Conversion of total leaf area to projected leaf area in lodgepole pine and Douglas-fir

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Summary Three definitions of leaf area index (LAI) in the literature have no predictable relationship with each other. Factors were derived for converting total LAI to projected LAI of horizontal leaves and to projected LAI for inclined leaves of lodgepole pine (Pinus contorta Dougl. var. latifolia Engelm.) and coastal Douglas-fir (Pseudotsuga menziesii (Mirb.) Franco) to allow comparison of results from different studies. An algorithm was derived to allow determination of these factors based on twig angles and the angles that the foliage subtends with the twig. Allowances were made for both the vertical and horizontal components of projection. The value of the factor for converting total LAI to projected LAI for inclined leaves was 0.229 + 0.0032 for lodgepole pine and 0.230 + 0.0037 for Douglas-fir. Sensitivity analysis established that this conversion factor was more sensitive to differences in vertical angles of the twigs than to twig rotation or foliar arrangement on the twig.

Keywords: leaf area index, Pinus contorta, Pseudotsuga menziesii, sensitivity analysis.

Introduction

Leaf area is a major determinant of photosynthesis in forests and hence the measurement of leaf area is important in assessing growth potential. There are currently at least five common measures of leaf area index (LAI): (i) total leaf area per unit area of horizontal land below, TLAI, is based on the total outside area of the leaves, taking leaf shape into account; (ii) total one-sided leaf area per unit area of horizontal land below (Watson 1947, Price 1993, Smith et al. 1993) is usually defined as half of the total leaf area, even if the two sides of the leaves are not symmetrical; it is a commonly used parameter because it represents the gas exchange potential; (iii) projected area of horizontal leaves per unit of horizontal land below, PLAI, (Running et al. 1986, Grace 1987, Gong et al. 1992) is defined as the area of horizontal shadow that would be cast beneath a horizontal leaf from a light at infinite distance directly above it; this measurement is common in remote sensing applications, because it represents the maximum leaf area that could be seen by sensors from overhead; (iv) projected area of leaves inclined to the horizontal (Smith et al. 1991, Stenberg 1996), called silhouette leaf area index (SLAI) by Smith et al. (1991), is a useful measure for modeling the effects of light penetration through a canopy (Chen and Black 1991, Lang 1991, Chen and Black 1992) and for remote sensing, because it is equivalent to the area for intercepting light and represents what would be observed by a nadir view from above, ignoring leaf overlaps; and (v) projected area of inclined leaves, but counting overlapping areas only once; this measure is common in remote sensing applications, because it represents the proportion of ground obscured by foliage in a remotely acquired image. This paper deals with the first (TLAI), third (PLAI) and fourth (SLAI) definitions listed above.

If leaves are fairly flat, horizontally projected leaf area can be directly measured on foliage samples with a video imaging system. Direct measurement of total leaf area can be done with calipers together with careful measurements of the shape of the leaf throughout its length (Madgwick 1964). Inclined leaf area can be assessed indirectly by measuring light transmission within stands with a modified photometer, such as the Decagon Devices Ceptometer (Decagon Devices, Inc., Pullman, WA) or the Li-Cor LAI-2000 (Li-Cor, Inc., Lincoln, NE) (Deblonde and Penner 1994). Other indirect methods of estimating LAI include measuring tree diameter, sapwood cross-sectional area and litter fall (Marshall and Waring 1986), as well as remote sensing (Running et al. 1986). Direct measurement is usually accurate but extremely time-consuming; in addition, significant sampling error may occur either as a result of small sample sizes or because sampling is restricted to certain parts of the tree. On the other hand, photometers require conversion factors for use with conifers to overcome biases caused by light interception by boles and branches and by non-randomness of the leaves (Gower and Norman 1991). For measurements made with the LAI-2000, leaves are assumed to be randomly oriented in space, which implies a spherical distribution of needle angles, with the three-dimensional angle probability uniformly distributed around a sphere. Although, leaf angle distributions are usually assumed to be spherical (Lang 1991, Chen and Black 1992) or elliptical (Campbell 1986, Wang and Jarvis 1988), the direct measurement of leaf angles has not been reported.

Most published values of LAI are for one-sided total LAI (e.g., Curran and Williamson 1987) or for horizontally projected LAI (e.g., Gower and Norman 1991). To make comparisons among studies, there is a need for factors to convert
among these three definitions of LAI. These conversion factors will presumably be specific to foliar growth patterns, because conifer species show different patterns of foliar arrangement that will translate into different mean proportional projections. Here the term projection coefficient is used to quantify the conversion between total LAI and silhouette LAI, and is taken to be SLAI/TLAI.

