Conversion of total to projected leaf area index in conifers

Hugh J. Barclay and Doug Goodman

Abstract: Several definitions of leaf area index (LAI) presently exist in the literature but the relationships among them are not clear. To compare the results of various studies, there is a need to convert from one definition to another. Factors for converting among four definitions of LAI are presented for six conifer species: *Abies grandis* (Dougl. ex D. Don) Lindl., *Thuja plicata* Donn ex D. Don., *Tsuga heterophylla* (Raf.) Sarg., *Picea sitchensis* (Bong.) Carr.), *Pinus contorta* Dougl., and *Pseudotsuga menziesii* (Mirb) Franco). Among the four definitions of LAI, the two extremes involve (*i*) the total area of the leaf and (*ii*) the projected area of nonhorizontal leaves, as they occur on the tree. If leaves are randomly oriented in space, then the conversion factor between definitions *i* and *ii* should be 0.25. Four of the six species have conversion factors very close to this value, and three of these four are relatively shade-intolerant,. The remaining two species, *A. grandis* and *Thuja plicata*, have conversion factors of approximately 0.35, owing to the approximately horizontal orientation of their leaves. These two species are both relatively shade-tolerant, and the trend toward horizontal leaves might be an adaptation to assist in shade tolerance. A sensitivity analysis indicated that the foliage of most of the species maximized the amount of light gathered when the light was coming from almost straight overhead, as is the case with many shaded forest trees.

Key words: leaf area index, conifers, leaf area index conversion.

Résumé : Il existe présentement plusieurs définitions de l’index de surface foliaire (LAI) dans la littérature, mais les relations entre elles ne sont pas claires. Afin de comparer les résultats de différentes études, on doit convertir les définitions de l’une à l’autre. Les auteurs présentent les facteurs pour convertir quatre définitions du LAI pour six espèces de conifères. *Abies grandis* (Dougl. ex D. Don) Lindl., *Thuja plicata* Donn ex D. Don., *Tsuga heterophylla* (Raf.) Sarg., *Picea sitchensis* (Bong.) Carr.), *Pinus contorta* Dougl. et *Pseudotsuga menziesii* (Mirb) Franco). De ces quatre définitons, les deux extrêmes impliquent (*i*) la surface foliaire totale et (*ii*) la surface projetée des feuilles non-horizontales, telles qu’on les observe sur l’arbre. Si les feuilles sont distribuées au hazard dans l’espace, le facteur de conversion entre les définitions *i* et *ii* devrait alors être de 0,25, et quatre des six essences montrent des facteurs de conversion très près de cette valeur, dont trois sont relativement intolérantes è l’ombre. Les deux autres, *A. grandis* et *Thuja plicata*, ont des facteurs de conversion d’environ 0,35, à cause de l’orientation approximativement horizontale de leurs feuilles. Ces deux espèces sont toutes deux tolérantes à l’ombre et la tendance vers des feuilles horizontales pourrait être une adaptation aidant à tolérer l’ombre. Une analyse de sensibilité indique que le feuillage de la plupart des espèces maximise la quantité de lumière recueillie, lorsque la luminosité vient pratiquement droit d’en haut, comme c’est le cas chez plusieurs essences forestières d’ombre.

Mots clés : conifères, conversion d’index de surface foliaire.

[Traduit par la Rédaction]

Introduction

Since leaf area is one of the prime determinants of photosynthesis, the measurement of the total leaf area of a forest stand is important in assessing forest growth potential. Leaf area is presently estimated by a variety of means, from direct measurement to inferences from remote sensing. In addition, leaf area is more easily estimated by remote sensing than total biomass, and so leaf area becomes important in updating forest inventories. There are at least five measures of leaf area index (LAI) in the literature: (*i*) the total external surface area of the leaves (TLAI) per unit area of horizontal land below (Kozlowski and Schumacher 1943; Cable 1958; Madgwick 1964); (*ii*) total one-sided leaf area (OLAI) per unit area of horizontal land below (Watson 1947; Price 1993), commonly used by botanists and usually taken as half the total leaf area; (*iii*) vertically projected area of leaves arranged horizontally per unit of horizontal land below (PLAI) (Running et al. 1986; Grace 1987; Gong et al. 1992); (*iv*) projected area of leaves inclined to the horizontal in their natural position on a tree, called silhouette leaf area index (SLAI) by Smith et al. (1991) and by Stenberg (1996); and (*v*) projected area of inclined leaves, but counting vertically overlapping areas only once—this measure is sometimes used in remote sensing applications, because it represents the proportion of ground covered by foliage in a remotely sensed image (D. Goodenough and O. Niemann,

Received September 16, 1999.

H.J. Barclay[1] and D. Goodman. Pacific Forestry Centre, 506 West Burnside Road, Victoria, BC V8Z 1M5, Canada.

[1] Author to whom all correspondence should be addressed (e-mail: hbarclay@pfc.forestry.ca).

personal communication). Numerical factors are required to convert among these five definitions to allow comparisons of data from different studies. In the absence of these conversion factors, relationships between (*i*) leaf area and forest growth and (*ii*) leaf area and remote-sensing measurements are incommensurate. This paper deals with TLAI, OLAI, PLAI, and SLAI and tries to provide a framework for unifying studies of leaf area in various disciplines that use different definitions of LAI.

