaf expansion was already completed in the lower sections of the canopy, possibly due to greater shading (Seiwa, 1998; Augspurger and Bartlett, 2003). The canopy remained planophile until the end of the summer, when senescence began at the canopy top, the petioles weakened and the distribution became plagiophile again.

A. incana showed minor but continuous changes throughout the growing season (Fig. 5). The leaf inclination angle distribution was strongly planophile in the spring over the entire vertical profile; the distribution remained planophile for most of the growing season, however, the proportion of horizontally oriented leaves decreased continuously. There was even some change toward uniform (upper canopy) or plagiophile (lower canopy) in autumn. Under calm conditions leaf inclination angles depend on petiole mechanical properties and the lamina load on petiole (Niklas, 1991, 1992). The seasonal change here was most likely caused by the increasing lamina size, which resulted in steeper leaf inclination angles. The change was again the greatest at the canopy top where the proportion of horizontally oriented leaves in the spring noticeably exceeded those at lower canopy levels.

P. tremula was planophile in the spring and mostly uniform throughout the rest of the growing season (Fig. 6). The leaves first appeared somewhat horizontally oriented. Subsequent seasonal change resulted in no real preferred orientation for the leaves. The leaves at the bottom of the canopy retained some of their horizontal orientation due to limited light availability (Niinemets, 1998). The rest of the tree had a uniform distribution. By the end of the
season the top turned plagiophile, most likely due to the aging of leaves.

*B. pendula* Roth (Fig. 7) was erectophile throughout the growing season with little seasonal or vertical variation. The only noticeable change was observed at the bottom of the canopy, where the downward hanging leaves lifted slightly and changed the distribution into plagiophile during the peak of the growing season (June–July), likely due to reduced light availability.

It has been noted that shade-tolerant tree species tend to have more horizontally oriented leaves, whereas the leaves of shade-intolerant tree species are characterized by steeper leaf inclination angles (McMillen and McClendon, 1979; Pearcy et al., 2004). Accordingly, as the shade-intolerant *B. pendula* Roth exhibits an erectophile distribution, slightly less shade-intolerant *P. tremula* has a uniform leaf inclination angle distribution and the leaves of shade-tolerant *A. platanoides* are oriented horizontally (Portsmouth and Niinemets, 2007).

It is apparent that for most of the studied tree species the change in leaf inclination angle distribution was the greatest in early spring, soon after the emergence of leaves. The direction of this change can go both ways toward steeper or more horizontal leaf inclination angles, depending on the cause of the change. The unfolding of leaves tended to decrease the leaf inclination angle (Figs. 3 and 4), whereas lengthening of the petiole and increase in lamina mass increased the leaf inclination angle (Niinemets, 1998). Yamada et al. (2000) showed that leaf blades expand faster compared to petiole elongation, thus indicating that some of the gradual change toward steeper angles (such as the small but continuous increase in leaf inclination angles for *A. incana*) can be caused by the petioles still lengthening while the leaves are already fully formed.

For the later part of the growing season the type of theoretical approximation remains the same for the majority of the studied tree species. An exception might be during late summer, when leaf inclination angles can again become steeper, possibly because of simultaneous increases in lamina mass and area with increasing leaf age (Gordon and Promnitz, 1976; Hamerlynck and Knapp, 1996). Furthermore, the seasonal changes are greater at canopy top and bottom than in the middle of crown. No other notable patterns
were found for differences in leaf inclination angle distributions at separate heights of the canopy for the studied tree species.

3.3. Variations in leaf inclination angle distribution due to different light exposure

The five previously discussed tree species were mainly observed in parks. Thus the studied trees were more exposed to light than they would be in a natural forest stand, with the exception of *A. incana* which was located in a dense plantation. In the following we investigate how different light exposure influences the leaf inclination angle distribution.

Fig. 8 illustrates the vertical variation of leaf inclination angle distributions for *B. pendula* Roth observed in Järveslja. It can be seen that the distribution was erectophile at the canopy top (Fig. 8B), similarly to the trees studied under higher light exposure (Fig. 7B), however, with decreasing height the leaf inclination angles were progressively more horizontally oriented, resulting in a planophile distribution at the bottom (Fig. 8D). Similar change with greater canopy depths was previously shown (e.g. Hutchinson et al., 1986; Hollinger, 1989; Niinemets, 1998). This variation might be caused by different light exposure at different height levels within the canopy. At the canopy top light is frequently received in excessive amounts, potentially resulting in water stress and photo-inhibition of photosynthesis during midday hours (Ball et al., 1988). Steeply inclined leaves help avoiding excessive light exposure, enable a greater amount of light penetration deeper into the canopy, and absorb solar radiation with a low incident angle more effectively (King, 1997). In contrast, the more horizontally oriented leaves at the bottom of the canopy produce an increasing efficiency of light interception at lower intensities (Ford and Newbould, 1971). With higher light availability this stratification is not necessary, explaining the lesser variation in leaf inclination angle distribution for the park-grown *B. pendula* Roth in Tõravere.