This paper has two goals: (i) to derive factors for converting total leaf area index to projected leaf area index of horizontal and inclined leaves for interior lodgepole pine (Pinus contorta Dougl. var. latifolia Engelm.) and coastal Douglas-fir (Pseudotsuga menziesii (Mirb.) Franco) by determining leaf angles and then calculating projection coefficients from these angles; (ii) to provide a methodology for determining these factors without having to measure the actual orientations of individual leaves in space. No attempt is made to calculate vertical or inclined leaf overlap, as would be required to estimate LAI from a remotely sensed image using the fifth definition of LAI above.

Materials and methods

For lodgepole pine, the actual leaf angles in space were measured, whereas for Douglas-fir, the twig angles and leaf arrangements around the twigs were measured and a transformation was then derived and applied to convert these measurements to leaf angles. Because branches and foliage tended to distort when stored for more than a few days, measurements were made as soon as possible after the trees were cut. Branches that were noticeably distorted were not measured.

Lodgepole pine

In mid-May 1996, five lodgepole pine trees were cut from a stand at Saturday Creek near Princeton, B.C., Canada (49°17′N, 120°35′W). The five trees ranged from 21.1 to 31.0 cm diameter at breast height, 13.8 to 20.9 m in height and 106 to 123 years old. Every 20th branch (including small shoots of the past year) was sampled, starting with the leader, for a total of 25 branches from the 5 trees, and the angle that the branch subtended with the bole was noted. The branches were transported to the laboratory and set up with these same branch angles; three to six foliated twigs were sampled from each branch. From each twig, 12 needle pairs were chosen to represent the distribution around the twig. In cross section, with the two halves pointing in slightly different directions. Total leaf area was taken as the area of the outside of the leaf plus the area of the inside of the leaf. The outside area is approximately \( \pi/2 \) times the largest projected area of a horizontal leaf, whereas the inside area, being approximately flat, is equivalent to the largest projected area. Thus, the factor to convert total leaf area (TLAI) to projected area of horizontal leaves (PLAI) is \( 2/(\pi + 2) = 0.3890 \). Because

needles are oriented in various directions, the angles along both the longitudinal and lateral leaf axes were considered when calculating projection coefficients to convert TLAI to SLAI. The longitudinal orientations of individual needles were measured, and the projected proportion for a given needle was calculated as the sine of its value from the vertical. The mean of these sine values was used to calculate the mean projected proportions associated with longitudinal obliqueness. This mean value was further modified by applying a reduction factor to account for lateral obliqueness. Although this reduction factor depends on the relative orientation of a needle pair with respect to the twig, a mean value was determined by finding the expected projected area of a hemi-cylinder held horizontally and rotated about its longitudinal axis, assuming the extent of rotation was random and varied according to the uniform probability distribution. The projected fraction of the hemi-cylinder from \( \delta = 0 \) to \( \delta = \pi/2 \) is \( (1 + \cos(\delta))/\pi \), and the mean projected proportion, \( p \), of the total area is:

\[
p = \int\left[1 + \cos(\delta)\right]/\pi d\delta = [\delta + \sin(\delta)]/\pi, \tag{1}
\]

evaluated when \( \delta \) goes from 0 to \( \pi/2 \) (Parzen 1960), which is \( (\pi + 2)/2\pi = 0.818 \). The other three quadrants have different formulations, but all give the same mean. This factor was then applied to the mean projected proportion to yield the overall projection coefficient (\( \lambda \)).

