

The use of multiple measurement techniques to refine estimates of conifer needle geometry

B. Bond-Lamberty, C. Wang, and S.T. Gower

Abstract: Knowledge of foliar surface area is important in many fields, but estimating the area of nonflat conifer needles is difficult. The primary goal of this study was to use optical scanning and immersion methods to test and refine the standard cross-sectional geometries assumed for black spruce (*Picea mariana* (Mill.) BSP) and jack pine (*Pinus banksiana* Lamb.) needles. Projected leaf area (PLA, measured using a flatbed scanner), and hemisurface leaf area (HSLA, estimated from water immersion) were compared for conifer samples from a 37-year-old even-aged stand in northern Manitoba, Canada. The HSLA–PLA relationship was used to infer information about needle cross-sectional geometry after assuming a basic form (rhombus for black spruce and hemiellipse for jack pine). The cross section of black spruce needles was best approximated as a rhombus with a major/minor diagonal ratio of 1.35. Jack pine needles were best described by a hemiellipse with major/minor axis ratio of 1.30. Minor but incorrect assumptions of needle cross-sectional geometry resulted in foliar area errors of 6–8% using scanning methods and 1–2% using immersion methods. Simple equations are presented to calculate hemisurface needle area from volume or projected needle area based on these refined parameters.

Résumé : Dans plusieurs domaines, il est important de connaître l'étendue de la surface foliaire mais il est difficile d'évaluer la surface des aiguilles de conifères car elles ne sont pas plates. L'objectif de cette étude consistait à utiliser des méthodes de balayage optique ou d'immersion pour tester et raffiner les formes géométriques standard qui sont utilisées pour représenter la section transversale des aiguilles d'épinette noire (*Picea mariana* (Mill.) BSP) et de pin gris (*Pinus banksiana* Lamb.). La projection de la surface foliaire (PSF, mesurée à l'aide d'un scanner à plat) et la moitié de la surface foliaire totale (MFST, mesurée par immersion dans l'eau) ont été comparées chez des échantillons de conifères provenant d'un peuplement équienne âgé de 37 ans du Nord du Manitoba, au Canada. La relation entre les valeurs de MFST et PSF a été utilisée pour inférer des informations sur la géométrie de la section transversale des aiguilles après avoir assumé une forme de base (rhombe pour l'épinette noire et demi ellipse pour le pin gris). La section transversale des aiguilles d'épinette noire était la mieux décrite par un rhombe avec un rapport de 1,35 entre la grande et la petite diagonale. Les aiguilles de pin gris étaient mieux représentées par une demi ellipse avec un rapport de 1,30 entre la grande et la petite diagonale. Une hypothèse erronée, même légèrement, au sujet de la section transversale des aiguilles entraîne des erreurs de 6 à 8 % dans la surface foliaire avec l'utilisation du scanner et de 1 à 2 % avec la méthode par immersion. Des équations simples permettant de calculer l'étendue de la moitié de la surface foliaire à partir du volume ou de la projection de la surface foliaire et basées sur des paramètres améliorés sont présentées.

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Introduction

Accurate estimation of foliar surface area is important for ecophysiologicals, biogeochemical models, remote sensing applications, and forest ecologists. At every scale (individual tree, stand, and landscape), leaf area is a key structural characteristic controlling many biological and physical processes in forest canopies. Direct and optical methods are used to estimate stand leaf area; estimates made using allometric models are usually the most accurate, especially in clumped conifer stands (Gower et al. 1999).

Leaf area is typically expressed on a hemisurface leaf area (HSLA) basis for both flat and nonflat leaves, with HSLA defined as one-half the total leaf surface area (Chen and Black 1992; Chen et al. 1997). However, projected leaf area (PLA) may be easier to measure than HSLA, especially for nonflat conifer needles. Numerous commercially available instruments can be used to estimate needle area. A generic flatbed scanner attached to a computer potentially offers the same functionality at a fraction of the cost, with the significant advantage that digital images can be stored indefinitely. One possible disadvantage of using a scanner is that image processing and area calculations are handled in software by the user and not by specialized hardware. Consistent methods should be followed to ensure reproducible results, especially in the conversion of PLA to HSLA.