Horizontally projected leaf area is usually measured on foliage samples with a video-imaging system. If the leaves are very thin, flat, and of uniform thickness throughout, then PLAI = OLAI. Most conifer leaves are curved in cross section, so that PLAI < OLAI. Inclined leaf area could be assessed indirectly by measuring light transmission within stands with the LI-COR LAI-2000 (LI-COR 1990) but, for conifers, this would require conversion factors to overcome biases caused by blockage of light by boles and branches and by nonrandom distribution of the leaves (Gower and Norman 1991).

SLAI is useful in modelling light penetration through a canopy (Lang 1991; Chen and Black 1991, 1992), although most values of LAI reported in the literature are for OLAI (e.g., Curran and Williamson 1987) or PLAI (e.g., Gower and Norman 1991). The factors for converting among these definitions of LAI will likely vary with different patterns of foliar arrangement, although direct measurement of conifer leaf angles, so far, is limited. The projection coefficient, λ (λ = SLAI/TLAI), is used to convert between TLAI and SLAI (Barclay 1998).

The objective of this study is to derive factors for converting TLAI and OLAI to PLAI and SLAI for western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), western red cedar (*Thuja plicata* (Donn ex D. Don)), Sitka spruce (*Picea sitchensis* (Bong.) Carr.), and grand fir (*Abies grandis* (Dougl. ex D. Don) Lindl.), by sampling the foliage, determining leaf angles, and calculating projection coefficients from these angles. In this way, certain patterns should emerge that will allow generalization to other coniferous species, as well as being consistent with known biological phenomena, such as differences in light tolerance among species. For comparison, conversion factors previously derived by Barclay (1998) for Douglas-fir (*Pseudotsuga menziesii* (Mirb) Franco) and lodgepole pine (*Pinus contorta* Dougl. var. *latifolia* Engelm.) are also presented.

Materials and methods

Sample trees

Three trees of each of four species (*A. grandis*, *Thuja plicata*, *Tsuga heterophylla*, and *Picea sitchensis*) were cut in the fall of 1997 from the Greater Victoria Water District land near Victoria, B.C. (48°30′N, 123°35′W, elevation 400 m). The three trees of each species ranged in age from 15 to ~50 years old and spanned conditions ranging from deep shade to full sunlight. The small and medium trees of each species except *Pinus contorta* were shaded by surrounding trees, while the larger trees had most of their crowns shaded but their tops in full sunlight. The *Pinus contorta* trees were from a relatively open stand where none of the trees were heavily shaded. Five or six branches per tree were sampled uniformly throughout the length of the crown, and the angle that each branch subtended with the bole was noted. Smaller trees were brought back to the laboratory intact but, for larger trees, branches and attached short stem sections were transported to the laboratory. Stems were mounted vertically to recreate the natural branch angles. From each branch, a subsample of twigs (a twig being defined as 1 year's growth on a single shoot) spanning all foliar ages was measured for azimuth and angle from the vertical, as well as for length. In most cases, 20–40 twigs were sampled from each branch, although some branches were too small to yield this number. Since the geometric pattern of leaves on twigs varied to some extent, several twigs were cut and examined to determine leaf arrangement around the twig and the angle of the leaves from the axis of the twig. Several typical twigs were cut and used to quantify these patterns. Each leaf arrangement was schematically characterized by a set of 20 leaf angles from the vertical with the twig held horizontally (estimated optically using a protractor; Table 1), for use in computation. These sets of 20 leaf angles were determined as the means of 20 quantiles (each representing 5% of the distribution) representing over 100 measurements for each leaf arrangement for each species. The leaf arrangements around the sample twigs were then categorized for each species (Table 1).

The leaves of all four species were flattened in cross section and, thus, different rotational orientations about the longitudinal axis exposed different aspects of the leaf to the ground for projection. However, the leaves were not exactly flat, and the total surface area was greater than twice the projected area of a horizontal leaf. These effects were allowed for in the algorithm, outlined below, that was used to compute the projection coefficients.

Twenty leaves of each species, taken from several twigs, were cross-sectioned and the microscope images photographed; measurements of diameter (D) and thickness (T) were then taken from the micrographs and from these an index, T/D, was recorded. The distance around the cross-sectional perimeter (P) of each leaf was measured along the top and bottom surfaces using a planimeter; this was compared with the diameter to produce a conversion factor to allow for this curvature, giving the conversion (λ_1) from OLAI to PLAI, so that λ_1 = leaf diameter/half the cross-sectional perimeter (i.e., $\lambda_1 = 2D/P$). The measurements taken on each twig were (*i*) the mean leaf angle from the twig axis, (*ii*) the leaf arrangement around the twig (Table 1), (*iii*) the axial angle that the foliage was rotated from the vertical, and (*iv*) the angle of the twig axis from the vertical. For western red cedar, the foliage over a small area was relatively flat and the measurements were made of the azimuthal and vertical angles of flat subsections of foliage rather than of individual twigs. In addition, for western red cedar, a typical leaf arrangement on a twig (Fig. 1) was determined.