Douglas-fir

In late July 1996, six Douglas-fir trees were cut from an experimental plantation at Shawnigan Lake, B.C. (48°38′N, 123°43′W, at an altitude of 270 m). The six trees ranged from 9.1 to 30.4 cm diameter at breast height, 11.1 to 24.1 m in height and 26 to 45 years old. Three trees were from a control plot (thinning level 1) and three from a plot that had been thinned to one-third of its original basal area (thinning level 2) in 1970 when the trees were age 24 (Crown and Brett 1975). One branch from every third whorl was sampled for a total of 35 branches from the 6 trees, although the leader and the first three whorls were sampled as a unit, and the angle that each branch subtended with the bole was noted. The branches were transported to the laboratory and mounted with these same branch angles. From each branch, a subsample of twigs was measured for azimuth and angle from the vertical as well as for length. Here a twig is defined as 1 year’s growth on a single shoot. In most cases, every fourth twig was sampled, although on small branches every twig was measured, whereas on large branches as few as every tenth twig was measured. In addition, five representative twigs along the length of the branch were cut and examined to determine leaf arrangement around the twig and the angle of the leaves along the twig in the plane of the leaf and twig. Leaf arrangements were categorized into three classes (Figure 1). Each class was schematically characterized by a set of 20 needle angles (estimated optically) from the vertical (Table 1) for use in computation. Because Douglas-fir needles are flattened in cross section, an allowance was made for the fact that different rotational orientations about the longitudinal axis would expose different
Table 1. Schematic angles of 20 representative leaves of Douglas-fir (degrees from vertical) associated with each of the three foliar arrangements around the twigs shown in Figure 1.

<table>
<thead>
<tr>
<th>Foliar arrangement</th>
<th>Leaf angles from the vertical (°)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>40, 45, 50, 55, 60, 70, 80, 90, 100, 110, 250, 260, 270, 280, 290, 300, 305, 310, 315, 320</td>
</tr>
<tr>
<td>2</td>
<td>5, 10, 15, 20, 30, 40, 50, 70, 100, 140, 220, 260, 290, 310, 320, 330, 340, 345, 350, 355</td>
</tr>
<tr>
<td>3</td>
<td>2, 5, 10, 15, 20, 30, 40, 60, 80, 100, 260, 280, 300, 320, 330, 340, 345, 350, 355, 358</td>
</tr>
</tbody>
</table>

Because the orientations of individual needles were not measured, a geometric algorithm was derived to calculate the distribution of needles in space from: (i) the mean needle angle from the twig; (ii) axial angle that the foliage was rotated from the vertical; (iii) angle of the twig from the vertical; and (iv) twig length.

Because the orientations of individual needles were not measured, a geometric algorithm was derived to calculate the distribution of needles in space from: (i) the mean needle angle from the twig; (ii) the arrangement of foliage around the twig (Figure 1); (iii) the axis of orientation of the foliar arrangement (Figure 2); and (iv) the vertical twig angles. The measurement taken on each twig were: (i) mean needle angle; (ii) the arrangement of foliage around the twig; (iii) angle of the twig from the vertical; and (iv) axial angle that the foliage was rotated from the vertical.

Because there are leaves pointing in many directions around the twig, several values around the twig were obtained and analyzed. When these values (Table 1) were substituted into the above steps they yielded many leaf projections on the x–y plane, from which mean values were calculated for a given twig. The twig length was then used to calculate weightings to be applied if there is significant variation in leaf angle with height, position on the branch, etc.

Algorithm for calculating projected length

The assignments and transformations required to compute leaf angles from the data available are described in order of application. Mathematical details are given in the Appendix.

(1) Place the leaf in a coordinate system with one end at the origin. Assign a unit vector to represent the leaf and let the twig be coincident with the x-axis.

(2) Based on the angle between the leaf and the twig, determine the coordinate values of the end of a leaf when the leaf is above the twig.

(3) Rotate the leaf through its appropriate angle around the longitudinal axis of the twig (Table 1) according to its position in the designated foliar arrangement (Figure 1). Determine the coordinates of the free end of the leaf. Repeat the process for each of the 20 needles in the designated foliar arrangement.

(4) Rotate the twig around its axis so that the axis of the foliar arrangement is at the measured axial angle, and recalculate the coordinates of the free end of each leaf (Figure 2).

(5) Rotate the twig vertically to its measured angle. Recalculate the coordinates of the free ends of the 20 leaves.

(6) Calculate the reduction in projection caused by longitudinal inclination of each leaf.

(7) Calculate the reduction in projection caused by lateral inclination of each leaf.

(8) Apply the factor 0.9/2 to eliminate the effects of curvature. The resulting values were then averaged to calculate the mean projection coefficient (λ).

Figure 1. Diagrammatic representation of the three foliar arrangements around the twigs noted in Douglas-fir.

Figure 2. One foliar arrangement around a twig in cross section, showing the axial angle (α) and the angle of one needle from the vertical (β) measured from the axial plane.
A sensitivity analysis was performed on the four foliar measures of: (i) angle of the leaves from the twig axis; (ii) type of foliar arrangement around the twig (Figure 1); (iii) axial angle of the foliage on the twig (Figure 2); and (iv) twig angle from the vertical. In each case, the angles with respect to each measure were incremented by 10° and the resulting projected proportions ($\lambda$) were recalculated, so that eventual rotation of a full circle was accomplished.