Hemisurface leaf area may be computed from PLA or from needle volume calculated by water immersion; both methods depend on assumptions of cross-sectional needle geometry (Beets 1977; Johnson 1984; Brand 1987), although more complicated regression techniques (e.g., area as a function of displaced volume and needle length) do not (Brand

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1987). Researchers generally assume that black spruce (*Picea mariana* (Mill.) BSP) and jack pine (*Pinus banksiana* Lamb.) needles may be approximated in cross section as a rhombus and hemicylinder, respectively (Chen et al. 1997), although the exact morphologies are rarely tested (Beets 1977). The goals of this study were to (i) use optical scanning and immersion methods to assess the standard cross-sectional geometries assumed for black spruce and jack pine needles and (ii) assess the impact of any geometric changes on each measurement method and on subsequent leaf area calculations. We used black spruce and jack pine, because they are important conifers in North American boreal forests and have similar ecological equivalents, of comparable needle shape, in the boreal forests of Eurasia. These two species, shaped, respectively, like a diamond and hemiellipse in cross section (Brand 1987), also encompass a broad range in needle geometry.

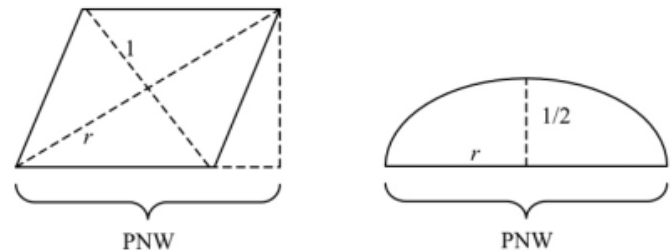
Materials and methods

Black spruce and jack pine needle samples were taken from a 37-year-old even-aged stand near Thompson, Man., and the BOREAS northern study area (55°53'N, 98°20'W). The stand originated from a stand-killing wildfire and was dominated by a mix of black spruce, jack pine, and trembling aspen (*Populus tremuloides* Michx.). Mean annual temperature was 0.8°C. Mean temperatures in January and July were -19.7 and 16.5°C, respectively. Mean annual precipitation was 438.5 mm.

Fifty foliage samples were taken for each species from randomly selected dominant or codominant trees. Deformed or diseased trees were not sampled. Samples were collected using clippers for small trees or a shotgun for tall trees, placed in airtight bags and 3°C coolers, and transported to Madison, Wis., for analysis. Simple linear regression was used to quantify the relationship between hemisurface leaf area (HSLA) and projected leaf area (PLA) for each group of needle samples (black spruce, jack pine scanned randomly, and jack pine scanned flat). This relationship (the slope of the regression line) was dependent on, and used to test, assumptions concerning needle geometry given r , the ratio of major to minor axis or diameter (Fig. 1). The regression line intercept is zero in theory (since a zero-area needle has PLA = HSLA = 0) but was initially included in all models for significance testing.

The volume of each sample was measured by the water displacement technique (Beets 1977; Johnson 1984; Brand 1987; Chen et al. 1997). Each sample consisted of 20–60 individual needles. Samples were also scanned at 800 dots/in. (1 in. = 2.54 cm) using a backlit flatbed scanner (Umax AstraNET e5470; Umax Technologies, Fremont, Calif.). All needles were physically separated before scanning. Jack pine samples were scanned twice, once randomly oriented and once taped flat to the scanner bed. This second scan was performed to quantify the error introduced by longitudinal twisting of longer needles, as scanning twisted (not taped) needles was a considerably faster procedure. The image files were converted from grayscale to black and white using a threshold luminosity of 170 (on a 0–255 scale). This threshold value yielded automatic pixel counts that agreed with hand counts performed on a subset of the samples ($R^2 =$

Fig. 1. Cross-sectional geometries assumed for black spruce (rhombus, left) and jack pine (hemiellipse, right). The value r is the ratio of major to minor diagonal, or major to minor ellipse axis, and is normalized here so that the minor diagonal or axis equals 1. Projected needle width (PNW) is shown and can be multiplied by needle length to calculate projected leaf area (PLA). For both shapes, hemisurface leaf area (HSLA) is equal to half the cross-sectional perimeter multiplied by needle length.