Samples of foliage were also taken along the sample branches of the two larger trees of each species, to determine specific leaf area (SLA) in units of square centimetres per gram (oven-dry weight) of leaf. Two samples of foliage were taken from each of several sample branches, one from near the bole and one from near the distal end of the branch. The horizontally projected areas of samples of 20 leaves were determined by means of a Delta-T Devices area meter, calibrated to a known standard. Leaves were laid flat with the ventral side up for these measurements. These samples of 20 leaves were subsequently dried at 65°C for 48 h and weighed to calculate the SLA. These measurements provided estimates of horizontally projected leaf area, which were then converted to the other measures of leaf area by the algorithm outlined below. Together with estimates of biomass, these estimates of leaf area can be converted to LAI, although the various measures of LAI are convertible without reference to biomass.

Algorithm for calculating projected area

A geometric algorithm was used to calculate the angle from the vertical of the plane of each leaf from the above four measure-

Table 1. Schematic angles of 20 leaves for the foliar arrangements around twigs for western hemlock, Sitka spruce, grand fir, and western red cedar.

Species	Foliar arrangement	Leaf angles from the vertical (°)
Western hemlock	1	22, 62, 83, 90, 90, 98, 106, 116, 121, 150
	1	72, 80, 82, 85, 90, 90, 93, 95, 100, 110
Grand fir	2	44, 45, 48, 50, 55, 58, 60, 65, 75, 85
	3	5, 20, 25, 30, 35, 45, 50, 60, 75, 90
Western red cedar	1	90, 90, 90, 90, 90, 90, 90, 90, 90, 90
	1	31, 56, 79, 90, 100, 101, 110, 113, 120, 148
Sitka spruce	2	7, 34, 56, 71, 79, 86, 99, 106, 119, 139
	3	6, 24, 43, 56, 72, 91, 108, 119, 137, 147

Note: Angles are given for 10 leaves only, all on one side of the twig axis, as the other 10 are located symmetrically on the other side. Western red cedar leaves were in the plane of the foliar sheet and the vertical angles were all 90°.

ments. The projection due to inclination was calculated for each of the leaves as the cosine of the angle of the leaf plane from the horizontal. Both the longitudinal and lateral orientations in space were included for each leaf, to estimate the reduction in projection caused by the leaf not being horizontal; this component is called λ_2, the proportional projection. The conversion of TLAI to SLAI thus involves conversion from TLAI to OLAI (i.e., division by two), then to PLAI (multiplication by λ_1), and then to SLAI (multiplication by λ_2). These were calculated for each leaf and then averaged to calculate the mean projection coefficient, λ, characteristic of a whole tree, where $\lambda = \lambda_1\lambda_2/2$.

Several transformations are required to compute leaf angles from the data available. The mathematical details for some of these transformations were given earlier by Barclay (1998). However, there is a fundamental difference in the method of handling the projection of the width axis of the leaves here. Previously, Barclay (1998) stated that Douglas-fir leaves were oriented so that a line normal to the plane of the leaf and through the centre of each leaf would pass through the twig axis. This yielded a simple method of dealing with the component of projection that depended on the orientation of the leaf width. This orientation is true in lodgepole pine but not in Douglas-fir or in any of the four species examined here. In these conifers, the leaves are oriented so that the plane of the leaf is coincident with the plane formed by the twig axis and the long axis of the leaf. This necessitates further transformations to calculate the total projection. The complete set of transformations is outlined below, and these were coded in a FORTRAN program to compute projections of the leaves for each species in space. Several leaf angles around the twig need to be supplied for the computations, because there are leaves pointing in many directions around a twig. In both grand fir and Sitka spruce, there was more than one leaf arrangement around the twig, and schematic representations of these are given in Table 1.

In the following transformations, we can assume without loss of generality that the flatter portion of the leaf is square, since it is the proportional projection that is required rather than the total amount of projection. We can further assume that the centre of each leaf is at the origin of a three-dimensional coordinate system and that the leaf simply rotates as the transformations are applied. The transformations are as follows:

1. Place the leaf in a 3-dimensional coordinate system with the leaf centre at the origin and letting the twig be parallel to the *x*-axis. The leaf starts by being horizontal and perpendicular to the twig axis. Establish two axes of the leaf, a longitudinal axis, down the middle of the leaf in the longest dimension, and a lateral axis, in the plane of the leaf width and perpendicular to the longitudinal axis, with both axes passing through the centre of the leaf. The coordinates of one end of the longitudinal axis at P_1 are then (0, 1, 0) and of one end of the lateral axis at P_2 are (–1, 0, 0) (Fig. 2*a*). The focus is on these axis ends in the following.
2. Rotate the leaf horizontally through an angle γ that the leaf makes with the twig. Determine the new coordinates of the ends P_1' and P_2' of the longitudinal and lateral axes (Fig. 2*b*).
3. For each of the 20 leaves in the designated foliar arrangement, rotate the leaf through its appropriate angle around the longitudinal axis of the twig according to the leaf's position in the designated foliar arrangement (Table 1). Determine the new coordinates of the ends of the two axes after rotation through angle β.
4. Rotate the twig around its axis so that the axis of the foliar arrangement is at the measured axial angle α, and recalculate the coordinates of the end of each leaf axis (P_1'' and P_2'' in Fig. 2*c*).

Fig. 1. Schematic representation of a typical western red cedar twig, displayed horizontally, showing the arrangement of the leaf angles.