**Results**

*Lodgepole pine*

The distribution of leaves in the vertical direction was not random, rather the leaves were oriented preferentially toward an angle somewhat above the horizontal (Figure 3) with a mean angle of 60° from the vertical. This distribution clearly does not follow either the spherical distribution or the elliptical distribution postulated by Campbell (1986), Wang and Jarvis (1988) and Chen and Black (1991), because both of these distributions are symmetrical about the horizontal. Hence, the parameters for the elliptical distribution were not fitted to the data here. The mean angle of 60° was based on the distribution from 0 to 180°. If a leaf angle $\theta$ is taken to be the same as 180° – $\theta$, on the grounds that they have the same projection (as was assumed by Wang and Jarvis 1988), then the mean angle taken from 0 to 90° is 56°, which is remarkably close to the mean angle of a spherical distribution of one radian (i.e., 57.3°).

The mean longitudinal projected proportions in lodgepole pine did not vary much with tree size ($P > 0.05$). The standard deviations were generally about 20 to 30% of the mean. Large standard deviations are to be expected, because the orientation of leaves varies considerably around the twig. Branch position had a slight effect on leaf orientation, with top branches (Branch 1) having leaves oriented slightly closer to the vertical than lower branches (Figure 4).

The lengths of the leaves varied little with tree size ($P > 0.05$), but showed a marked increase with branch height within the trees, although most of the differences resulted from leaves on the highest and lowest branches. This implies that sampling for foliage within a tree should be done either throughout the crown or at least in the intermediate branches to avoid bias.

The value of the overall factor ($\lambda = \text{SLAI}/\text{TLAI}$) for converting total leaf area index (TLAI) to projected leaf area index for inclined leaves (SLAI) was the product of the factors for converting TLAI to PLAI and PLAI to SLAI. The former is $2/(\pi + 2) = 0.3890$. The factor for converting PLAI to SLAI is the product of (i) the mean of the sines of the angles, 0.7184, and (ii) the reduction factor due to random rotation of the hemi-cylinder, 0.818; this product was 0.588, for a sample size of 1488 needle pairs. Thus the overall factor $\lambda = (0.3890)(0.588) = 0.2287$, with a standard error of 0.0032 based on the mean projection coefficients for the five trees.

Although this estimate should be accurate for lodgepole pine trees of similar age growing under similar conditions, it is not known how well it represents other site qualities and other ages. However, the small variation in this estimate with tree size and age suggests that values for other stands will not differ greatly from 0.23.

If leaves were oriented randomly in all directions, the mean value of the sines of the longitudinal angles can be found by...
obtaining the mean of $\sin(\theta)$ where $\theta$ varies according to a spherical distribution over the interval $(0, \pi)$. The spherical distribution is given by the density function, (Feller 1971):

$$f(\phi, \theta) = \cos(\theta)/4\pi,$$

for $-\pi < \phi < \pi$, and $-\pi/2 < \theta < \pi/2$,

where $\phi$ is equivalent to longitude (or azimuth) and $\theta$ is equivalent to latitude (or altitude) on the sphere and is measured from the horizontal. The angles measured in the samples taken from the field were the angles from the vertical rather than the horizontal, so that in calculating the means of the sines of the vertical angles, we substituted $90^\circ - \theta$ for $\theta$. The mean of $\sin(90^\circ - \theta)$ is given by:

$$E[\sin(90^\circ - \theta)] = \int \cos(\theta) \cos(\theta)/2 \, d\theta,$$

evaluated from $-\pi/2$ to $\pi/2$, which equals $\pi/4 = 0.7854$. This is only slightly greater than the observed value of 0.7184.

**Douglas-fir**

The angles of the needles from the axis of the twig were significantly affected only by tree diameter ($P < 0.0001$) and ranged from about $53^\circ$ for trees of large diameter to $64^\circ$ for trees of small diameter with a grand mean of $58^\circ$ (SD = 10°, SE = 0.8°, $n = 160$). Because thinning had virtually no effect on needle angle, it was used as a replicate in the statistical analysis. Foliar arrangement appeared to be affected by diameter and height within the tree (Figure 5), but these were not tested statistically because foliar arrangement category is only a nominal variable.