0.995) and should be considered specific to the scanner used. Projected needle area was computed by dividing the number of black pixels in the image by the scan resolution in pixels per unit area.

Total needle area was calculated from needle volume. It is commonly assumed that, in cross section, a black spruce needle is a rhombus with diameter ratio $r = 1.5$; a jack pine needle is assumed to approximate a hemicylinder (a hemiellipse with axis ratio $r = 1$) (Johnson 1984; Brand 1987; Grace 1987; Chen et al. 1997). The PLA, HSLA, and volume of a hemiellipse or rhombus can be derived from basic geometric definitions (Table 1). For example, the perimeter of an ellipse with axes a and b is $\pi((a^2 + b^2)/2)^{0.5}$. Normalized by b , the axes are a/b (which is r by definition) and 1. The perimeter of the hemiellipse (the ellipse cut on the long axis a) is then $r + \pi/2((r^2 + 1)/2)^{0.5}$, which multiplied by needle length l becomes the approximated surface area of the needle. We assumed a constant cross-sectional area and geometry over the length of individual needles, as needle taper is probably a relatively small source of error (Brand 1987). Thus, in Table 1, PLA is rl (i.e., the flat side of the jack pine needle) and HSLA is half the total surface area. The volume equation in Table 1 is derived in a similar manner starting with $\pi ab/4$, by definition the area of an ellipse with axes a and b .

From these definitions, total needle area was calculated from measured needle volume, an assumed r , n (number of needles), and l (mean needle length). Hemisurface leaf area (HSLA) was calculated as one-half of total leaf area, and PLA was known from the scanning procedure. Finally, the unitless HSLA/PLA ratio was calculated. For example, the ratio of HSLA to PLA is $(1 + \pi/2)/2 = 1.29$ for a hemiellipse with $r = 1$, and $(1.5^2 + 1)/1.5^2 = 1.44$ for a rhombus with $r = 1.5$.

Theoretically, the HSLA/PLA computed using the equations in Table 1 should equal the slopes of the regression lines relating HSLA and PLA, if the assumed needle shapes are correct. Water immersion and an assumed value of r were used to calculate HSLA. Flatbed scanning was used to measure PLA directly, with no assumption needed for r . Thus, the regression slopes and respective confidence intervals of the HSLA/PLA relationship were used to test the sample needles' assumed geometric fit for different values of r .

Table 1. Equations for hemisurface leaf area (HSLA), projected leaf area (PLA), and volume of conifer needles whose cross-sectional profile approximates a hemiellipse or rhombus.

| Needle shape | Geometric equation for | | |
|--------------|---|---|------------------------------------|
| | HSLA | PLA | Volume |
| Hemiellipse | $\left(r + \frac{\pi}{2} \sqrt{\frac{r^2 + 1}{2}} \right) \frac{l}{2}$ | rl | $\left(\pi \frac{r}{4} \right) l$ |
| Rhombus | $(\sqrt{r^2 + 1}) l$ | $\left(\frac{r^2}{\sqrt{r^2 + 1}} \right) l$ | $\left(\frac{r}{2} \right) l$ |

Note: Equations are in terms of r , the ratio of major to minor axes (for hemiellipse) or major to minor diagonals (for rhombus), and l , needle length. The theoretical relationship between HSLA and PLA for a range of r values is shown in Fig. 2.

As a check on some of the assumptions underlying this study, several independent samples of black spruce and jack pine needles (from the same 37-year-old stand, as well as other stands) were taken and measured by hand. Midneedle width and height were measured to the nearest 0.01 mm using digital calipers. This allowed for an independent computation of r , the major/minor axis or diagonal ratio, to compare with the indirect results obtained from the scanning-immersion protocol described above.