In the case of *A. rubrum* the vertical variation in leaf inclination angles was much smaller compared to *B. pendula* Roth (Fig. 9). As with *A. platanioides* (Fig. 4), the leaf inclination angle distribution was plagiophile in the spring and remained planophile throughout
the rest of the growing season for the entire vertical profile. Despite the fairly constant distribution type it can be seen that the leaf inclination angles were slightly less horizontal in the upper canopy. However as the tree is planophile, it was not possible to observe a strong exposure-related vertical difference similar to B. *pendula* Roth.

Analogous to *A. rubrum*, the leaf inclination angle distribution of *Q. rubra* was mainly planophile throughout the season (Fig. 10). Again, seasonal variation was clearly seen in the spring before full leaf expansion, while the rest of the season was rather invariant. Considering the horizontal orientation of the leaves, vertical variation in leaf inclination angle distributions related to different exposure was not observed.

*B. alleghaniensis* is the suppressed tree species in Harvard Forest (Fig. 11). As light availability is limited over the entire vertical profile, the leaf inclination angle distribution was planophile at all heights to maximize light use (our results for *B. pendula* Roth suggest this might be different in more exposed locations). With the exception of the bottom of the canopy no seasonal change was observed (Fig. 11D). This can be due to earlier budburst and leaf growth for sub-canopy tree species (Augspurger, 2008), resulting in close to fully developed leaves by the time of the first measurement.

Among the four studied tree species only *B. pendula* Roth clearly exhibited vertical differences in leaf inclination angle distributions characteristic of a closed forest stand (Hutchinson et al., 1986; Niinemets, 1998). The lack of variation for the remaining tree species mainly resulted from dominant horizontally oriented leaves regardless of light exposure. Although supporting a uniformly planophile canopy is not the most effective strategy in terms of maximizing single tree productivity, it allows shading out other tree species and thus gives a competitive advantage over tree species with steeper leaves, which is likely the cause of planophile tree species dominating late-successional forests (Hikosaka and Hirose, 1997).
The findings for *B. pendula* Roth confirm the vertical variation of leaf inclination angles reported by e.g. Kull et al. (1999), Werner et al. (2001), and Utsugi et al. (2006). The example of *B. pendula* Roth also suggests that leaf orientation can vary greatly with light exposure, thus we recommend to obtain actual leaf inclination angle measurements whenever feasible.

4. Conclusions

In this study seasonal and vertical changes for deciduous broadleaf tree species characteristic for temperate and hemiboreal ecolimatic regions were examined by tracking leaf inclination angle changes of eight selected tree species at three different height levels throughout the growing season. Additionally, the leveled digital camera method used to measure leaf inclination angles was tested in terms of user subjectivity and uncertainty. Based on our findings, we conclude:

- The leveled digital camera method is relatively robust and provides similar leaf inclination angle distributions irrespective of the user. However, when measuring leaf inclination angles of tree species with more complex leaf structure (e.g., elongated leaves as for *O. europaea*) some previous practice with the technique is warranted.
- The leaf inclination angle distribution is the most variable in spring and remains comparatively constant throughout the remainder of the growing season. Some tree species also exhibit different distributions in late summer. The change in distribution tends to be the most pronounced at the top of canopy, whereas middle and bottom vary less throughout the season.
- Different light exposure has a strong effect on species with steeper leaf inclination angles. In contrast, the leaf inclination angles of canopies with more horizontally oriented leaves do not vary considerably with different light exposure.

As leaf inclination angle distribution can be a highly variable characteristic depending on a number of factors, it is recommended to use leaf inclination angle distributions derived from actual measurements whenever feasible. However, if this is not possible, the generalizations found in this paper for the given tree species can be considered a useful first-order approximation.

Acknowledgments

This study was supported by the funding from the Estonian Science Foundation Grant no. PUT232 ‘EST-SEEDS’. The authors would like to thank the undergraduate students from Université de Montréal and University of Tartu who volunteered to participate in the subjectivity component of our study. The authors are indebted to Andrew Oliphant for English style corrections. We also greatly acknowledge the anonymous reviewer whose comments greatly helped to improve the original manuscript. All the leaf inclination angles measured in this study will be made publicly available through the TRY database (https://www.try-db.org).

References