Axial angle and twig angle were not affected by thinning or tree height (whorl), but variability in both measures was considerable. Mean axial angle was $32^\circ$ (SD = 40°, SE = 1.3°, $n = 921$) and mean twig angle was $87^\circ$ from the vertical (SD = 36°, SE = 1.2°, $n = 921$). The projection coefficients also did not vary much with thinning or whorl position (Figure 6), although top branches (Whorl 1) had needles oriented somewhat closer to the vertical than branches on lower whorls. Thus, position of sampling within the crown and tree size are of minor importance when designing a sampling scheme to determine leaf orientation. The standard deviations were generally about 20 to 30% of the mean, because the orientation of leaves varies considerably, even around the twigs.

The distribution of the leaf angles from the vertical indicated a preference for angles somewhat above the horizontal, with a mean of $72^\circ$ from the vertical (cf. Figures 3 and 7) based on taking the mean from 0 to 180°. If the supplementary angles are considered equal, this mean is reduced to $57^\circ$, which is the same as for a spherical distribution of one radian between 0 and 90°.

The value of the overall factor ($\lambda$) for converting TLAI to SLAI was $\lambda = 0.230$ (SD = 0.0477, SE = 0.0016, $n = 921$); the standard error based on the mean projection coefficients of the six trees was 0.0037. The component due solely to longitudinal projection was 0.786 (with a standard deviation of 0.223), with the reduction due to lateral leaf projection and the curvature of the two faces of the leaves accounting for the difference. If the leaves were oriented randomly in all directions, then the mean value of the sines of the angles equals $\pi/4 = 0.7854$, which is almost identical to the measured value of 0.786.

The sensitivity analysis is shown in Figure 8. Even with a full circle of rotation, little variability of the projection coefficients ($\lambda$) was obtained. The calculated value was 0.230 and the values under rotation of the four foliar quantities varied between 0.21 and 0.26, with the greatest variation resulting from perturbing the vertical angles of the twigs and the least variation from perturbing the axial angles of the foliar arrangements.
Discussion

In a few lodgepole pine leaf pairs, the two halves lie against each other forming a cylinder. Some are twisted, but in most cases the two halves lie slightly apart and must be treated as two leaves. The twigs were slightly curved, which necessitated the sampling of foliage along the length of the foliated part of each twig. The method of computation of the projection coefficient for lodgepole pine was time-consuming, but the result appears robust (SE = 0.0053). The sensitivity analysis applied to the Douglas-fir needles was not appropriate for lodgepole pine, because the twig angles were not recorded making calculation of needle angles on twig rotation impossible.

Both lodgepole pine and Douglas-fir needles are arranged in a highly regular fashion. The directions spanned by the needles are predictable, because the needles are arranged in repeating patterns around the twig, which accounts for most of the variability on any given twig. Hence when sampling foliage for measurement of leaf orientation, it may be sufficient to sample relatively small numbers of twigs, provided that care is taken to sample from representative locations around the tree, with an adequate representation of different twig orientations. In aggregate, the leaves span the range of vertical orientations but with a distribution quite different from either a uniform or spherical distribution, both of which are symmetrical. However, the projection coefficients for both lodgepole pine and Douglas-fir (0.23) are close to values obtained for a variety of shapes under random orientations with a spherical distribution (0.25) (Chen and Black 1992), as also are the mean angles from the vertical, if supplementary angles are taken as being equal for the purpose of projection. Thus, it appears that the spherical distribution describes certain aspects of needle distribution quite well, even though the distribution of directed needle angles (base to tip) is quite different from the spherical distribution.

The sensitivity analysis showed that twig angle makes the greatest difference to the calculated projected proportion in Douglas-fir, indicating the importance of sampling twigs throughout their vertical angle distribution. The curves for needle angle and twig angles are relatively smooth, because there is little or no interaction with the other measures. The curves for axial angle and foliar arrangement are irregular, because these two measures interact strongly with each other, and different leaf arrangements will yield different effects of changing axial angle. Varying the twig angle simulates changing the direction of view from vertically above the tree, down through the horizontal, through vertically beneath the tree and back up to the zenith again. Alternatively, it also simulates the effect of a beam of light swinging through a circular arc including both the zenith and nadir. In neither case does the resulting value of $\lambda$ vary greatly.