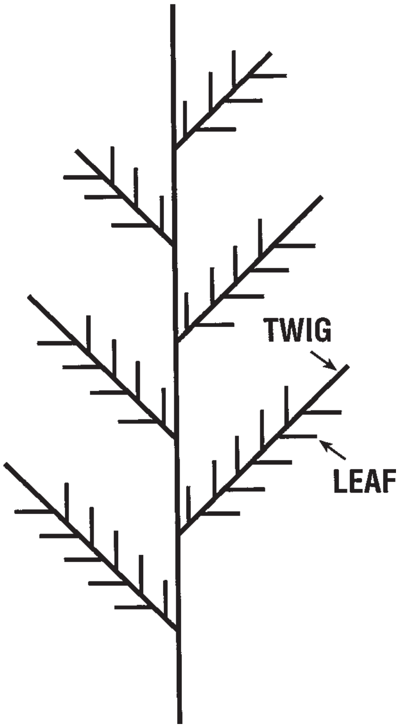
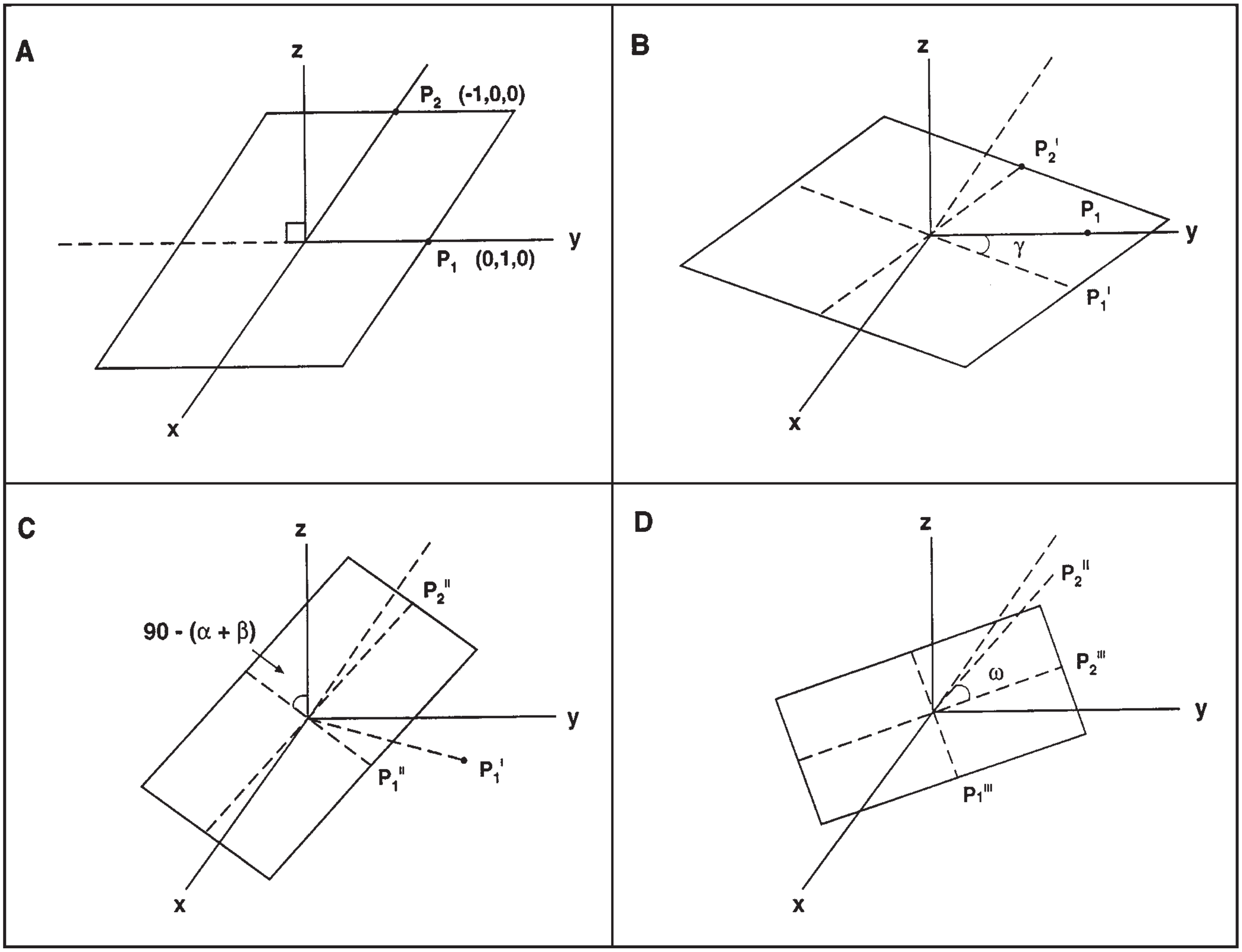


Fig. 2. (A) The unit square leaf shown in the *XY*-plane with sides parallel to the *x*- and *y*-axes. (B) The unit square leaf in the *XY*-plane but rotated through a horizontal leaf angle, γ. (C) The unit square leaf further rotated about its width axis by an angle $\alpha + \beta$, where α is the complement of an angle shown in Table 1 and β is the axial angle of the foliar arrangement. (D) The unit square leaf further rotated vertically by the twig angle, ω.