Results

The mean length of the sample black spruce needles was 0.86 cm with a SD of 0.10. In the regression relating PLA to HSLA ($N = 50$, $R^2 = 0.91$, $MSE = 0.15$), the intercept was not significant ($p = 0.45$) and was removed. (This agrees with theory, since a zero-area needle should have PLA = HSLA = 0.) Assuming the needle cross-sectional profile of black spruce was a rhombus (diamond) with major to minor axis ratio $r = 1.50$ (Chen et al. 1997), the slope of the regression between HSLA and PLA was 1.58, with a 95% confidence interval (CI) of 1.55–1.61. The theoretical HSLA/PLA ratio for this geometry was 1.44, outside of the confidence interval, implying a too-large r value. Repeated model-fitting iterations decreased the axis ratio r by 0.05 with each iteration. The theoretical HSLA/PLA ratio fell inside the confidence interval only at $r = 1.35$ (Fig. 2). At this geometry the theoretical HSLA/PLA ratio was 1.55, and the observed value (slope of the regression line) was 1.55 with a 95% CI of 1.53–1.58 (Table 2). (Using different r values amounts to a linear scaling of HSLA in the HSLA–PLA relationship and does not affect the regression fit as expressed in R^2 and MSE above.) Changing the geometry from $r = 1.50$ to $r = 1.35$ reduced the computed needle surface area of black spruce needles by 1.8% if using the immersion method and by 7.2% if scanning.

The mean length of the sample jack pine needles was 2.25 cm with a SD of 0.51. In the PLA–HSLA regression for needles taped flat on the scanner bed ($N = 50$, $R^2 = 0.95$, $MSE = 0.26$), the intercept was not significant ($p = 0.56$) and was removed. Assuming a needle cross-sectional shape of a hemicylinder (Johnson 1984; Brand 1987; Grace 1987; Chen et al. 1997), the slope of the HSLA/PLA regression line was 1.19, with a 95% CI of 1.16–1.21. The theoretical HSLA/PLA ratio for a hemicylinder is 1.29, implying that

Table 2. Formulas to compute hemisurface leaf area (HSLA) for black spruce and jack pine needles from projected leaf area (PLA) and volume.

| Species | Formula for HSLA computed from | | |
|--------------------------------|--------------------------------|---------|-------------------|
| | r | PLA | Immersion |
| Black spruce | 1.35 | 1.55PLA | $2.05(Vnl)^{0.5}$ |
| Jack pine (flat orientation) | 1.30 | 1.20PLA | $1.79(Vnl)^{0.5}$ |
| Jack pine (random orientation) | 1.00 | 1.29PLA | $1.77(Vnl)^{0.5}$ |

Note: Formulas are based on a particular geometric shape (rhombus for black spruce, hemiellipse for jack pine) with major/minor diagonal or axis ratio of r . Immersion-based equations depend on needle volume (V), number of needles (n), and mean needle length (l).