The calculations were made only on individual twigs and the results averaged; the azimuths of the twigs were ignored. This average variation in projection coefficient with varying twig angle represents an overestimate for a tree because few branches on the tree will undergo the full vertical change for any given change in vertical viewing aspect; many branches will be oriented obliquely and this change in viewing aspect (rotation of the twig) will be better described by an axial rotation, which has little effect on the projection coefficient. In addition, views of trees from slightly off nadir in remotely sensed optical images will be little biased by the lack of a vertical view. Even Synthetic Aperture Radar (SAR), in which the whole image has a slant view, will not be strongly biased in terms of the apparent needle angles it sees. This, however, does not take account of branch geometry (Horn 1971, Ross 1981); the outline of the crown itself will be quite different
from the side than when viewed vertically, and this may significantly affect the apparent leaf area index.

The sun at mid-latitudes usually lies between 30 and 60° altitude. In this range, the effect of twig angle is to increase the projection coefficient, especially nearer 45°. This implies that foliage is nearly optimally oriented to catch maximal radiation for much of the day. On cloudy days the light from the sun will be diffused and will come from all directions in the sky. Thus, the optimal foliage orientation will be different from that on clear days. In addition, unpredictable shading from other trees will render parts of the foliage less efficient. Thus, the orientation of the foliage would appear to be a compromise between optimality for a clear sky and that for a cloudy sky and unpredictable shading.

Values of the projection coefficient for lodgepole pine and Douglas-fir were similar, suggesting that such a value is nearly optimal for capturing sunlight under a variety of conditions. Corresponding values for other species with similar foliage growth patterns will probably be similar, because evolution in all tree species would be expected to result in foliage arrangements that optimize the light gathering ability of foliage, although selection may result from other factors as well, such as cold stress (Smith and Brewer 1994).

Acknowledgments

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References


Appendix

Description of the algorithm

(1) First construct a rectangular parallelepiped to represent a leaf as the unit vector \((x_1, y_1, z_1)\) (Figure 9). The attached end of the leaf then has coordinates \((0, 0, 0)\) and the free end has coordinates \((x_1, y_1, z_1)\). Assuming that azimuth is unimportant, we can consider without loss of generality that the attached end of the leaf is at the origin and the twig is coincident with the \(x\)-axis in the positive direction. The assumption that the leaf is one unit in length is unimportant because we only need the projected proportion. For a vector \(V\) of unit length with one end at \((0, 0, 0)\):

\[
\sum_{i=1}^{3} x_i^2 = 1.
\]

This vector makes angles \(\chi, \omega,\) and \(\zeta\) with the \(x, y\) and \(z\)-axes, respectively, and \(x = \cos(\chi), y = \cos(\omega)\) and \(z = \cos(\zeta)\). Then \(x, y\) and \(z\) are direction cosines of the three angles.
The projection of the vector V onto the x-y plane is the vector A, whose length is:

\[ x_1^2 + y_1^2 = \cos^2(\chi) + \cos^2(\omega) = 1 - \cos^2(\zeta) = 1 - z_1^2 \]  
(5)

(Figure 9).

(2) Next determine the coordinates of the free end of the leaf when it is directly over or under the x-axis. In this case \( y_1 = 0 \) and the projection of V onto the x-y plane is \( x_1 = \cos(\chi) \) and \( z_1 = \sin(\chi) \), where \( \chi \) is the angle measured between the leaf and the axis of the twig.

(3) Establish the coordinates of a set of leaves in one of the three arrangements in Figure 1. As the vector V rotates around the x-axis, as the leaf would if the twig were rotated around its longitudinal axis, the locus of points \((x_1, y_1, z_1)\) at the end of V form a circle of radius \( r \), where \( r = \sin(\chi) \), which equals \( z \) when \( y = 0 \). This circle is in a plane parallel to the y-z plane but going through the point \((x_1, y_1, z_1)\). The equations of the locus of points in this circle are:

\[ x = x_1, \quad y^2 + z^2 = r^2. \]  
(6)

If the vector V is initially above the x-axis and is rotated about the x-axis through an angle \( \alpha \), then \( x = x_1, \quad y = r \sin(\alpha), \quad z = r \cos(\alpha) \). In this way the free end of each of the leaves in a given arrangement in Figure 1 would be assigned coordinates.