5. Rotate the twig vertically to its measured angle, ω, and recalculate the coordinates of the ends of the axes (P_1''' and P_2''' in Fig. 2*d*) for each of the 20 leaves. The two leaf axes must still be perpendicular after these transformations.
6. Calculate the reduction in projection caused by the longitudinal inclination of each leaf.
7. Compute the coordinates of the end of the unit line normal to the plane of the two axes and passing though the leaf centre. This normal line is calculated by computing the inner product of it with each of the two axes and solving, since the inner product gives the cosine of the angle between the two lines.
8. Calculate the angle between the normal line and the *XY*-plane (the horizontal plane). The complement of this angle gives the angle that the plane of the leaf makes with the *XY*-plane, and the cosine of this angle is the projection coefficient (λ), unless the leaf is inclined sufficiently that the thickness obscures the lower edge.
9. To assess the possibility that the thickness of the leaf obscures the edge, the angle that the lateral leaf axis makes with the *z*-axis (vertical) must be computed, and this can be done by computing the line perpendicular to the longitudinal axis that lies in the *XY*-plane and calculating the angle between it and the lateral leaf axis. The criterion for the leaf thickness obscuring the lower edge is that the tangent of the angle between the lateral axis and the *z*-axis is greater than $(d_1 - d_2)/2d_2$, where d_1 is the leaf width and d_2 is the leaf thickness, assuming that the leaf is a cylindrical biconvex lens (Fig. 10 in Barclay 1998). These measurements have been made from the sectioned leaves. The appropriate projection was then used on the basis of this criterion.
10. Apply a factor for curvature of the leaf in cross section to convert from total two-sided area to horizontally projected area, $\lambda_1/2$. This was also based on the micrographs of the lateral leaf sections.

This algorithm was used for grand fir, western hemlock, western red cedar, and Sitka spruce, although for western red cedar, a simplification was possible because of the growth pattern of the foliage. In western red cedar, the foliar arrangement consisted of a single angle, viz., 90° (Table 1). There was considerable variability in foliar patterns in western red cedar, but a "typical" pattern was chosen that seemed to represent an average (Fig. 1), in which half the leaves were parallel to the main twig axis and half were perpendicular. In sampling the foliage of western red cedar, only small sections of foliage were sampled, to ensure that the entire sample would be in one plane, since the foliar sheet was often bent under its own weight. In the foliar pattern illustrated in Fig. 1, about half the leaves point forward, one quarter point to the left, and one quarter point to the right, so in the computer program, four leaves were described, two pointing forward and the other two at right angles to the first two. The total number of leaves was not important, only the relative frequency of the various angles represented.

Statistical analysis

The three trees of each species were used as replicates, although in fact they varied in age, size, and height within the canopy. Nested analyses of variance (Table 2) were done on each of the measures T/D, SLA, diameter/semiperimeter (λ_1), proportional projection (λ_2), and SLAI/TLAI (λ), using species as the independent variable and trees as a nesting factor. To assess equality of variances, $F_{\max}$ tests were done on the variances and, where necessary (for SLA and λ_1), logarithmic transformations were performed on the data prior to analysis and these transformations yielded homogeneous variances. Lodgepole pine was not included in this analysis, because leaf angles were determined differently, and not all of the five variables above were measured for this species.

Sensitivity analysis

A sensitivity analysis was performed on the three foliar measures: angle of the leaves from the twig axis, axial angle of the foliage on the twig, and twig angle from the vertical. In each case, every twig measured was included, with the initial conditions being the measured leaf and the axial and vertical angles for that twig, with every twig being oriented in the same azimuthal direction. These three angles were then systematically changed in 10° increments, and the resulting projected proportions (λ) were recalculated through a full rotation. These values of λ were then averaged for all twigs in a given 10° increment and for a given foliar measure, to yield the curves shown in the sensitivity analysis.

Results

Conversion of TLAI to PLAI

Results are presented here for the four species examined, as well as for Douglas-fir and lodgepole pine, which were originally studied by Barclay (1998). The leaves varied considerably in thickness among species (Table 2), with western hemlock, grand fir, and western red cedar being thin, about 22% of the diameter, while Sitka spruce, Douglas-fir, and lodgepole pine were relatively thick, about 43–50% of the diameter (Table 3). This is reflected in the T/D ratios, in the values of SLA, and also in the diameter/semiperimeter ratio (λ_1); species with thinner leaves generally have higher values of λ_1 and lower values of T/D (Table 3). Analyses of variance showed that the values for T/D differed significantly among species (Table 2), with western hemlock, grand fir, and western red cedar forming one group, and Sitka spruce and Douglas-fir forming separate groups. The values of SLA just failed to show differences among species (p = 0.0664), while the values of λ_1 differed significantly among species (Student–Newman—Keuls (SNK) test) forming two overlapping groups, one group containing western hemlock, grand fir, western red cedar, and Douglas-fir and the other group containing western hemlock, Douglas-fir, and Sitka spruce (Table 2). However, variability of λ_1 was low, with values of λ_1 only varying between 0.839 for Douglas-fir and 0.920 for grand fir.

Table 2. Nested analyses of variance for the effects of species differences on thickness-to-diameter ratio (T/D), specific leaf area (SLA), diameter-to-semiperimeter ($2D/P = \lambda_1$), the proportional projection (λ_2), and the projection coefficient (λ) in western hemlock, grand fir, western red cedar, Sitka spruce, and Douglas-fir.