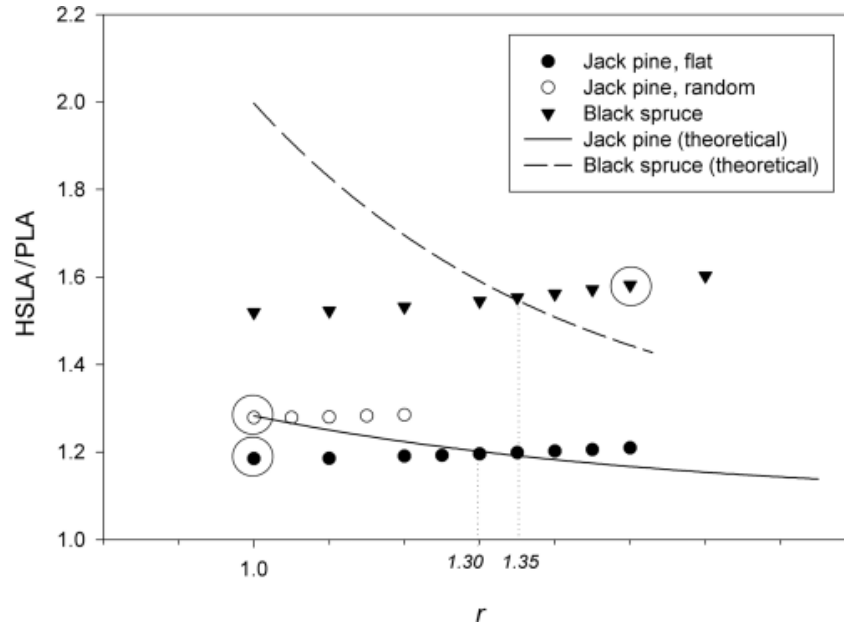
the assumed value of $r = 1.0$ was too small. The theoretical and observed ratios converged as the long axis of the hemicylinder was “stretched” (Fig. 2). The theoretical HSLA–PLA relationship first fell within the observed 95% confidence interval at $r = 1.25$ (a hemiellipse with axes ratio of 1.25), where the theoretical HSLA/PLA was 1.21 and the observed value was 1.19 (95% CI 1.16–1.22). The “best” fit was for $r = 1.30$, where the theoretical value was 1.20 and the observed value was 1.20 (95% CI 1.17–1.22; Table 2). The last r value at which the theoretical HSLA/PLA fell within the observed confidence interval was $r = 1.40$, where the theoretical value was 1.18 and the observed value was 1.20 (95% CI 1.17–1.23). The changed geometry, from $r = 1.00$ to $r = 1.30$, increased the computed leaf area of jack pine by 0.9% if using the immersion method and decreased it by 6.6% if scanning.

Randomly oriented jack pine needles had a slightly poorer fit and larger error ($N = 50$, $R^2 = 0.94$, $MSE = 0.33$) than needles taped flat. The intercept was not significant ($p = 0.23$) and was removed. Under the assumption of $r = 1.00$, the slope of the HSLA–PLA regression line was 1.28 (95% CI 1.25–1.31) compared with the theoretical value of 1.29. This was the best fit, although the theoretical HSLA/PLA was within the observed confidence interval up to $r = 1.10$. Thus, there was no evidence against the null hypothesis ($r = 1$) for randomly oriented jack pine needles.

There was some evidence that treating jack pine needles as hemicylinders ($r = 1$) became more problematic with increased needle length. For the shortest half of the samples ($N = 25$, length 1.86 ± 0.29 cm (mean \pm SD), taped flat to the scanner bed), the observed and predicted HSLA/PLA ratios most closely matched at $r = 1.25$, whereas for the longest half of the samples ($N = 25$, length 2.65 ± 0.34 cm), the ratios most closely matched at $r = 1.35$. The change implies that longer needles were flatter in cross section and, thus, more poorly approximated as hemicylinders.

The independent hand-measured samples exhibited variable r values (Table 3). The black spruce needle samples from the same 37-year-old stand sampled in the rest of the study had a measured $r = 1.35$ ($N = 32$), exactly the same value as determined by the combination immersion–scanning protocol. The jack pine samples from this stand had a measured $r = 1.51$ ($N = 32$), which is higher and significantly different ($p < 0.001$) than the $r = 1.25$ seen with the immersion–scanning protocol.

Fig. 2. Relationship of hemisurface leaf area (HSLA) to projected leaf area (PLA) versus needle geometry for black spruce and jack pine needles, both theoretical and observed. Black spruce and jack pine needle shapes were assumed to be a diamond (rhombus) and a hemiellipse, respectively, in cross section. Lines (broken for black spruce, solid for jack pine) show the theoretical HSLA–PLA relationship as a function of r , the ratio of the major to minor diagonals (for black spruce) or axes (for jack pine). Circled values are the results of using standard assumptions ($r = 1.0$ for jack pine and 1.5 for black spruce). The observed and theoretical lines cross at $r = 1.35$ (black spruce), 1.30 (jack pine, scanned flat), and 1.00 (jack pine, random needle orientation). Confidence intervals are given in the text but, for clarity, are not shown here.