(4) Rotate all the leaves in a foliar arrangement by an angle \( \alpha \). If the vector was already at a rotated angle \( \beta \) from being above the twig, then a rotation of angle \( \alpha \), as in Figure 2, would yield the point:

\[ x = x_1, \quad y = r \sin(\alpha + \beta), \quad z = r \cos(\alpha + \beta). \]  
(7)

In this scheme, \( \beta \) is the clockwise angle that any given needle is from the vertical axis of one of the arrangements of the twig (as in Figure 1; here all leaves are assumed to be straight, although most are slightly curved) and \( \alpha \) is the angle of axial rotation that was measured, and is the angle through which all the leaves in the appropriate arrangement in Figure 1 must be rotated. We thus obtain a new vector of leaf angles in space.

(5) We then correct for the twig angle, which was initially assumed to be horizontal. The twig must be rotated up or down in the \( x-z \) plane until its angle from the vertical is that which was measured.

(6) The orientation and projection of the vector, V, are then recalculated for each leaf. In the rotation of the twig, the \( x \) and \( z \) values along both the twig and the leaf vary, whereas the \( y \) values do not. In performing this rotation, the end of the vector \((x_1, y_1, z_1)\) describes a circle in a plane parallel to the \( x-z \) plane with constant \( y \) coordinate \( (y_1) \). This circle has a radius:

\[ s = (x_1^2 + z_1^2)^{1/2}. \]  
(8)

The angle \( \theta \) that the vector V projected onto this circle (in the plane defined by \( y = y_1 \)) will subtend with the horizontal can be determined from \( z_1/s = \sin(\theta) \). If the twig is to be rotated in the \( z \) direction by an angle \( \phi \), then the point at the end of V will subtend an angle \( \theta + \phi \) on the circle and its coordinates can be found by using:

\[ x_2 = s \cos(\theta + \phi), \quad y_2 = y_1, \quad z_2 = s \sin(\theta + \phi). \]  
(9)

This transformation again must be performed on every leaf in the array for a given twig. Because the twig angles that were measured were from the vertical, those angles were subtracted from 90° to conform to the above conditions.

(7) We now correct for curvature of the lateral plane of the needle. Douglas-fir leaves are nearly flat and the plane of each leaf is such that a line normal to the plane and passing through the end of the leaf \((x_1, y_1, z_1)\) would also pass through the axis of the twig. The thickness of the leaf is approximately 40% of the width. An approximation to the projection due to lateral rotation of the leaf around the twig is obtained by considering a doubly convex lens-shaped object rotating about its centre (Figure 10). If \( d_1 \) is the width of the lens and \( d_2 \) is the thickness, and if the two curved faces are both parts of congruent circles, then the length of the vertical projection will be:

\[ p = d_1 \cos(\alpha + \beta), \]  
(10)

if the vertical lines touch the ends of the lens and are not tangent to the curves, where \( \alpha + \beta \) is the rotational angle the leaf subtends with the top of the twig. The radius of curvature of the circular arcs is:

\[ r = (d_1^2 + d_2^2)/4d_2, \]  
(11)

which is 0.725 if \( d_1 = 1.0 \) and \( d_2 = 0.4 \). If the vertical lines are tangent to the two curves and do not touch the ends of the lens, then the projected length will be:

\[ p = (d_1^2 + d_2^2)/2d_2 - (d_1^2 - d_2^2)\sin(\alpha + \beta)/2d_2. \]  
(12)

Figure 9. Direction cosines of a needle (the vector V) oriented in 3-D space with the attached end at the origin of the coordinate system. Here \( \chi, \omega \) and \( \zeta \) are the angles between V and the \( x, y \) and \( z \)-axes, respectively. The vector A is the projection of V on the \( x-y \) plane.
The angle where these two conditions intersect is given by:

\[
\tan(\alpha + \beta) = \frac{(d_1^2 - d_2^2)}{2d_1d_2},
\]

which is 46.4° if \(d_1 = 1.0\) and \(d_2 = 0.4\). In this scheme, \(d_1\) is taken as 1.0 to yield proportional projections. More precise values of this thickness/width ratio were determined by measuring samples of six leaves from each of the foliar arrangements and the two thinning treatments with a micrometer caliper. These ratios for the foliar arrangements 1, 2, and 3, respectively, were 0.358, 0.437 and 0.424 for control plots and 0.409, 0.445 and 0.482 for thinned plots; these values were used in Equation 13. In Figure 10, \(\beta\) was taken as zero for the derivation.

(8) The projection is then multiplied by 0.9/2 to account for the curvature of the two sides of the leaf and the conversion of total to one-sided area.