Dependant variable	Source	df	MS	F	p
	S	4	0.368	27.5	0.0005
T/D	T(S)	6	0.013	5.92	0.0001
	W	1	0.006	2.52	0.1156
	S	4	0.828	4.45	0.0664
SLA	T(S)	5	0.186	10.6	0.0001
	W	1	0.996	56.7	0.0001
	S	4	0.018	10.7	0.0115
λ_1	T(S)	5	0.002	5.03	0.0004
	W	1	0.000	0.04	0.8385
	S	4	4.451	3.16	0.0510
λ_2	T(S)	13	1.410	50.6	0.0001
	W	1	3.677	131.8	0.0001
	S	4	1.147	4.29	0.0199
λ	T(S)	13	0.268	50.0	0.0001
	W	1	0.734	136.9	0.0001

Note: Independent variables were species (S) and trees within species (T(S)); whorl number (W) was used as a covariate.

Conversion of PLAI to SLAI

The factor λ_2 for converting PLAI to SLAI reflects the leaf arrangement; grand fir and western red cedar have the highest values (Table 3) and, generally, the most nearly horizontal leaves throughout much of the tree, and Douglas-fir and lodgepole have the lowest values, with both species having appreciable proportions of their leaves oriented away from the horizontal. Sitka spruce and western hemlock were intermediate. These differences were all but significant (p = 0.051), but these three groups were not separable by a SNK test.

Conversion of TLAI to SLAI

The combined conversion factors, λ, were all between 0.23 (lodgepole pine) and 0.36 (grand fir). These values fell into two relatively homogeneous and statistically different groups (Table 2), with western hemlock, Douglas-fir, Sitka spruce, and lodgepole pine all having values close to 0.25, the expected value from a random distribution, and grand fir and western red cedar having values close to 0.35.

Sensitivity analyses

The effects of twig angle, axial angle, and needle angle from the twig on the projection coefficient, λ, are shown in Fig. 3 for each of the four species. The effects of twig angle and axial angle were pronounced in grand fir and western red cedar, as the foliage tends to be fairly flat with many leaves being in nearly the same plane. The effects on western hemlock and Sitka spruce were much smaller, in keeping with the greater array of leaf angles around the twigs in these species. Needle angle from the twig had hardly any effect in grand fir and western red cedar, for the same reason as above, while there was a small effect for western hemlock and Sitka spruce.

Table 3. Factors for converting OLAI to PLAI (λ_1), PLAI to SLAI (λ_2), and TLAI to SLAI (λ) for western hemlock, grand fir, western red cedar, Sitka spruce, Douglas-fir, and lodgepole pine.

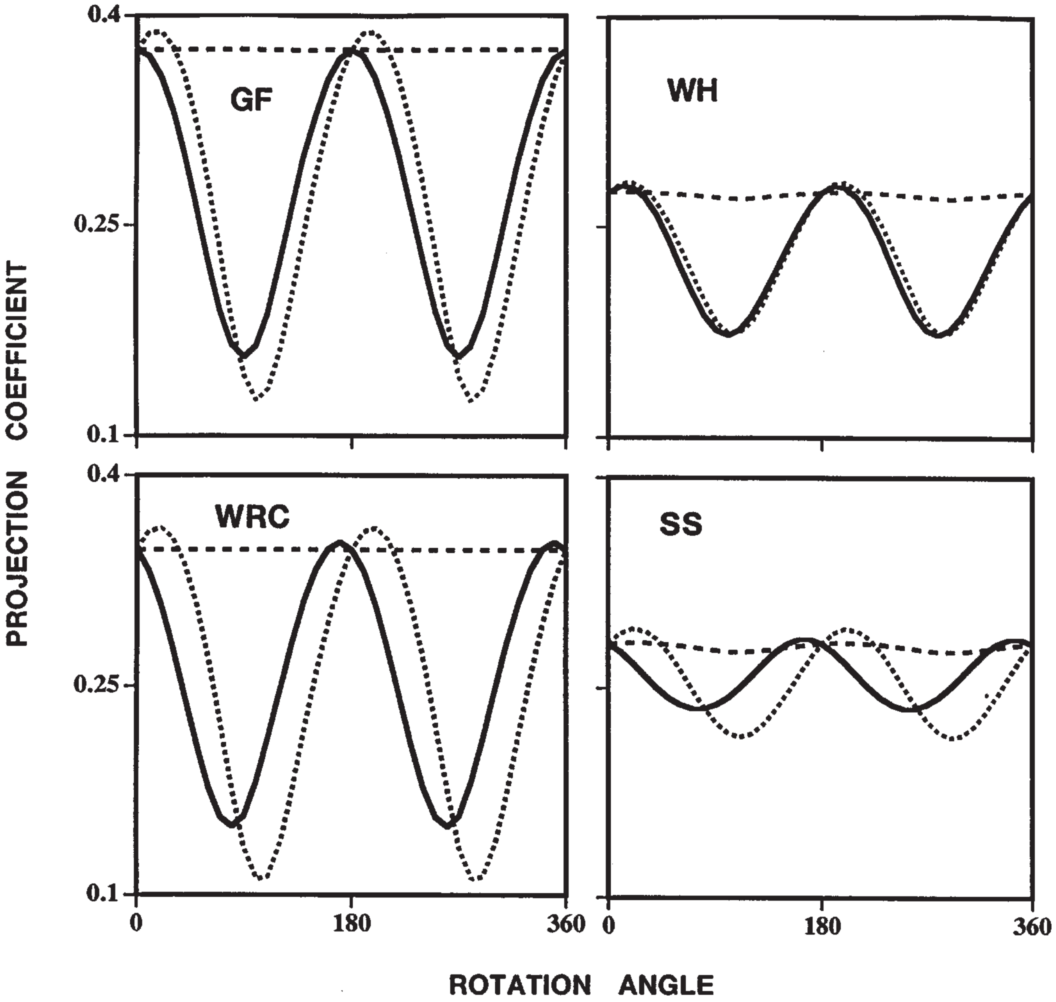
Species	*T*/*D*	SLA	λ_1	λ_2	λ	SE
Western hemlock	0.233*a*	60.4*a*	0.873*ab*	0.629*a*	0.275*ab*	0.005
Grand fir	0.223*a*	65.5*a*	0.920*b*	0.779*a*	0.358*b*	0.006
Western red cedar	0.227*a*	74.6*a*	0.879*b*	0.790*a*	0.347*b*	0.003
Sitka spruce	0.505*c*	45.7*a*	0.864*ab*	0.632*a*	0.273*ab*	0.005
Douglas-fir	0.431*b*	53.4*a*	0.839*a*	0.585*a*	0.245*a*	0.003
Lodgepole pine	0.500*	37.3	0.778†	0.588	0.229	0.003