Discussion

The black spruce and jack pine needles sampled here, from a 37-year-old, even-aged stand in northern Manitoba, are somewhat inaccurately described by the “standard” cross-sectional geometries used for these species. Within a species, leaf morphology can vary with soil conditions, foliage age, canopy position, growth rate (Lambers and Poorter 1992; Gower et al. 1995; Kozłowski and Pallardy 1997), and leaf longevity (Reich et al. 1992; Gower et al. 1993; Reich et al. 1997). Thus, while using a black spruce morphology of $r = 1.5$ may be reasonable for the mature 151-year-old BOREAS stand (as testing these hand-measured samples for a mean of 1.5 gave $p = 0.041$), it may not be reasonable for a younger group of trees in the same region (Table 3). The jack pine r values measured using hand measurements and the scanning–immersion protocol did not agree with each other; however, both were significantly larger than the theoretical value of $r = 1.0$. It is possible that this disagreement is an artifact of sampling variability (as the hand measurements were made on a separate sample) but assuming a single value of $r = 1.0$ for jack pine trees is problematic nevertheless. Such an assumption may affect leaf area estimates by 5–10% or more, depending on the method of measurement.

Three different types of measurement were used in this study to refine estimates of conifer needle geometry. Hand measurement is precise but time consuming and poorly suited for measuring needle area. Immersion techniques must be performed with care (Johnson 1984; Brand 1987) but give accurate measurements of volume. Flatbed scanning, in contrast, gives exact measurements of projected area

Table 3. Variability in needle cross-sectional geometry from hand measurements.

| Species | Stand age | | | |
|--------------|-----------|----------|-----------|----------|
| | (years) | <i>N</i> | <i>r</i> | <i>P</i> |
| Black spruce | 151 | 16 | 1.61±0.19 | 0.041 |
| | 37 | 32 | 1.35±0.25 | 0.002 |
| | Total | 48 | 1.43±0.26 | 0.433 |
| Jack pine | ~50 | 12 | 1.23±0.22 | 0.004 |
| | 37 | 32 | 1.51±0.29 | <0.001 |
| | ~20 | 16 | 1.42±0.32 | <0.001 |
| | Total | 60 | 1.43±0.30 | <0.001 |

Note: The r values are the major/minor diagonal or axis ratio (mean ± SD) for each particular geometric shape (rhombus for black spruce, hemiellipse for jack pine). The 37-year-old stand is that sampled in the rest of the study; the 151-year-old stand is the northern BOREAS stand. The P value given is for the two-sided t test of the null hypothesis $r = r_0$, where r_0 is 1.50 for black spruce and 1.00 for jack pine.

and permits easy sampling of very large numbers of needles (more than 2000 black spruce needles were sampled in this study). In addition, the scanned images can be preserved easily and indefinitely. However, scanning is more sensitive than immersion methods to errors in the cross-sectional geometry assumptions, and calculated leaf area can change significantly because of this problem.

There are numerous potential implications of such errors in leaf area estimates, as the correct measurement of forest leaf area is critical to both scientists and managers. Leaf area and leaf area index (LAI, the amount of leaf area per unit ground area) strongly influence energy, water, and carbon di-

oxide exchange between terrestrial ecosystems and the atmosphere (Campbell and Norman 1998; Law et al. 2001). Leaf area is tightly coupled with photosynthesis, litterfall, microclimate, and productivity (Gower et al. 1999) and is a central parameter in terrestrial biogeochemical models and remote sensing (Bonan 1993; Chen et al. 1997). Optical methods may underestimate leaf area in coniferous forests because of foliage clumping at the whorl, shoot, and branch levels and the difficulty of distinguishing wood from foliage tissue (Smith et al. 1991; Stenberg et al. 1995; Chen et al. 1997; Küßner and Mosandl 2000). Allometry is the most accurate approach in such stands (Gower et al. 1999) but depends on destructive harvests and, often, determination of specific leaf area based on assumptions about the cross-sectional geometry of conifer needles.

Small systematic errors in leaf area calculations can be particularly insidious, as such systematic errors cannot be detected or minimized by increasing data set size. Thus, larger errors may be introduced when scaling instantaneous fluxes that are subject to systematic, rather than random, biases (Moncrieff et al. 1996). Given the importance of accurate leaf area values in many areas of earth systems science research, and the variability in needle morphology seen in this small study, such errors in leaf area calculation should be explored further.

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References

- Beets, P. 1977. Determination of the fascicle surface area for *Pinus radiata*. *N.Z. J. For. Ecol.* **7**: 397–407.
- Bonan, G.B. 1993. Importance of leaf area index and forest type when estimating photosynthesis in boreal forests. *Remote Sens. Environ.* **43**: 303–314.
- Brand, D.G. 1987. Estimating the surface area of spruce and pine foliage from displaced volume and length. *Can. J. For. Res.* **17**: 1305–1308.
- Campbell, G.S., and Norman, J.M. 1998. An introduction to environmental biophysics. Springer-Verlag, New York.
- Chen, J.M., and Black, T.A. 1992. Defining leaf area index for non-flat leaves. *Plant Cell Environ.* **15**: 421–429.
- Chen, J.M., Rich, P.M., Gower, S.T., Norman, J.M., and Plummer, S. 1997. Leaf area index of boreal forests: theory, techniques, and measurements. *J. Geophys. Res.* **102**: 29 429 – 29 443.
- Gower, S.T., Reich, P.B., and Son, Y. 1993. Canopy dynamics and aboveground production of five tree species with different leaf longevity. *Tree Physiol.* **12**: 327–345.
- Gower, S.T., Isebrands, J.G., and Sheriff, D.W. 1995. Carbon allocation and accumulation in conifers. *In Resource physiology of conifers. Edited by W. Smith and T.M. Hinckley. Academic Press, San Diego, Calif.* pp. 217–254.
- Gower, S.T., Kucharik, C.J., and Norman, J.M. 1999. Direct and indirect estimation of leaf area index, f_{APAR} , and net primary production of terrestrial ecosystems. *Remote Sens. Environ.* **70**: 29–51.
- Grace, J.C. 1987. Theoretical ratio between “one-sided” and total surface area for pine needles. *N.Z. J. For. Ecol.* **17**: 292–296.
- Johnson, J.D. 1984. A rapid technique for estimating total surface area of pine needles. *For. Sci.* **30**: 913–921.
- Kozlowski, T.T., and Pallardy, S.G. 1997. The physiological ecology of woody plants. Academic Press, San Diego, Calif.
- Küßner, R., and Mosandl, R. 2000. Comparison of direct and indirect estimation of leaf area index in mature Norway spruce stands of eastern Germany. *Can. J. For. Res.* **30**: 440–447.
- Lambers, H., and Poorter, H. 1992. Inherent variation in growth rate between higher plants: a search for physiological causes and ecological consequences. *Adv. Ecol. Res.* **23**. pp. 187–261.
- Law, B.E., Cescatti, A., and Baldocchi, D.D. 2001. Leaf area distribution and radiative transfer in open-canopy forests: implications for mass and energy exchange. *Tree Physiol.* **21**: 777–787.
- Moncrieff, J.B., Malhi, Y., and Leuning, R. 1996. The propagation of errors in long-term measurements of land-atmosphere fluxes of carbon and water. *Global Change Biol.* **2**: 231–240.
- Reich, P.B., Walters, M.B., and Ellsworth, D.S. 1992. Leaf life-span in relation to leaf, plant, and stand characteristics among diverse ecosystems. *Ecol. Monogr.* **62**: 365–392.
- Reich, P.B., Walters, M.B., and Ellsworth, D.S. 1997. From tropics to tundra: global convergence in plant functioning. *Proc. Natl. Acad. Sci. U.S.A.* **94**: 13 730 – 13 734.
- Smith, F.W., Sampson, D.A., and Long, J.N. 1991. Comparison of leaf area index estimates from tree allometrics and measured light interception. *For. Sci.* **37**: 1682–1688.
- Stenberg, P., DeLucia, E.H., Schoettle, A.W., and Smolander, H. 1995. Photosynthetic light capture and processing from cell to canopy. *In Resource physiology of conifers. Edited by W.K. Smith and T.M. Hinckley. Academic Press, San Diego, Calif.* pp. 3–38.