Note: *T*/*D* is the mean thickness-to-width ratio for the leaves and SLA is specific leaf area. Values within a given column followed by common letters are not statistically different (SNK test). SE is for λ.

*Determined geometrically.

†Determined as the mean projection of a randomly rotated hemicylinder.

Fig. 3. Sensitivity analyses to determine the effects of the leaf angles on the projection coefficient (λ), by systematically purturbing (*i*) mean leaf angle from the axis of the twig (dashed line), (*ii*) axial angle of the foliar arrangement (dotted line), and (*iii*) angle of the twig from the vertical (solid line) for western hemlock (WH), grand fir (GF), western red cedar (WRC), and Sitka spruce (SS).



Discussion

Species differences in the projection coefficient, λ

The six species considered here can be grouped nicely into two groups consisting of (*i*) western hemlock, Sitka spruce, Douglas-fir, and lodgepole pine and (*ii*) grand fir and western red cedar, based on their projection coefficients (λ). Grand fir and western red cedar have leaves that are more nearly horizontal and Sitka spruce, Douglas-fir, and lodgepole pine have leaves that are more inclined to the horizontal. These correspond approximately to the degree of shade tolerance of the respective species. Sitka spruce, Douglas-fir, and lodgepole pine are of intermediate shade tolerance, while grand fir and western red cedar are relatively shade-tolerant. Western hemlock is the exception here, having less nearly horizontal leaves but also being quite shade-tolerant. The species with lower values of λ and more inclined leaves have values of λ that approximate those expected if the leaves were randomly oriented in three-dimensional space (Lang 1991), even though on any twig the leaves are arranged in a highly predictable fashion. These same species have lower values for SLA than grand fir and western red cedar.

Light and temperature conditions help explain variation in leaf shape and arrangement between plant species and individuals (Campbell 1977; Wilson 1984). Planar horizontal leaves are suited to the lower canopy or the understory, where most light arrives from near-vertical angles. The flatter leaves and leaf arrangements of grand fir (λ = 0.36) and western red cedar (λ = 0.35), two shade-tolerant species that often regenerate in the understory, may be adaptations for efficient light collection. In contrast, western hemlock (λ = 0.28), Douglas-fir (λ = 0.24), Sitka spruce (λ = 0.27), and lodgepole pine (λ = 0.23) all had more variable leaf angles and ratios of SLAI to TLAI that were close to those for randomly arranged leaves (λ = 0.25; Lang 1991). The shape and arrangement of the leaves of latter three species are not surprising, as they usually grow in more open conditions. According to this reasoning, it is surprising that western hemlock, as a prominent understory species, doesn't have a flatter leaf arrangement to accompany its fairly flat leaves. However, western hemlock in the understory may be able to acquire carbon via ectomycorrhizal links with some of the tree species under which it grows, as has been shown for Douglas-fir (Griffiths et al. 1991; Simard et al. 1997). It may be that western hemlock does not require as efficient a light-gathering apparatus, because of this ability. This option is often unavailable to western red cedar, which is arbuscular mycorrhizal and frequently regenerates in the understory of ectomycorrhizal trees such as Douglas-fir and western hemlock.

Although the arrangement of leaves on a twig is predictable for all species considered here, the variation in twig angles throughout the tree creates the illusion of randomness when whole trees are considered, so that when taken in aggregate for the whole tree, all except western red cedar and grand fir have values of λ close to 0.25, the expected value for a spherical (random) distribution of leaf angles (Chen and Black 1992).

The SE values for λ (Table 3) are really underestimates, as T/D and $2D/P$ were determined with far fewer samples (about 24 leaves per species) and were taken as constant when calculating the various conversion factors. Better determination of these values would improve precision, but this should not alter the conclusions drawn here.

Sensitivity analyses

Systematically varying needle angle from the twig had hardly any effect on the value of λ. This is not surprising given the array of values for the axial and twig angles, and was especially true for the two species with nearly horizontal foliage, grand fir and western red cedar, as variations in needle angle in horizontal leaves would not change the projection.

Varying axial angle and twig angle both had profound effects on the mean value of λ, with the highest values of λ being found for the measured angles for twig angle and for about 20° more than the measured angles for axial angle. This implies that the foliage is nearly ideally aligned to receive light from the vertical direction, but with a variability in alignment that allows considerable flexibility in receiving light from other angles, although not from near the horizon where the efficiency abruptly declines(Fig. 3).

In remote sensing applications, the nadir view (vertically downwards) would yield nearly the highest apparent value of LAI (Fig. 3). Also, there would be greater variability in apparent LAI in remotely sensed images of western red cedar and grand fir as the view angle changes than there would be for western hemlock and Sitka spruce, owing to the more nearly horizontal angles of the leaves in western red cedar and grand fir. However, the extensive overlapping of leaves would tend to smooth out the variations in apparent LAI, as leaves would enter and leave the view as the view angle changed. The fifth definition of LAI (involving overlapping leaves) probably appears less variable than the others as the view angle changes, but it is also the most difficult to quantify, except perhaps by measurement from photographs and remotely sensed images.

Acknowledgements

We are grateful to Gordon Joyce, Chief Forester of the Greater Victoria Water District, for permission to cut 12 trees in their protected land. We thank Dr. Alan Mitchell, for the use of his laboratory and area meter, and Dan Hall and Emil Wegwitz, for assistance in procuring two trees.

References

Barclay, H.J. 1998. Conversion of total leaf area to projected leaf area in lodgepole pine and Douglas-fir. Tree Physiol. **18**: 185–193.

Cable, D.R. 1958. Estimating surface area of ponderosa pine foliage in central Arizona. For. Sci. **4**: 45–49.

Campbell, G.S. 1977. An introduction to environmental biophysics. Springer Verlag, New York.

Chen, J.M., and Black, T.A. 1991. Measuring leaf area index of plant canopies with branch architecture. Agric. For. Meterol. **57**: 1–12.

Chen, J.M., and Black, T.A. 1992. Defining leaf area index for non-flat leaves. Plant Cell Environ. **15**: 421–429.

Curran, P.J., and Williamson, H.D. 1987. Estimating the green leaf area index of grassland with airborne multispectral scanner data. Oikos, **49**: 141–148.

Gong, P., Pu, R., and Miller, J.R. 1992. Correlating leaf area index of ponderosa pine with hyperspectral CASI data. Can. J. Remote Sens. **18**: 275–281.

Gower, S.T., and Norman, J.M. 1991. Rapid estimation of leaf area index in conifer and broad-leaf plantations. Ecology, **72**: 1896–1900.

Grace, J. 1987. Theoretical ratio between "one-sided" and total surface area for pine needles. N.Z. J. For. Sci. **17**: 292–296.

Griffiths, R.P., Castellano, M.A., and Caldwell, B.A. 1991. Hyphal mats formed by two ectomycorrhizal fungi and their association with Douglas-fir seedlings: a case study. Plant Soil, **134**: 255–259.

Kozlowski, T.T., and Schumacher, F.X. 1943. Estimation of stomated foliar surface of pines. Plant Physiol. **18**: 122–127.

Lang, A.R.G. 1991. Application of some of Cauchy's theorems to estimation of surface areas of leaves, needles and branches of plants, and light transmittance. Agric. For. Meteorol. **55**: 191–212.

LI-COR. 1990. LAI-2000 plant canopy analyzer: instruction manual. LI-COR, Lincoln, Nebr.

Madgwick, H.A. 1964. Estimation of surface area of pine needles with special reference to *Pinus resinosa*. J. For. **62**: 636.

Price, J.C. 1993. Estimating leaf area index from satellite data. IEEE (Inst. Electr. Electron. Eng.) Trans. Geosci. Remote Sens. **31**: 727–734.

Running, S.W., Peterson, D.L., Spanner, M.A., and Teuber, K.B. 1986. Remote sensing of coniferous leaf area. Ecology, **67**: 273–276.

Simard, S.W., Perry, D.A., Jones, M.D., Myrold, D.D., Durall, D.M., and Molina, R. 1997. Net transfer of carbon between ectomycorrhizal tree species in the field. Nature (London), **388**: 579–582.

Smith, W.K., Schoettle, A.W., and Cui, M. 1991. Importance of the method of leaf area measurement to the interpretation of gas exchange of complex shoots. Tree Physiol. **8**: 121–127.

Stenberg, P. 1996. Simulations of the effects of shoot structure and orientation on vertical gradients in intercepted light by conifer canopies. Tree Physiol. **16**: 99–108.

Watson, D.J. 1947. Comparative physiological studies on the growth of field crops: I. Variation on net assimilation rate and leaf area between species and varieties, and within and between years. Ann. Bot. **11**: 41–76.

Wilson, B. 1984. The growing tree. University of Massachusetts Press, Amherst.